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ENZA ZADEN

THE ROLE OF MOBILE RNAS IN GRAFTING-INDUCED TRAITS IN *SOLANACEOUS* CROPS.

by

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Declaration

Statement regarding published works

A significant proportion of the thesis introduction in Chapter 1 has been independently published by the author as a review paper in Frontiers in Plant Science under the title "Long distance signalling and epigenetic changes in crop grafting" (https://doi.org/10.3389/fpls.2023.1121704). Similarly, portions of Chapter 2 have been made publicly available as a preprint manuscript (https://doi.org/10.1101/2024.08.19.608270). With this declaration we state that the cited manuscripts contain work belonging to Katherine Jeynes-Cupper, whom is figuring as the first author, and are direct outputs of the research undertook during her PhD project, which are also described in the thesis. In these publications, Katherine Jeynes-Cupper is credited as main contributor for the writing and editing of the text. The Katherine Jeynes-Cupper's supervisor Dr Marco Catoni is cited as senior co-authors in these publications, and he contributed to the works by providing supervision, critical analyses of the methodologies and the datasets, and by contributing to writing and editing the manuscripts.

Katherine Jeynes-Cupper [redacted] Dr. Marco Catoni [redacted]

Abstract

Across Europe and America, tomato cultivation exploits plant grafting to combines plant traits from two different genotypes into a single plant. For example, drought resistance to a productive cultivar. This example can be explained by the intrinsic properties of the rootstock. Yet, other traits that alter the architecture and physiology of the scion may not be as easily or simply explained. In research, plant grafting has been extensively used as an experimental tool to discover and demonstrate the short- and long-distance signalling of proteins, hormones and RNAs in plants. This includes the movement of small RNAs and their ability to introduce epigenetic alterations in the destination tissue. Interestingly, epigenetic alterations have been linked to responses to environmental and developmental stimuli to regulate proper growth and development. However, researchers have yet to fully describe whether mobile small RNAs are a primary driver of grafting-induced traits. To further understand the role of mobile RNAs in grafting-induced traits, these works aim to improve upon existing detection methods and investigated the mobility of RNAs in solanaceous plants using grafting.

Throughout the previous studies there lacked a standardised computational approach to characterise mobile RNAs using Next Generation Sequencing (NGS) technology. Using real and simulated data, we demonstrate that previous methods generate high levels of false positives and background data noise. Inspired by pan-genomes, we devised an alternative method which showed a remarkedly improved ability to discriminate and place reads to their genome of origin. This method was wrapped into a Bioconductor/R package,

mobileRNA, to support further research efforts. As of December 2024, *mobileRNA* has 1,805 downloads from Bioconductor.

Unlike other plant families, species within the *Solanaceous* family can be joined via grafting, known as interspecific grafting. In industry, it's popular to graft productive tomato scions onto hybrids rootstocks to further boost crop vigour in non-stress conditions, yet the underlying mechanisms introducing these alterations is poorly understood. To further understand how rootstocks drive architectural changes to the scion, we investigated tomato and eggplant heterografting using a comprehensive approach that integrated three different angles: phenotypic analysis, physiological analysis, and genomic analysis. The results indicate that a relatively small population of mobile RNAs could have profound effect on the scion architecture. More specifically, the rootstock altered the fruit weight, and we observed an increase in triose phosphate utilisation in the leaves. The results highlight the possible role of mobile sRNA in re-programming the re-allocation of carbon to stress responses, such as cell wall modifications, instead of fruit production. We further suggest that based on a statistical enrichment, mobile messenger RNAs could be the source of the rootstock-derived sRNAs in the scion. This delivery method could possibly ensure greater RNA stability before reaching the destination. Overall, we demonstrate how grafting could be a valuable tool as an alternative perspective to investigating the molecular basis of phenotypic traits, thereby laying the groundwork for further investigations aimed at optimizing crop yields.

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List of Abbreviations

NGS	Next-generation sequencing
CRISPR-Cas9	Clustered Regularly Interspaced Short Palindromic Repeats and CRISPR-associated protein
RNA	Ribonucleic acid
DNA	Deoxyribonucleic acid
sRNA	Small RNA
mRNA	Messenger RNA
TGS	Transcriptional gene silencing
vsiRNA	Virus-derived small interfering RNA
Spp	Species
Ci	Intercellular CO_2 concentrations
WUE_i	Water use efficiency
RdDM	RNA-directed DNA methylation
TE	Transposable element
TF	Transcription factor
gbM	Gene body methylation
miRNA	Micro RNA
siRNA	Small interfering RNA

PTGS	Post-transcriptional gene silencing
RT-PCR	Reverse-transcriptase PCR
qRT-PCR	Quantitative RT-PCR
sRNA-seq	Small RNA sequencing
McrBC-PCR	Methylsensitive-PCR
MSAP	Methylation sensitive amplification polymorphism
BS-seq	Bisulfite sequencing
tRNA	Transfer RNA
kDa	Kilodalton
MPs	Movement proteins
TLS	Transfer RNA like structures
mRNAseq	Messenger RNA sequencing
cDNA	Complementary DNA
SNPs	Single-nucleotide polymorphisms
TRAPseq	Translating ribosome affinity purification followed by RNA sequencing
RPM	Reads per million
FPKM	Fragments Per Kilobase of transcript per Million mapped reads
GO	Gene ontology
Kb	Kilobases
FDR	False discovery rate
phasiRNAs	Phased secondary small interfering RNAs
ROS	Reactive oxygen species
TPU	Triose phosphate usage
Ci	Internal Carbon dioxide
A	Assimilation rate
DEGs	Differentially expressed genes
KEGG	Kyoto Encyclopedia of Genes and Genomes
logFC	Log2 fold change
CC	Cellular component
BP	Biological process
MF	Molecular function

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CHAPTER 1: INTRODUCTION

At the centre of many supply chains, including biofuel manufacturing and food production, is agricultural production. Yet, supply could be threaten due to shifts in demand for products studies in line with the exponential growth of the human population (Jeynes-Cupper and Catoni 2023). To estimate this effect, researchers have generated projections based on ~2.5 million agricultural statistics taken from around the globe across four key crops and demonstrated that the expected yield increase will not satisfy the demand expected in 2050 (Ray, Mueller et al. 2013). These projections are concerning, and yet do not factor in the adverse effects of the climate change crisis which is expect to hinder food production (Food and Organization 2013, Ray, Mueller et al. 2013, Jeynes-Cupper and Catoni 2023). To increase crop production, it has been widely suggested that increasing the hectare devoted to cultivation is not the most effective or sustainable approach (Green, Cornell et al. 2005, Matson and Vitousek 2006, Godfray, Beddington et al. 2010, Foley, Ramankutty et al. 2011, Phalan, Balmford et al. 2011, Tscharntke, Clough et al. 2012). As an alternative, many suggest to increase existing crop yields, which has indeed been shown to be an effective method to support communities dependent on subsistence crops to tackle food poverty (Evans 1997, Green, Cornell et al. 2005, Matson and Vitousek 2006, Godfray, Beddington et al. 2010, Foley, Ramankutty et al. 2011, Phalan, Balmford et al. 2011, Tscharntke, Clough et al. 2012). Despite this appearing as an obvious solution, there are many barriers to entry. For instance, in the early days of modern crop breeding, breeders fundamentally increased yields by developing new phenotypes including alterations to the tiller number,

number of seeds, stem branching and dwarfism (Peng, Richards et al. 1999, Spielmeyer, Ellis et al. 2002, Long, Marshall-Colon et al. 2015). However, in this modern age growers are beginning to experience a plateauing in crop yield improvements in numerous global regions (Cassman 1999, Peltonen-Sainio, Jauhiainen et al. 2009, Brisson, Gate et al. 2010, Finger 2010, Lin and Huybers 2012, Ray, Ramankutty et al. 2012).

Today, scientists work to tackle these issues using modern research techniques and technological advancements. In the past three decades, there has been a significant boom in scientific knowledge and understanding lending to the discovery of underlying mechanisms in fundamental biological processes. These advancements can be credited to major technological advancements which have introduced new ways to research biological systems. For one, it has encouraged computational modelling of whole populations including epidemiological spread to single cellular activity, such as cellular and metabolic pathways. Similarly, the advancements in genetic-genomic studies, facilitated by Next-Generation Sequencing (NGS), provides insight into the regulation of genes (Morrell, Buckler et al. 2012). Together these developments support researchers to predict every imaginable change from up- or down- regulating specific genes in a tissue, to introducing or removing specific endogenous or foreign genes, proteins, or pathways. And in the wake of genetic engineering, these alterations can be applied to connect the dots and prove computational predications, hopefully supporting real-world applications. A key example is the application of this approach to improve the efficiency of converting light energy into chemical energy during photosynthesis. With the use of computational models to simulate the effect of alterations to photosynthetic

genes, successful modification could be introduced into crops using genome editing tools (Long, Marshall-Colon et al. 2015).

To translate research findings and develop crops with improved agronomic traits, it is important to maintain perspective within plant research and consider the whole organism using the sum of its parts. Plants, by nature, are sessile making them unable to physically evade predators, pests, or abiotic stress. To survive, plants have developed advanced and complex systems of non-linear interactions among pathways, factors, and genes to detect and respond to these cues. These ongoing systemic interactions are responsible for communication between organs and the triggering developmental processes. The complexity of plants, as a whole organism, can be studied using plant grafting alongside the use of NGS technologies and molecular laboratory experiments to directly associate changes to phenotypical traits. Plant grafting is a technique that combines compatible plants that then grow as one. Typically, this involves joining two plants where one plant contributes the shoot, known as the scion, while the other contributes the roots and is called the rootstock (Figure 1.1) (Jeynes-Cupper and Catoni 2023). Grafting is a popular technique in agriculture due to its ability to introduce favourable agronomic trait that increase crop production in stress or non-stress conditions.

Figure 1.1. An example of a plant grafting technique. This technique is known as the cleft technique. Two plants are joined, where one contributed the shoot, known as the scion, and the other contributes the roots, known as the rootstock. The end of the scion is cut into a wedge shape using a single cut and a single vertical cut is made within the end of the rootstock. The scion wedge is placed within the cleft of the rootstock, and they are held in place with a clip or tape. Created using BioRender.com.

Plant grafting is referenced to in texts from ancient China, Greece and the Bible; making it challenging to pin-point the exact time grafting was first utilised by man-kind (Melnyk 2017). Regardless, since grafting can occur naturally in plants it thought that its deployment in agriculture was derived from observations of this natural event (Dallimore 1917). In China, records from more than 4,000 years ago demonstrate grafting in fruit trees to improve anchorage, dwarfism and to improve propagation (Mudge, Janick et al. 2009). Fast-forward to the 21st century, and grafting of woody perennials is still utilised to introduce these traits (Gaion, Braz et al. 2018, Jeynes-Cupper and Catoni 2023). This is particular prominent in the wine industry where grafting has been famously used to introduce resistance to the soil-borne insect

phylloxera (*Phylloxera vastatrix*) in grapevine (*Vitis* spp.) in the European wine industry (Pouget 1990). In terms of herbaceous crops, it was not till the early 20th century, that grafting of these was shown to be possible and advantageous for commercial markets. Among these the most commonly and economically grafted families are:

- *Solanaceae*: Tomato, Eggplant, Sweet Pepper.
- *Cucurbitaceae*: Watermelon (*Citrullus lanatus*), Melon (*Cucumis melo*), and Cucumber (*Cucumis sativus*)

The discovery of herbaceous grafting has allowed growers to combine favourable traits without cross-breeding (Jeynes-Cupper and Catoni 2023) which can be timely and expensive. A key example is the prolific grafting of tomatoes (*Solanum lycopersicum*) to increase marketable fruit yields by up to 41% (Djidonou, Simonne et al. 2016) (Velasco-Alvarado, Castro-Brindis et al. 2016). Together tomato, eggplant and cucumber accounted for almost 50% of the increase in global vegetable production (Jeynes-Cupper and Catoni 2023). Up to 40% of the global production of tomatoes stems from grafting, where alone in the USA and the Netherlands all soilless tomatoes are grafted transplants (Phani, Gowda et al. 2023). Whereas the production of grafted watermelons and cucumber in Japan and Korea hold 90% and 75% of all agricultural land, respectively (Phani, Gowda et al. 2023). Interestingly, companies are heavily investing in the development of robots and machinery to undertake the grafting task, while others focus on producing grafted seedlings which are exported globally to other production companies to grow to season (Bie ZhiLong, Nawaz et al. 2017, Pardo-Alonso, Carreño-Ortega et al. 2018, Spanò, Ferrara et al. 2020). This rising global interest in the international trading of grafted crops has

prompted many seed companies to invest in rootstock breeding programs to develop rootstocks that introduce highly specific traits to a designated crop line. Typically, rootstocks are hybrid plants bred from wild or unproductive varieties from the same family or species as the scion and tend to be naturally highly generative or are intrinsically resistant pathogens (Thompson, Pico et al. 2017). In comparison, the use of grafting for subsistence crops may not be suitable. Subsistence agriculture is a method used by farmers typically in developing countries to produce enough crops to meet the demand of their families or community on a smallholding. Utilising grafting in this form could introduce a level of risk and uncertainty for farmers since the grafting technique adds a level of additional labour and potential crop loss if not correctly implemented.

Grafting routinely utilises wild varieties as a source for diverse plant traits without the need for crossing or selection processes. The application of this has greater scope if plants from genetically distant relative can be compatible. A recent study looked into exactly that and showed that tobacco could be used successfully as a grafting partner to genetically distant relative species, including soybean, *chrysanthemums indicum* as well as an additional 38 representative flowering plant (Notaguchi, Kurotani et al. 2020). This indicates that there is the possibility to graft a wide range of different plant combinations, also impossible to hybridise by interspecific crossing, to support the introduction of specific traits into crops.

Despite the extensive use of plant grafting, the underpinning mechanisms of graft-induced traits are not fully characterised. Some traits, such as resistance,

have been attributed to the intrinsic properties of rootstocks, while changes induced in the scion are not well understood. Hence, improving our knowledge of the underpinning mechanisms which give rise architectural changes in the scion, including changes to vigour, would provide valuable insights for researchers to develop novel approaches to crop breeding. Here, advanced technologies, such as CRISPR-Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats and CRISPR-associated protein), alongside genomics and proteomics could facilitate precision breeding and high-throughput screening of scion-rootstock combinations to enable researchers to develop crops that thrive under various environmental conditions. Ultimately, by integrating the molecular insights from grafting-induced traits with practical applications, we may increase the crop production per hectare.

1.1 Graft Formations and Compatibility

The bulk of our understanding on graft compatibility stems from research aimed to investigate and understand how plants can be grafted in the first place (Melnyk 2017). Immediately after grafting intact cells on either side of the graft junction adhere and fuse, strengthening over time through polysaccharide deposits. A callus is then formed around at the junction which contains stem cell-like tissue to rebuild the phloem and xylem connections across the junction (Melnyk 2017, Sala, Karcz et al. 2019). Although the full extent of the molecular mechanism for graft formation remains unclear, recent findings have begun to make great strides in this area. Transcriptomic studies have identified transcription factors (TFs) that could play key roles in graft formation through promotion of tissue adhesion, callus formation and in cell-differentiation (Melnyk, Gabel et al. 2018, Canher, Lanssens et al. 2022, Zhang, Matsuoka et al.

2022). One such is *PHYTOCHROME A SIGNAL TRANSDUCTION 1* (*PAT1*), a possible core regulator of graft healing. And more recently, cell-wall-related *β-1,4-glucanase* genes have been shown to be essential to graft formation and attachment (Notaguchi, Kurotani et al. 2020, Kurotani, Huang et al. 2022). Other genes including *WUSCHEL-RELATED HOMEOBOX13* (*WOX13*) and *WOUND INDUCED DEDIFFERENTIATION1 (WIND1)* have been found to be important early activators for callus formation (Iwase, Mitsuda et al. 2011, Ikeuchi, Iwase et al. 2022). Moreover, hormones including auxin and cytokinin have been indicated as activators of expression to encourage graft formation (Melnyk and Meyerowitz 2015, Matsuoka, Sugawara et al. 2016, Ntatsi, Savvas et al. 2017, Reeves, Tripathi et al. 2022).

To be compatible, partners must have the ability to successfully form a continuous vascular connection across the graft junction with the resulting grafted plant continuing to survive as a single organism (Harrison and Burgess 1962, Moore 1984). By contrast, graft incompatibility might depend upon many factors, yet there are two types of incompatibility: 1) immediate incompatibility. 2) delayed incompatibility (Mendel 1936, Argles 1937). Immediate incompatibility refers to immediate death of the scion due to dehydration with no signs of any initial healing at the graft junction. Whereas delayed incompatibility occurs when the grafted plant appears to be healed but within there is a lack of cohesive fusion of the vascular tissues. For example, in some cucurbit combinations graft incompatibility could be observed 25 days after grafting or in some trees it can appear years later (Mosse 1962, Wutscher 1979, Tuttle and Gotlieb 1985, Edelstein, Burger et al. 2004, Aloni, Karni et al. 2008). Some have sought to identify physical characteristics to detect delayed

compatibility, however they are poorly backed (Webber 1948, Wutscher 1979). The most likely cause of incompatible is the presence of substances that are exchanges at the junction. Despite most *Solanaceous* species being compatible, tomato and pepper are not (Thomas, Van den Broeck et al. 2022, Thomas, Gevorgyan et al. 2023, Thomas, Gevorgyan et al. 2024). Its thought that the cross-species leucine-rich repeat receptors promoted the synthesis of defence compounds and programmed cell death (Thomas, Gevorgyan et al. 2024). Similar findings were observed in interstock grafting in pear cultivation (Tukey 1978, Parry 1981, Wertheim 2000). Interstock grafting allows to combine two incompatible genotypes by placing tissue from a third plant within the graft junction, which is compatible with both partners. In pear cultivation, it is preferable to graft productive varieties onto quince (*Cydonia oblonga*) to introduce dwarfism. However, directly grafting the productive pear cultivars onto quince is not possible and thought to be due to the passage of secondary metabolites from the quince rootstock into the pear shoot tissue where it is converted into cyanide that kill the surrounding cells. This failure is overcome by using an alternative un-productive pear cultivar as interstock (Tamura 2012). Ultimately, while the determinants of grafting compatibility are not fully known, it might be due to defence and immune responses, genetic backgrounds, growth characteristics, plant architecture such as structural weakness, physiological, age, and biochemical factors such as metabolic imbalances (Johkan, Mitukuri et al. 2009, Mudge, Janick et al. 2009, Martínez-Ballesta, Alcaraz-López et al. 2010, Goldschmidt 2014, Fan, Yang et al. 2015, Gratão, Monteiro et al. 2015).

A grafted plant that contains partners of the same genotype is referred to as a self- or homograft (Melnyk 2017, Reeves, Tripathi et al. 2022). In contrast, grafted plants that combine multiple genotypes are called heterografts. The most compatible pairings usually occur between plants of the same species (intraspecific grafting) while pairings between different species within the same family (interspecific) are usually compatible (Mudge, Janick et al. 2009, Kurotani, Huang et al. 2022). As the two partners become more distantly related the less compatible they can be, yet it is still challenging to predict graft-compatibility (Schöning and Kollmann 1997, Flaishman, Loginovsky et al. 2008). However, typically, grafting partners from different families are incompatible (Mudge, Janick et al. 2009). Few examples exist, but interspecific grafting is prevalent within the *Solanaceous* family which includes potato (*Solanum tuberosum),* tobacco, eggplant (*Solanum melongena*) and tomato or, similarly it can occur between pear (*Pyrus* spp.) and apple trees (*Malus* spp.) or, finally, between plants from the *Fabaceae* family including soybean and common bean (*Phaseolus vulgaris*) (Melnyk 2017, Li, Wang et al. 2021, Li and Zhao 2021).

1.2 Plant Grafting as a Tool in Scientific Research

Due to the sessile nature of plants, they have evolved complex communication networks and transport systems from the cellular level up to the whole organism level. These signals are required to coordinate both development and responses to environmental cues (Liu and Chen 2018). To propagate the signals to distant tissues, they are transmitted by the vascular system. The vascular system is comprised of the xylem which transports inorganic salts and water and the phloem which transports phytohormones, photosynthates, amino acids

and RNA molecules (Hu, Ham et al. 2016). Our understanding of plant signalling has been elucidated by using plant grafting as a research technique. Facilitating the discovery of short- and long-distance interactions, such as the exchange of genetic material between cell layers (Hertle, Haberl et al. 2021) and the discovery of hormones, proteins and RNAs as signalling molecules (Melnyk and Meyerowitz 2015).

Plant grafting assisted the discovery of hormones, proteins and RNAs as long-distance systemic signals. For which this evidence had been collected using plant species other than *Arabidopsis* (Tsutsui and Notaguchi 2017). To peoples surprise, it was not until 2002 when viable grafting methods for *Arabidopsis* were developed, further known as micrografting (Turnbull, Booker et al. 2002). Traditionally, these proof-of-concept experiments would graft a plant that could elicit a phenotype due to the presence of specific molecule onto another that lacked the molecule. If the response is observed in the grafted partner which was previously lacking that ability, then the desired molecule has demonstrated mobilisation. Famously, this method was used to uncover the movement of the FLOWERING LOCUS T (FT) protein that triggers flowering (Lifschitz, Eviatar et al. 2006, Zeevaart 2006, Notaguchi, Daimon et al. 2009). In a similar way, a graft transmissible hormone signal was demonstrated to control branching in pea plants (Foo, Turnbull et al. 2001). Other examples include the works that showed the movement of assimilates in a source-to-sink manner (de Stigter 1966). As well as the cellular processes of protein exchange (Golecki, Schulz et al. 1998, Golecki, Schulz et al. 1999), the role of phytohormones on growth and development (Aloni, Cohen et al. 2010). In addition to the transmission of proteins and hormones, grafting has been instructive in

uncovering the role of small RNAs (sRNAs) in transcriptional and post-transcriptional gene silencing. These grafting studies demonstrated that sRNAs have the ability to move in bulk across long-distances and integrate into epigenetic pathways to elicit regulatory action upon genes expression (Molnar, Melnyk et al. 2010, Lewsey, Hardcastle et al. 2016). Moreover, the systemic movement of sRNAs has been linked to the coordination of abiotic and biotic stress responses (Buhtz, Springer et al. 2008, Lin, Chiang et al. 2008, Ruiz-Ferrer and Voinnet 2009, Molnar, Melnyk et al. 2010, Zhang, Kollwig et al. 2014). sRNAs coordinate these responses by acting as key regulators of gene expression through several mechanism of action, including messenger RNA (mRNA) inhibition or cleavage and, or through the modification of DNA or chromatin, such as methylation (Baumberger and Baulcombe 2005, Lee and Cui 2009). These studies not only demonstrated sRNA action but also their capacity to move across a graft junction between partnering genotypes.

A significant amount of research and understanding of sRNAs has derived from research focused on plant immunity. These early works were fundamental in understanding the role of sRNAs in transcriptional gene silencing (TGS) across plant and pathogen species (Kong, Yang et al. 2022). Grafting experiments were utilised to demonstrate the mobilisation of sRNAs and their ability to be transmitted systemically, to induce tolerance or resistance to specific pathogen. Here, researchers would utilise a transgenic line producing a sRNA capable of targeting a specific virus and graft it onto a non-transgenic susceptible line to confer resistance. Some pathogens, like viruses, can use the plant vascular system to spread and establish systemic infections. In response to such attacks, plants have evolved a defence system that utilises sRNAs from the

viral genome to degrade the viral RNAs, preventing further viral replication. These sRNA with a defence function are known as virus-derived siRNAs (vsiRNAs), and can be generated by the presence of exogenous viral RNA or circular extrachromosomal DNA (Kong, Yang et al. 2022). For example, a transgenic tomato rootstock known to be resistant to the Tomato Spotted Wilt Virus (TSWV) through the action of a vsiRNA was found to delay symptoms and significantly reduce viral load in grafted scions (Catoni, Lucioli et al. 2013). Likewise, plants produce sRNA in response to bacterial pathogens to quickly manipulate the expression of endogenous genes involved in plant immunity and initiate a defence response (Kong, Yang et al. 2022).

Plant grafting has also been employed to demonstrate the movement of large genetic materials including complete genomes. Using tobacco as a model, the initial work generated transgenic lines with reporter and marker genes in the nucleus and chloroplast genomes unique to either the scion or rootstock (Stegemann and Bock 2009). This model alongside further validation with PCR and Northern blotting, demonstrated the mobilisation of the DNA across the graft junction (Stegemann and Bock 2009). Later works soon demonstrated the transfer of plasmid and mitochondrial genomes across a cell-to-cell interface and across the grafting junction (Stegemann, Keuthe et al. 2012, Fuentes, Stegemann et al. 2014, Gurdon, Svab et al. 2016). These results have helped pave the way for research in horizonal genome transfer through grafting from which finds suggest that this mechanism could be exploited as an alternative traditional method to introduce transgenes.

1.3 Grafting-Induced Phenotypical Traits

Plant grafting is known to introduce a wide degree of desirable traits, and in this section, we discuss grafting-induced traits in herbaceous crops. To investigate the presence of grafting-induced traits researchers compare heterografted plants to self- or homo-grafted plants rather than non-grafted controls. This is because the grafting procedure itself is a stressful experience, and alone can introduce changes to the plant (Kumari, Kumar et al. 2015, Spanò, Mascia et al. 2015). This has been observed in studies investigating viral infection which suggested that resistance or tolerance to infection was attributed to a combination of the grafting method and the genotype combinations. In tomato, recovery from infection by Potato Virus Y (PVY) was significantly improved regardless of grafting the scion with a susceptible or resistant rootstock (Spanò, Ferrara et al. 2020). Likewise, the same level of resistance to Cucumber Mosaic Virus (CMV) could be introduced by simply grafting (Spanò, Gallitelli et al. 2017).

In the *Cucurbitaceous* family, watermelon, melon and cucumber are regularly grafted to provide resistance to abiotic and biotic stress. In the case of watermelons, they are regularly grafted onto Bottle Gourd (*Lagenaria siceraria*), Pumpkin (*Cucurbita pepo L.*), Squash (*Cucurbita moschata Duch.*) or interspecific hybrid Squash to introduce resistance to soilborne pathogens including *Fusarium oxysporum*, *Verticillium* species and root-knot nematodes (Davis, Perkins-Veazie et al. 2008, King, Davis et al. 2010, Lee, Kubota et al. 2010, Louws, Rivard et al. 2010, Khankahdani, Zakeri et al. 2012, Mohamed, Abd El-Hamed et al. 2014). For example, grafting watermelon onto a *C. maxima* × *C.*

moschata hybrid introduces resistance to the soilborne pathogen *Fusarium* as well as increasing the watermelon fruit size and yield compared to non-grafted plants (Miguel, Maroto et al. 2004, Álvarez-Hernández, Castellanos-Ramos et al. 2015). Similarly, the rootstocks demonstrate extensive rooting systems which provide tolerance to drought and nutrient deficiency (Miguel, Maroto et al. 2004, Rouphael, Cardarelli et al. 2008, Lee, Kubota et al. 2010, Huang, Li et al. 2013). Areas which cultivate watermelon are regularly faced with droughts, hence, grafting mini-watermelon onto interspecific hybrid squash rootstocks has been shown to improve the yield and improves water use efficiency (Rouphael, Cardarelli et al. 2008). Whereas, in exposure to nutrient deficiency in the soil of nitrogen, potassium, and magnesium specific grafting combination can facilitate the improved uptake and transport of these nutrients and mitigates any needs for fertilizers (Pulgar, Villora et al. 2000, Huang, Li et al. 2013). That said, some combination of watermelon on squash and interspecific rootstocks have been associated with adverse crop traits, specifically a reduction in fruit quality even though the rootstocks facilitated greater nutrient uptake (Shinbori, Kota et al. 1981, Davis, Perkins-Veazie et al. 2008, King, Davis et al. 2010, Soteriou, Kyriacou et al. 2014). Considering these were strange findings, the authors discussed how these finds were likely associated to the time of fruit collection, as fruits were collected at the same time as the non-grafted plants yet grafted plants require ~5-10 days longer to fully ripen fruits (King, Davis et al. 2010, Soteriou, Kyriacou et al. 2014). Even so, these grafted watermelons displayed fruits with higher lycopene levels and improved pulp textures, but typically have a reduced level of resistance to soil-borne pathogens than other rootstocks (King, Davis et al. 2010, Villocino Jr and Quevedo 2015, Fallik, Alkalai-Tuvia et al. 2016, Kyriacou, Soteriou et al. 2016). Unsurprisingly,

melons are grafted onto the same rootstocks as watermelons, or species of cucumber and wax guards as rootstocks (King, Davis et al. 2010, Lee, Kubota et al. 2010). The grafting of melons is mainly employed to introduce resistance to soilborne pathogens (Cohen, Pivonia et al. 2000, Dhall 2015) whereby wax guards introduce resistance to nematodes (*Meloidogyne incognita and M. javanica*) and squash rootstocks introduce resistance to the fungus *Stagonosporopsis* spp in melon (Ito, Charlo et al. 2009, Galatti, Franco et al. 2013). It is challenging for breeders to develop rootstocks that offer complete resistance to the *Fusarium oxysporum* f. sp. *melonis* strain as it has four distinct races but several genes in rootstocks which are absent in melon have been shown to confer resistance (Zink and Gubler 1985, Zink and Thomas 1990, Oumouloud, Arnedo-Andrés et al. 2010, Oumouloud, El-Otmani et al. 2013, Zhou, Wu et al. 2014, Dhall 2015). Indeed, some grafting combinations between melon and closely related rootstocks can confer adverse effects to fruit yield and quality. But typically, these combinations show limited compatibility with melon in a cultivar-dependant manner (Nisini, Colla et al. 2002, Calatayud, San Bautista et al. 2013, Salar, Salehi et al. 2014). Furthermore, an additional condition of grafting the melon cultivar 'Dikti' onto an interspecific hybrid illustrated a greater nitrate uptake, a higher photosynthetic ability and improved crop yield (Neocleous 2015). Using a method of double grafting in melon, increased crop yields were observed and linked to greater mineral and water uptakes (San Bautista, Calatayud et al. 2011). However, double grafting is more laborious and potentially uneconomical. The use of melon grafting has also observed some improvements of tolerance to nutrient deficiency and salt stress (Edelstein, Plaut et al. 2011, Orsini, Sanoubar et al. 2013). Finally, cucumber grafting is used to accomplish three main traits: *Fusarium* wilt tolerance, cold tolerance, salt

tolerance, temperature stress tolerance and improvements to the appearance of fruits (Huang, Bie et al. 2010, Savvas, Ntatsi et al. 2013, Cao, Ju et al. 2014, Li, Wang et al. 2014, Zhen, Liu et al. 2014, Dhall 2015, Liu, Li et al. 2016, Velkov and Pevicharova 2016). For example, grafting cucumber onto a squash rootstock ('Chaojiquanwang') can lower the sodium (Na) content in the cucumber scion and support tolerance to high salinity (Huang, Li et al. 2013, Xu, Guo et al. 2017). Similarly, squash rootstocks produce wax-free cucumber fruits which are preferred by buyers and consumers (King, Davis et al. 2010).

In the *Solanaceous* family, grafting is used regularly for tomato and eggplant cultivation but also in potatoes and sweet pepper (Gaion, Braz et al. 2018). Potato, unlike other grafted plants, produces the crop below ground making it challenging to pair with a grafting partner improves the above ground traits. Amazingly, potato can be grafted to tomato to generate tomato fruits above ground and potatoes below ground (Arefin, Zeba et al. 2019). In comparison, sweet pepper has limited compatibility with other solanaceous species (Johkan, Mitukuri et al. 2009, Gaion, Braz et al. 2018, Thomas, Gevorgyan et al. 2024). Tomatoes were traditionally grafted to introduce resistance to soilborne pathogens (Hamdi, Boughalleb et al. 2009, Polizzi, Guarnaccia et al. 2014, Yin, Zhao et al. 2014, Owusu, Kwoseh et al. 2016), but with the growing global demand for tomatoes it has promoted seed companies to develop rootstocks that introduce abiotic stress tolerance, improved nutrient or water uptake or improved crop vigour in non-stress conditions (Ntatsi, Savvas et al. 2013, Albacete, Martínez-Andújar et al. 2015, Asins, Raga et al. 2015, SEMİZ and Suarez 2015, Savvas, Öztekin et al. 2017). Grafting induced abiotic stress tolerance spans tolerance to salinity, drought, extreme temperatures, light

stress, flooding, heavy metal toxicity and nutrient deficiency (Black, Wu et al. 2003, Savvas, Colla et al. 2010, Ntatsi, Savvas et al. 2013, Nilsen, Freeman et al. 2014, Albacete, Martínez-Andújar et al. 2015, Kumar, Lucini et al. 2015, Velez-Ramirez, van Ieperen et al. 2015). For example, under low temperature and low light conditions, grafting productive tomatoes onto interspecific hybrid rootstocks can improve the nutritional qualities of the fruits, including increased vitamin C and lycopene accumulation (Riga, Benedicto et al. 2016). Of all abiotic traits to develop tolerant lines, a keen focus has been to develop rootstocks with tolerance to high salinity (Fernández-García, Martínez et al. 2002, Fernández-García, Martínez et al. 2004, Voutsela, Yarsi et al. 2012). This is to support intense greenhouse production which utilises fertigation and high rates of soil moisture evaporation. Similar to the cucurbit rootstocks, tomato rootstocks that supply tolerance to salinity show reduced accumulation of sodium and chloride under stress and support higher yields than the non-grafted and self-grafted controls (Fernández-García, Martínez et al. 2002, Fernández-García, Martínez et al. 2004, Voutsela, Yarsi et al. 2012, SEMİZ and Suarez 2015). That said, it has become highly popular for seed companies to develop rootstocks for tomato cultivation that increase fruit yields under non-stress environments – hence, producing a greater fruit yield per hector (King, Davis et al. 2010). These rootstocks are derived from interspecific hybrid cultivars generated from modern tomato lines and wild tomato species, such as *Solanum habrochaites.* A key example is the grafting of tomatoes (*S. lycopersicum* cv. Florida 47, *S. lycopersicum* cv. El Cid) to 'Beaufort' or 'Multifort' rootstocks to increase marketable fruit yields by up to 41% (Djidonou, Simonne et al. 2016, Velasco-Alvarado, Castro-Brindis et al. 2016).

In Eggplant, grafting utilises rootstock from tomato hybrids or wild species such as *Solanum integrifolium*, *Solanum torvum* and *Solanum sisymbriifolium.* There have been some reports that grafting Eggplant onto traditional rootstocks can lead to loss of tolerance and negative effects on crop yield (Honma 1977, Kawaguchi, Taji et al. 2008, King, Davis et al. 2010). The use of wild species has generally been employed to provide resistance to bacterial wilt (from *Fusarium* spp. and *Verticillium* spp.) and root-knot nematodes, but recent studies have shown they can also improve crop yield and change crop quality. For example, the rootstocks of *S. torvum* and *S. sisymbriifolium* can provide resistance to *Verticillium* wilt but in non-infected soil *S. torvum* rootstock can increase crop production (Bletsos, Thanassoulopoulos et al. 2003, Sabatino, Iapichino et al. 2016). Note that this depends on the eggplant scion. Moreover the *S. torvum* rootstock can alter the nutrient content and physical characteristics of the fruits. Such as improved levels of phenolic antioxidants and darker fruits (Moncada, Miceli et al. 2013, Sabatino, Iapichino et al. 2016). In comparison, the use of interspecific tomato hybrid rootstocks on eggplant has shown to enhance crop vigour – including higher yields, improved fruit quality, tolerance to root-knot nematodes and tolerance to *Verticillium* wilt (Figure 1.2) (Gisbert, Prohens et al. 2011, Gisbert, Prohens et al. 2011, Johnson, Inglis et al. 2014, Kacjan Maršić, Mikulic-Petkovsek et al. 2014, Miles, Wimer et al. 2014, Cerruti, Gisbert et al. 2021). For example, the tomato interspecific hybrid rootstocks 'Beaufort' F1 and 'Emperador RZ' improves the fruit yield and quality in Eggplant cultivars (Gisbert, Prohens et al. 2011, Kacjan Maršić, Mikulic-Petkovsek et al. 2014).

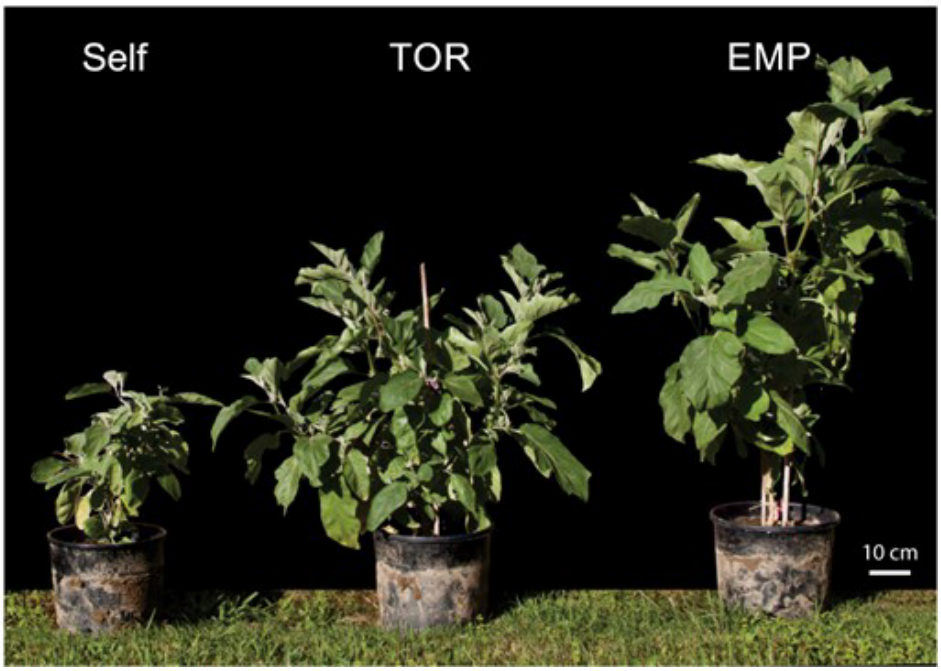


Figure 1.2. Images of grafting traits in Solanaceous species. Image displays differences in vigour between self-grafted eggplant (Self, Solanum melongena var. 'Ecavi'), eggplant grafted onto Solanum torvum rootstocks (TOR), and eggplant grafted onto tomato 'Emperador RZ' (Solanum lycopersicum) rootstocks (EMP). Taken from (Cerruti, Gisbert et al. 2021).

Technological developments allow researchers to estimate the photosynthetic capacity of a plant including the photosynthetic rate (A), stomatal conductance (gs), intercellular CO_2 concentrations (Ci), transpiration rate, water use efficiency (WUE_i), chlorophyll florescence, leaf temperature, and vapor pressure deficit (VPD). To increase crop yields, researchers aim to increase the carbon assimilation through a greater photosynthetic rate. To date, very few studies have investigated changes in photosynthetic performance between heterografts and self-grafts. In non-stress condition, rootstocks derived from wild tomato species found in hostile conditions alter the scion architecture by reducing leaf biomass and improved WUE_i (Cantero-Navarro, Romero-Aranda et al. 2016). At a cellular level, changes to the leaf cell structure have been observed in heterografts, including alterations to the thickness of the leaf mesophyll layer and spongy parenchyma (Nawaz, Wang et al. 2017, Žanić, Vuletin Selak et al.

2018). Whereas in stress conditions, grafting either tomato, pepper (*Capsicum*), or beans (*Fabaceae*) onto either wild or commercial/rootstocks increased the WUE_i compared to self-grafted plants and did not affect crop yield (Fullana-Pericàs, Conesa et al. 2020). Similarly, grafting cucumber onto a salt-tolerant rootstock appears to enhance the activity of Rubisco and increases the expression of related genes. As a result, the grafted plant's is more tolerant to salt stress through improvements in photosynthetic performance and the conversion of nitrates to amino acids (Liu, Bie et al. 2013). In agreement, grafting sweet pepper (*Capsicum annuum*) onto commercial rootstocks increased crop yields under drought conditions and these plants showed an improved net carbon assimilation rate, stomatal conductance and sub-stomatal carbon dioxide concentration (López-Marín, Gálvez et al. 2017). Collectively, these findings demonstrate that the use of both wild-relatives or commercial rootstocks can manipulate and optimise the carbon fixation in the scion. Yet, it is unlikely that a rootstocks ability to uptake more nutrients or water is driving these changes.

Although we are focused on herbaceous plants, it is important to recognise the grafting-induced traits in woody species. Prior to the insurgence of herbaceous grafting, fruit trees were routinely grafted to induce tolerance to pests or alteration to scion vigour. For instance, it is almost always employed for grapevine grafting to ensure resistance to the devasting effects of the soil-borne pest, phylloxera. Alternatively, woody tree grafting can alter vigour by introducing dwarfism. Popular for apple, kiwi and peach cultivation, this method significantly reduces the associated labour costs (Basile and DeJong 2018).

1.4 Regulation of Gene Expression

Gene expression is the fundamental level at which the genome controls an organism's phenotype. Across multicellular organisms, coding regions in the DNA sequences are transcribed into mRNA and translated into proteins (Figure 1.3). These proteins govern biological functions required to support life (Clancy and Brown 2008) (Figure 1.3). The diversity of the transcriptome is enhanced by alternative splicing which is a process that allows a single gene to produce more than one mature mRNA variant (Kornblihtt, Schor et al. 2013, Reddy, Marquez et al. 2013).

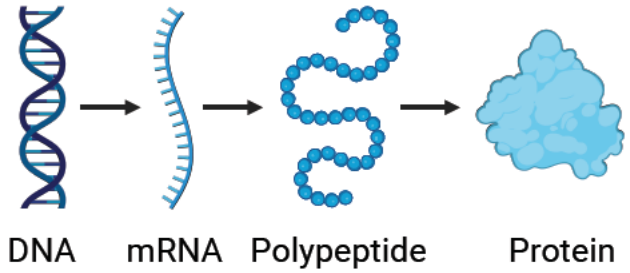


Figure 1.3. The central dogma of biology: gene expression. Gene expression involves the transcription of a gene structure from the DNA sequence into messenger RNA (mRNA). The mRNA is translated into a protein. Created using BioRender.com.

Across years of research, mRNAs have been demonstrated to act as signalling molecules conveying messages cell-to-cell or across long-distances (Kitagawa, Tran et al. 2023). Over the course of a day, a plant will alter the pattern of gene expression. These alterations can be in response to the circadian rhythm and in response to stimulus such as development or environmental cues. The regulation of gene expression relies on many different molecular mechanisms before, between and after gene transcription or translation. In this section we will discuss different molecular mechanisms that regulate gene expression

including epigenetic mechanisms and RNA interference (Figure 1.4). Mainly, DNA methylation and sRNA activity.

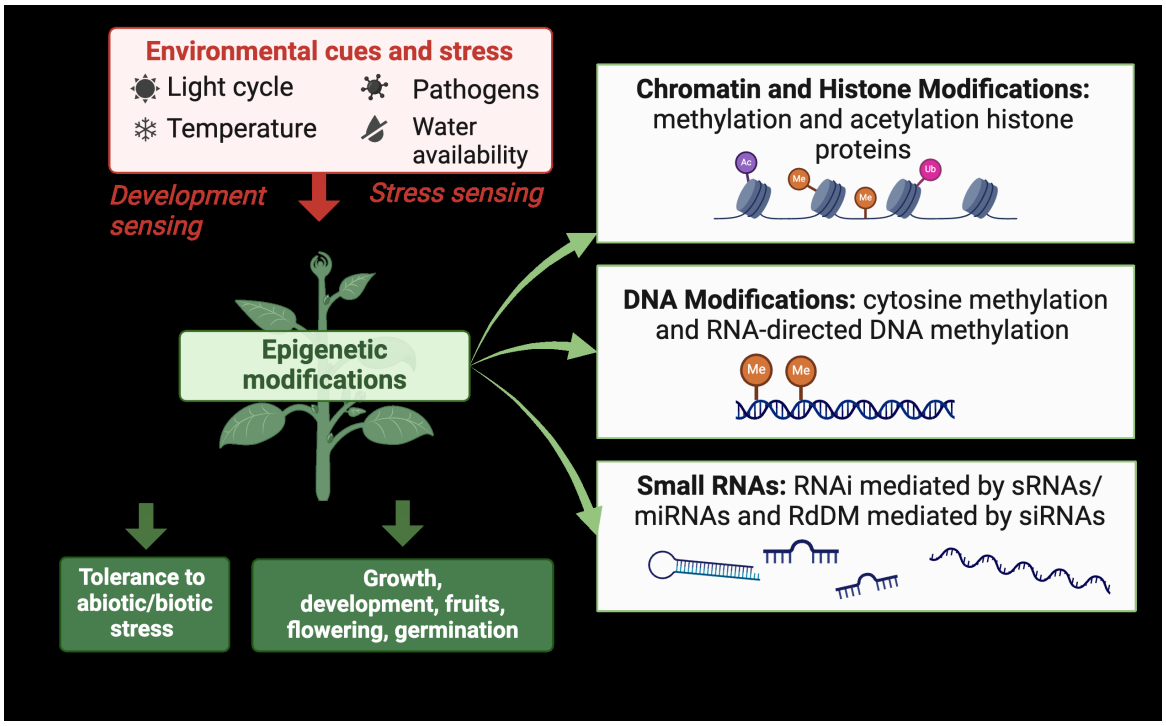


Figure 1.4. Epigenetic regulation in plants in response to environmental and developmental cues. This illustration showcases the role of epigenetic mechanisms in regulating and maintaining the plant growth and development. Several key plant processes, including growth and flowering, are controlled by epigenetic mechanisms including DNA methylation, histone modifications, and small RNAs in gene expression. Created using BioRender.com.

DNA methylation an Epigenetic Mechanism

DNA methylation is a pivotal epigenetic mark involved in the regulation of gene expression and the silencing of transposable elements (TEs). DNA methylation occurs on DNA cytosine residues on carbon five (5-mC) through the action of DNA methyltransferase enzymes (Law and Jacobsen 2010) (Figure 1.5). In plants, 5-mC occurs in three sequence contexts: CHH, CHG and CG where H refers to any nucleotide base bar G (Law and Jacobsen 2010) (Figure 1.5). This epigenetic modification has been associated with the control of

developmental processes including flowering time, seed dormancy, fruit ripening and crop productivity, as well as responses to environmental stimuli (Mercé, Bayer et al. 2020). Similarly, growing evidence not only demonstrates the role of DNA methylation in plant evolution but its role in plant domestication through agricultural practises (Liu and Wendel 2003, Zhang, Fischer et al. 2013, Song, Zhang et al. 2017).

The establishment of *de novo* methylation is initiated by the RNA-directed DNA methylation (RdDM) pathway, which is described further later in the text. The maintenance of cytosine methylation is operated differently for each context, and each requires a specific set of methyltransferases. This is illustrated by the disparage in the distribution of each context within a genome. For instance, in *Arabidopsis* 10-20% of CHH sites maintain methylation, CG sites show the highest degree of methylation (40%) and the majority of CHG sites are unmethylated (Cokus, Feng et al. 2008, Catoni and Zabet 2021). In comparison, in tomato on average 23% of cytosines are methylated - with 55% of CG sites and 85% of CHG sites are methylation (Messeguer, Ganal et al. 1991). The methylation at CG contexts occurs during DNA replication and is driven by the enzyme methyltransferase 1 (MET1) (Woo, Dittmer et al. 2008) (Figure 1.5). In comparison, methylation at CHH contexts is implemented by domain rearranged methylase 2 (DRM2) or chromomethylase 2 (CMT2) with the RdDM pathway and methylation at CHG context is performed by chromomethylase 3 (CMT3) and CMT2, facilitated by factors such as set domain-containing proteins 4-6 (SUVH4, SUVH5, SUVH6) (Figure 1.5) (Du, Zhong et al. 2012, Stroud, Greenberg et al. 2013, Zemach, Kim et al. 2013, Du, Johnson et al. 2014, Liu, Shao et al. 2014, Stroud, Do et al. 2014). In contrast the methylation can be

removed through processes of DNA de-methylation, either in an active or passive process. Active DNA de-methylation is promoted by DNA glycosylase enzymes like REPRESSOR OF SILENCING 1 (ROS1) and DEMETER (DME) through the base-excision repair (BER) pathway. While, passive DNA de-methylation occurs when there is either a lack of methyl donors or by a lack of maintenance during DNA duplication (Almeida and Sobol 2007, Li, Kumar et al. 2018).

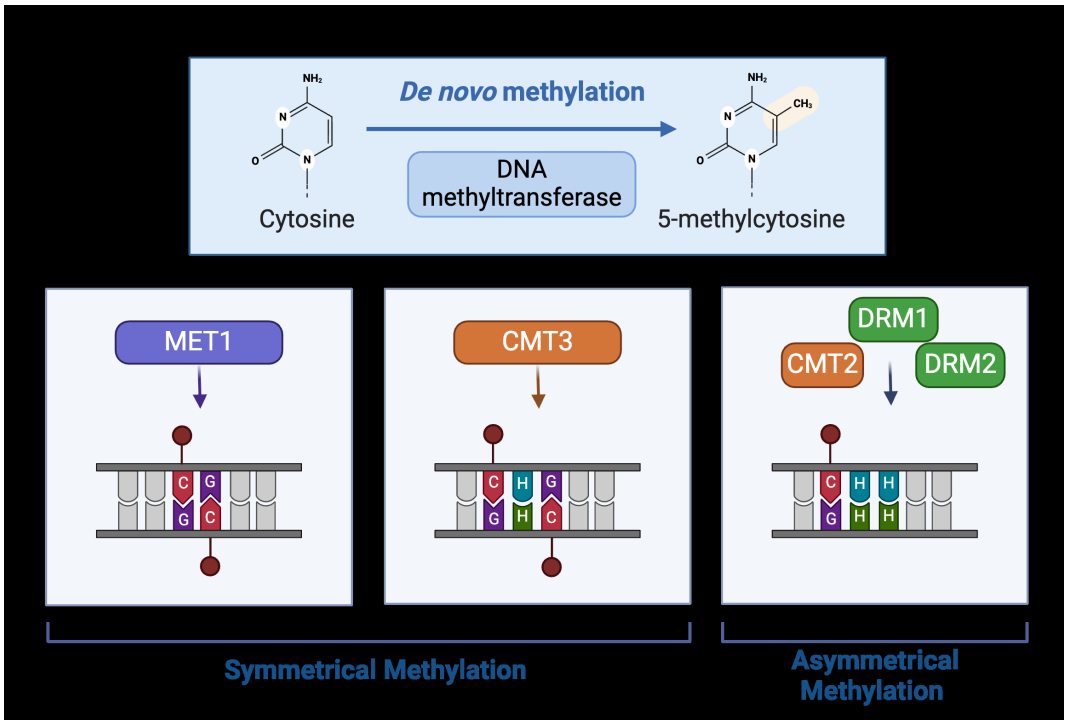


Figure 1.5. Cytosine Methylation of DNA on the 5' carbon. In plants, there are three cytosine methylation contexts and are initiated and maintained by different DNA methyltransferases. The CG methylation context is maintained by methyltransferase 1 (MET1). The CHG methylation context is maintained by chromomethylase 3 (CMT3). The CHH methylation context is maintained by domain rearranged methylase 1 (DRM1), domain rearranged methylase 2 (DRM2) and chromomethylase 2 (CMT2). Both the CG and CHG methylation contexts are symmetrical while CHH methylation context is asymmetrical. Created using BioRender.com.

TEs are the most heavily methylated regions and is predominantly in CHH and CHG contexts (Kumar and Mohapatra 2021) and acts to inhibit TE activation since their activity can threaten genome stability (Kumar and Mohapatra 2021).

When placed within promoter regions, methylation can repress expression, for example by blocking TF binding and generating a repressive-chromatin structure by interacting with DNA-binding proteins specifically recognising methylated DNA. However, it can also activate gene expression by enhancing interactions with TFs, for example observed in the promoter region of the ROS1 gene in *Arabidopsis thaliana*. Lastly, DNA methylation can also occur within the gene body (gbM), mainly in the CG context (Bewick and Schmitz 2017). Interestingly, the functional role of gbM remains largely unknown, primarily because it appears to more than one role. For instance, it has generally been associated with housekeeping genes (Bewick and Schmitz 2017) and maintains its constitutive expression through the control of splicing, prevention of intragenic transcription and promotion of transcriptional elongation (Tran, Henikoff et al. 2005, Zilberman, Gehring et al. 2007, Regulski, Lu et al. 2013, To, Saze et al. 2015). Whereas other results imply that gene body could be an artefact of TEs. More recently, researchers have suggested that gbM could have a much smaller role than anticipated and instead works in hand with additional chromatin factors (Choi, Lyons et al. 2020). This includes cooperation with the histone H1 protein which binds to nucleosomes and the linker DNA (Choi, Lyons et al. 2020).

RNA-directed gene regulation

Small RNAs represent a group of non-coding RNAs with a nucleotide length between 20-25 (Hamilton and Baulcombe 1999, Hamilton, Voinnet et al. 2002). Within this group, there are two types – micro RNAs (miRNAs) and small interfering RNAs (siRNAs) – each with a distinct nucleotide length,

biosynthesis pathway and molecular function (Borges and Martienssen 2015, Kamthan, Chaudhuri et al. 2015, Singh, Gautam et al. 2018).

The first, miRNAs, facilitate post-transcriptional gene silencing (PTGS) which inhibits mRNA translation either via the blocking or cleavage of target mRNA transcripts (Dong, Hu et al. 2022) (Figure 1.6). This mechanism affects gene expression and regulates important aspects of plant physiology, including organs morphogenesis, growth and development, hormone production, systemic signal pathways, and can alter responses to external stress and environmental stimuli (Liu, Li et al. 2009, Yokotani, Nakano et al. 2009, Naqvi, Sarwat et al. 2012). The miRNA producing loci are usually located between genes and are transcribed in the nucleus by RNA Polymerase II (Pol II).

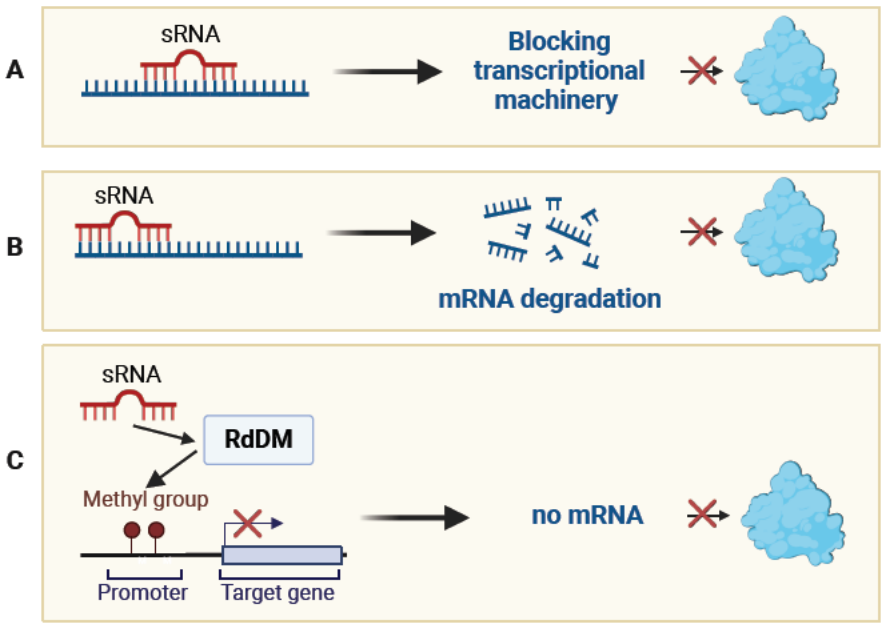


Figure 1.6. Summary diagram of examples of RNA silencing including A) mRNA cleavage. B) inhibition. C) sRNA action through RNA-directed DNA methylation (RdDM) pathway. Created using BioRender.com.

The second group of endogenous sRNAs have a length of 24-nucleotides (24nt) and have a distinct role in the RdDM pathway. RdDM functions to maintain methylation patterns and to add *de novo* methylation to previously unmethylated regions (Figure 1.6) (Hamilton, Voinnet et al. 2002, Qi, He et al. 2006, Henderson and Jacobsen 2007, Matzke and Mosher 2014). This pathway recruits epigenetic factors which add repressive methylation to initiate TGS. The RdDM pathway is critical for several biological processes including cell-to-cell signalling, response to stress and the external environment, and then maintenance of genome stability via the silencing of TEs (Erdmann and Picard 2020). To initiate the DNA methylation, the siRNAs guide the machinery to cDNA sequences. To do so, the siRNAs are loaded into ARGONAUTE (AGO) proteins and bind to an RNA scaffold produced RNA Polymerase V using a complex of Suppressor of Ty insertion 5-like (SPT5L), the Involved in de novo 2-IDN2 Paralog (IDN2-IDP) complex, and the Pol V subunit NRPE1 (Erdmann and Picard 2020). This process recruits the DNA methyltransferase enzyme, DRM2, to added methyl groups to cytosines at the loci (Figure 1.7). Described was the canonical RdDM pathways, in contrast the non-canonical RdDM pathway represents the known variations in the RdDM pathway and represents the pathway to initiate do novo methylation in previously unmethylated regions (Figure 1.8). This has been largely understood in terms of the silencing of newly inserted TEs. When newly inserted and expressed TEs are acknowledged the PTGS/RNAi pathways target these loci to induce silencing and maintain genome stability.

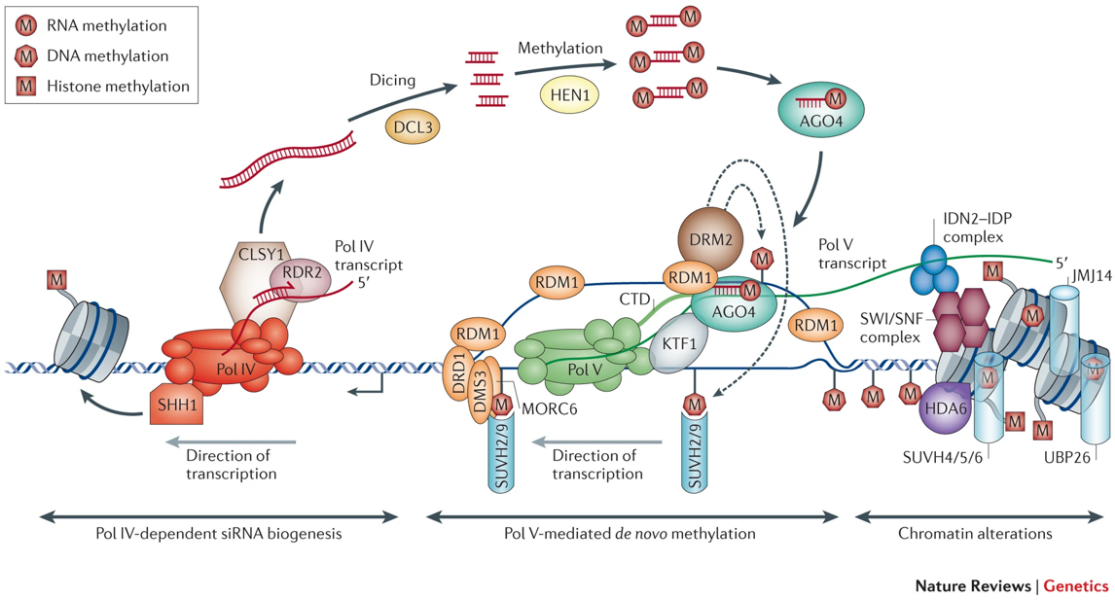


Figure 1.7. Diagram of the Canonical RNA directed DNA Methylation (RdDM) pathway in plants. Single stranded RNA transcripts (ssRNA) are synthesized by RNA polymerase IV (Pol IV) and processed to form 24-nucleotide double stranded small interfering RNAs (siRNAs). The siRNAs are loaded onto Argonaut 4/6 to generate the RNA induced silencing complex (RISC). The complex is imported into the nucleus and directs the enzymatic action of the cytosine methyltransferase DRM2 to establish de novo DNA methylation. Taken from (Matzke and Mosher 2014)

To consistently silence these loci, the system recruits the non-canonical RdDM system, and the new methylation patterns are maintained by the canonical RdDM system. The non-canonical RdDM pathway utilises a different pathway to synthesis siRNAs, and unlike the canonical pathway, it synthesises siRNAs with a length of 21-22nts known as secondary siRNAs. Secondary siRNAs are transcribed from non-coding gene transcripts, such as TAS genes, or protein-coding genes from large gene families, such as pentatricopeptide repeats (*PPR*s) (Kong, Yang et al. 2022). The processing of these secondary siRNAs means many are phased-siRNAs which not only silence the sequence origin in cis but also extends the silencing effect in trans to gene homologues in the same family (Kong, Yang et al. 2022). As secondary siRNAs are transcribed from many different regions it allows de novo DNA methylation to be introduced to a range of loci. Note that these secondary siRNA also act in PTGS alongside

miRNAs. To process transcripts for non-canonical RdDM, some will be first targeted and cleaved by PTGS. These fragments are converted into dsRNAs by RDR6, processed by Dicer/Dicer-like (DCL)2, DCL3 or DCL4 into 21-22nt sRNAs and loaded into AGO6 leading to RdDM (Marí-Ordóñez, Marchais et al. 2013, Nuthikattu, McCue et al. 2013, McCue, Panda et al. 2015). Another way sRNAs can be produced for non-canonical RdDM is from Poll II transcripts – these contain inverted repeat sequences which shape the transcript and generates double-stranded hairpin-like structures. Likewise, miRNA precursors generate similar hair-pin structures. These structures are cleaved by DCL proteins into either PolIV-dependent siRNAs (p4-siRNAs) or secondary siRNAs (Cuerda-Gil and Slotkin 2016). Unlike of types of sRNAs, p4-siRNAs they do not target mRNAs or function outside the nucleus (Hudzik, Hou et al. 2020). These siRNAs become associated with AGO proteins (AGO4, AGO6, or AGO2) to initiate DNA methylation and chromatin remodelling at target loci. In the non-canonical RdDM pathway, the siRNAs guide the protein complex, Needed for RDR2-independent DNA methylation (NERD), towards to loci which in turn attracts DRM2 to mediate the methylation (Figure 1.8) (Pontier, Picart et al. 2012). It is important to recognise that non-canonical RdDM is not fully characterised, hence, there are possibly additional sources of sRNA production not yet known (Pingali 2012).

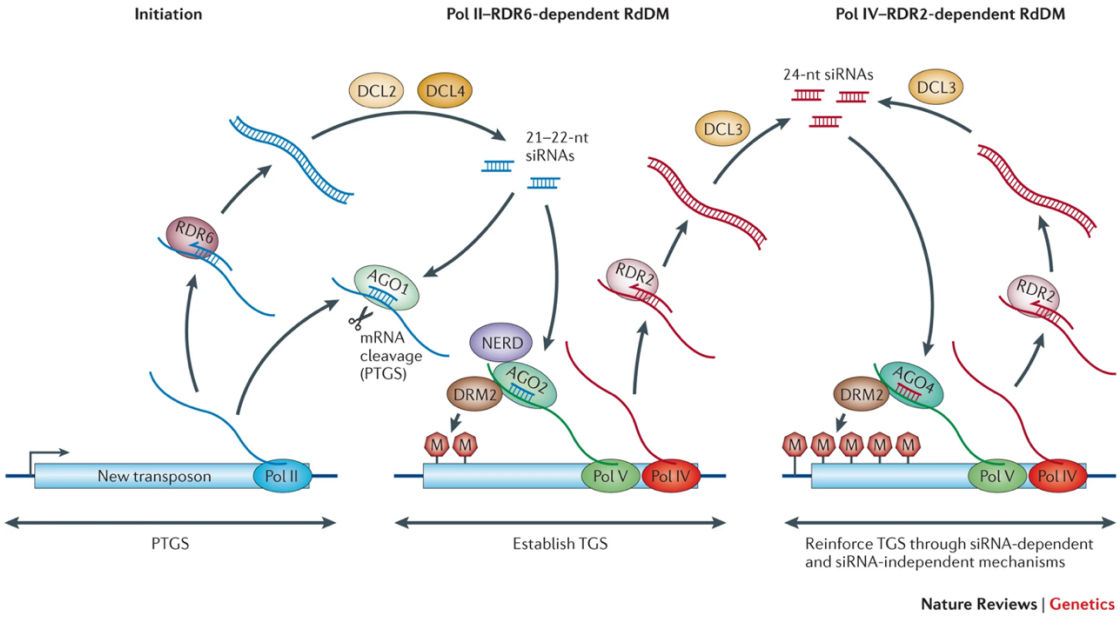


Figure 1.8. Diagram of the Non-canonical RNA directed DNA Methylation (RdDM) pathway in plants. From the left, a newly inserted transposon is visible and is transcribed by RNA polymerase II (Pol II) and converted into double-stranded RNA (dsRNA) by RNA-DEPENDENT RNA POLYMERASE 6 (RDR6). The dsRNAs are processed into 21-22-nucleotide small interfering RNAs (siRNAs) by DICER-LIKE 2 (DCL2) and DCL4. The siRNAs form a complex with ARGONAUTE 1 (AGO1) to guide the cleavage of transposon transcripts through post-transcriptional gene silencing (PTGS). The middle panel illustrates the ability of some 21-22-nt siRNAs to initiate a low level of DNA methylation through the action of DOMAINS REARRANGED METHYLTRANSFERASE 2 (DRM2), Pol V, AGO2 and NEEDED FOR RDR2-INDEPENDENT DNA METHYLATION (NERD). This action recruits' canonical RNA-directed DNA methylation which reinforces transcriptional gene silencing (TGS). Taken from (Matzke and Mosher 2014).

1.5 Molecular Mechanisms Underpinning Grafting-Induced Vigour Changes

While the benefits of grafting are well-documented, the underpinning mechanisms that drive grafting-induced traits remain an area of scientific inquiry. A large proportion of grafting-induced traits can be explained by the intrinsic characteristics of the genotypes within the rootstock. Nevertheless, alterations to the scion's architecture cannot be as easily explained.

Grafted traits such as tolerance to abiotic/biotic stress are typically attributed to the intrinsic properties of a rootstock (Gaion, Braz et al. 2018). Late blight resistance can be induced in tomatoes by grafting onto resistant potatoes and differentially expressed genes (DEGSs) were witnessed in both the scion and rootstocks (Li and Zhao 2021). In melon grafting, pumpkins can be utilised as a rootstock to improve nutrient deficiency tolerance. Specifically, the 'TZ-148', 'RD841' and 'RS-841' cultivars which have been shown to limit the transport of sodium ions from the roots to the shoots by storing an accumulation in the roots in comparison to self-grafted and nongrafted melon plants. A rootstocks' ability to introduce saline tolerance through increased sodium exclusion and potassium uptake is thought to be credited to changes in hormonal regulation resulting in greater control of stomatal functions (Edelstein, Plaut et al. 2011, Orsini, Sanoubar et al. 2013, Neocleous 2015). Likewise, cucumber grafted onto figleaf guard (*Cucurbita ficifolia*) exhibit a higher tolerance to high soil salinity and low temperature tolerance. This was associated to increased antioxidant activity resulting in reduced Na/K leakage, reduced malondialdehyde levels, increase catalase activity, and greater proline accumulation (Huang, Bie et al. 2010, Zhen, Liu et al. 2014, Li, Liu et al. 2015). Conversely, high temperature tolerance can be induced into cucumber by grafting onto luffa (*Luffa cylindrica* (L.) M. Roem) rootstock. Both the luffa and figleaf guard rootstocks induce upregulation of the genes *Cu/Zn-SOD, MYB , MAPK1,* and *MYC* in response to temperature stress (Li, Wang et al. 2014, Li, Liu et al. 2015). The luffa rootstock has also been noted to introduce drought tolerance to grafted cucumbers by improving their water use efficiency and reducing the transpiration rate (Liu, Li et al. 2016). This is thought to be due to the rootstocks heightened sensitivity to changes in water availability leading to a swifter

response resulting in the upregulation of abscisic acid (ABA) biosynthesis and its accumulation in the roots, vascular system, and leaves (Liu, Li et al. 2016).

Grafting can alter the development and physiology of the scion which manipulates the crop's vigour. Yet, the mechanisms giving rise to these changes are not fully understood, and hence, still under active investigation (Ghanem, Albacete et al. 2011, Djidonou, Simonne et al. 2016, Grieneisen, Aegerter et al. 2018, Cerruti, Gisbert et al. 2021). So far, its thought that intrinsic rootstock traits are harder to associated to these changes in scion architecture; suggesting that there are additional interactions in play. Historically, it has been hypothesised that grafting-induced vigour could be associated with the a rootstocks more extensive and efficient root system, with a greater capacity to draw water, minerals and nutrients from the soil (Lee 1994). Indeed some grafting combinations are more efficient at absorbing and trafficking nutrients from root-to-shoot (MASUDA and GOMI 1984, Ruiz and Romero 1999, Pulgar, Villora et al. 2000, Rivero, Ruiz et al. 2005, Rouphael, Cardarelli et al. 2008, Colla, Rouphael et al. 2010, Colla, Suárez et al. 2010, Salehi, Kashi et al. 2010). However, in these studies they have recognised that the source of the vigour is unclear and investigators could not rule out the possibility that vigour was an indirect consequence of alteration in scion gene expression (Rouphael, Cardarelli et al. 2008). Similarly, hormones are known to play a role in systemic signalling and thought to play a role in grafting-induced vigour. For example, one study used a grafting of tomato with an engineered rootstock that overexpressed a cytokinin biosynthesis enzyme and they observed higher crop yields than non-grafted controls in high salinity (Ghanem, Albacete et al. 2011). In tree grafts, studies suggest hormones play a role in a rootstocks ability to

introduce dwarfism – dwarfism is a form of improved crop vigour in trees as it generated higher yield efficiencies which is thought to be due to greater partitioning of hormones and carbohydrate into fruit production (Habibi, Liu et al. 2022).

More recent findings imply that grafting-induced crop vigour could be associated with genetic and epigenetic reprogramming. Specifically, the systemic movement of endogenous RNAs between the scion and rootstock leading to the silencing or activation of specific genes. This dialog also stipulates alterations to epigenetic marks, such as DNA methylation and histone modifications, which can alter the transcriptome without altering the DNA sequence. Recent studies have associated DNA methylation changes to crop vigour (Yang, Sanchez et al. 2020, Cerruti, Gisbert et al. 2021) and have contributed to drought tolerance, fruit development and ripening in grafted orange trees (Neves, Almeida et al. 2017, Huang, Liu et al. 2019). As well as the association between the reprogramming of the transcriptome and the abundance of specific sRNA populations (Cookson and Ollat 2013, Ahsan, Hayward et al. 2019). For example, in avocado trees the abundance of miR156, miR172 and the miR156, known to target the SPL4 gene, control juvenility and flowering (Ahsan, Hayward et al. 2019). Moreover, sRNAs and mRNAs mobility across the graft junction has been demonstrated (Molnar, Melnyk et al. 2010, Thieme, Rojas-Triana et al. 2015, Zhang, Thieme et al. 2016). The mobile sRNAs have been associated to changes in DNA methylation and transcriptomic patterns in the grafted plants, yet these investigations lack direct implications to grafting-induced traits (Buhtz, Springer et al. 2008, Molnar,

Melnyk et al. 2010, Lewsey, Hardcastle et al. 2016, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022).

1.6 The RNA Mobilome and Plant Traits

Regulating plant growth and development incorporates vast mechanisms and circuitry. At the centre are signalling molecules that transmit, coordinate, and control these mechanisms. One such are non-cell autonomous RNA molecules including mRNAs and sRNAs, both of which have been well-characterised as systemic signalling molecules in plant graft systems (Molnar, Melnyk et al. 2010, Lewsey, Hardcastle et al. 2016, Heeney and Frank 2023).

1.6.1 RNA Mobilomes

In the past decade studies have isolated putative mobile RNAs produced by one grafting partner and located in the tissues of the other. Many of which have been more focused on mobile mRNAs and have associate their transmission with phenotypical changes. However, very few studies have assessed the sRNAs mobilome and their impact on plant phenotypes. By using interspecific grafting, we can detect mobile RNAs based on sequence variations between the genotypes. While it is near impossible to track mobile RNAs produced by the same genotype.

The Messenger RNA Mobilome

Long-distance signalling in plants can be mediated by non-cell autonomous mobile mRNA molecules travelling in the phloem and have the potential to directly contribute to protein synthesis and fluctuations in protein abundances

in distant tissues (Lee and Cui 2009, Jeynes-Cupper and Catoni 2023). At their destination, these proteins might act as TFs to inhibit or promote gene expression which could contribute to observed phenotypical and physiological difference (Lee and Cui 2009, Jeynes-Cupper and Catoni 2023). The possibility of mRNA mobility was first demonstrated by showing the ability of mRNAs to move across the phloem plasmodesmata. Initial studies investigated the mRNA of the sucrose transporter 1 (SUT1) whereby the SUT1 gene is expressed only in the companion cells and not in the sieve tube elements, yet, the mRNA accumulates in the sieve tube elements suggesting mobilisation (Kühn, Quick et al. 1996, Kühn, Franceschi et al. 1997). Similarly, the mobility of a functional mRNA transcript was described in experiments using tomato. The mutant *Me* tomato line produces a chimeric mRNA transcript produced by the fusion between PYROPHOSPHATE-DEPENDENT PHOSPHOFRUCTOKINASE (*PFP*) and HOMEOBOX PROTEIN KNOTTED-1-LIKE *(LeT6) (Kim, Canio et al. 2001, Tsiantis 2001)*. This transcript encodes a TF from the KNOX gene family, and the *Me* mutation results in altered leaf morphology. When the mutant line is utilised as a rootstock, the same alterations in leaf morphology are observed in the wild-type scion. Using *in situ* reverse-transcriptase PCR (RT-PCR), *Me* mRNA transcripts were located in the phloem (Kim, Canio et al. 2001, Tsiantis 2001). Similarly, the abundance and localisation of the *Me* mRNA transcripts were comparable between the mutant shoots and the wild-type shoots grafted on a mutant rootstock, which suggest that mobilisation of distant mRNAs can be directly responsible for plant traits. Using a similar method with *Arabidopsis thaliana*, a dwarfed transgenic line with a deficiency in gibberellins (GA) synthesis, reverted its phenotype if grafted onto a wildtype rootstock (Peng, Carol et al. 1997, Magome, Yamaguchi et al. 2004). Remarkably, a similar

observation was replicated in tomato, where a mutant line was utilised as a rootstock and induced dwarfism in the scion (Wang, Liu et al. 2012). Together, the dwarfism was associated with a root-to-shoot mobile transgenic mRNA transcript. Similar observations were described in pumpkin (*Cucurbita pepo*) where it has been determined that the mobile transcripts responsible for the phenotype was root-to-shoot mobile. These results showed that an accumulation of mRNA in specific tissues regulated GA-response genes (Haywood, Yu et al. 2005). Mobile mRNA molecules were also found using RT-PCR and *in situ* hybridisation for the transcripts of the potato homeobox1 (POTH1) gene and BEL1-type *BEL5* gene (Kim, Canio et al. 2001). These mobile mRNAs were linked with changes in hormone levels, leaf architecture and improved tuber formation in potato (Banerjee, Chatterjee et al. 2006, Mahajan, Bhogale et al. 2012). These examples were found in *Solanaceous* crops, and similar findings have been found in other crop families. In the *Cucurbitaceae* and *Brassicaceae* families, mobile mRNAs related to auxin signally have been found in plant grafts and thought to have driven phenotypical changes. Unlike the previous examples, this transcript was shown to move shoot-to-root and impair lateral root formation (Omid, Keilin et al. 2007, Notaguchi, Wolf et al. 2012). Moreover, in cucumber and pumpkin grafting for drought tolerance, elevated levels of ABA have been observed in the scion of heterografts. And, it was surmised that the presence of mobile mRNA transcripts drove the increased accumulation of ABA which facilitated the drought tolerance in cucumber crops (Davoudi, Song et al. 2022).

The Small RNA Mobilome

To investigate sRNAs, researchers are widely used *Arabidopsis thaliana* and cucurbits as models. Here, *Cucurbits* and *Brassica* species were used from the early days to access RNA populations and mobility whereas *Arabidopsis thaliana* has been used to understand the mechanistic role of mobile sRNAs (Yoo, Kragler et al. 2004, Buhtz, Springer et al. 2008). One of the pinnacle studies in *Arabidopsis thaliana* demonstrated systemic movement of sRNAs from shoot-to-root and illustrated their ability to direct *de novo* DNA methylation in the rootstock tissue via the RdDM pathway (Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016, Zhang, Lang et al. 2018).

Since, there has been a growing interest in translating these findings into crops due to their significance in understanding grafting-induced traits including eggplant, pumpkin, cucumber, potato, *N. benthamiana*, grapevine, beans and soybean (Tournier, Tabler et al. 2006, Bai, Kasai et al. 2011, Zhang, Kollwig et al. 2014, Cerruti, Gisbert et al. 2021, Li, Wang et al. 2021, Davoudi, Song et al. 2022, Rubio, Stammitti et al. 2022). For instance, in potato several miRNAs have been found to be graft transmissible including miR156, miR339, miR395 and miR172 (Pant, Buhtz et al. 2008, Buhtz, Pieritz et al. 2010, Kasai, Kanehira et al. 2010). These miRNAs were identified using assays which comprised of miRNA validation using RT-PCR and miRNA levels were determined using stem-loop quantitative RT-PCR (qRT-PCR). Of which, the miR156 was found to target specific genes related to plant architecture and tuberization causes these characteristics to change (Bhogale, Mahajan et al. 2014).

Some crop grafting studies set out to primarily identify whether grafting-induced traits were linked to changes in DNA methylation and forgoes mobile sRNA analysis. This was initially explored in grafting of cucumber and melon as scions to a pumpkin rootstock which is linked to improved tolerance to salinity. With Methylation Sensitive Amplification Polymorphism (MSAP) analysis, grafting-induced hypermethylation in CHG and CG profiles in scions was observed (Avramidou, Kapazoglou et al. 2015). Whereas, other studies have utilised methylsensitive-PCR (McrBC-PCR) to associate mobile sRNAs in grapevine grafting with TGS at target loci (Rubio, Stammitti et al. 2022). Later, additional researchers utilised Bisulfite sequencing (BS-seq) to determine whole-genome wide DNA methylation changes in eggplant heterograft with *Solanaceous* hybrid rootstocks which are known to introduce improved crop vigour. This study found that vigour was associated with genome-wide hypomethylation in the CHH context and the transcriptomics found that the methyltransferases SmelCMT3b and SmelMET1 were upregulated, suggesting that epigenetics regulation may be controlled differently in the heterografts compared to self-grafts. Moreover, keeping in mind that TEs are silenced by DNA methylation, they found more TEs were downregulated in the heterografts while the most upregulated TEs were retrotransposons (Cerruti, Gisbert et al. 2021). Unlike the previous study, a pattern of genome-wide CHH hypomethylation was observed, although in the previous work CHH methylation was not measured (Cerruti, Gisbert et al. 2021).

The mobility of sRNA has been demonstrated in proof-of-concept studies conducted in *Arabidopsis thaliana* used gene knock-out mutants and transgenes (Molnar, Melnyk et al. 2010, Lewsey, Hardcastle et al. 2016), and recent studies

have mirrored these approaches in crops. For example, transgenic lines of *N. benthamiana* containing artificial sRNA producing-transgenes which have been utilised as the scion grafting partner to a wild-type rootstock (Bai, Kasai et al. 2011). In this study the shoot-to-root movement of an artificial siRNA was observed to induce TGS via the RdDM pathway on endogenous genes (Bai, Kasai et al. 2011). The authors later followed up this investigation using interspecific grafting between the same *N. benthamiana* transgenic line and potato where potato was utilised as a rootstock, and the resulting grafted plants demonstrated siRNA induced TGS and changes in tuber formation (Kasai, Bai et al. 2016). Remarkably, the TGS was maintained also in offspring of these plants which lacked the transported siRNA, indicating that the epigenetic alterations induced by the mobile siRNA are transgenerational stable. This outcome suggest that mobile sRNAs could be exploited, in combination with grafting, as transient tools for epigenetic editing and crop breeding (Kasai, Bai et al. 2016). For example, this mechanism has been exploited to improve the CRISPR-*Cas9* process. The *CRISPR-Cas9* technology allows for genome editing including the removal, addition, or alteration of nucleotide regions. The discovery of *CRISPR-Cas9,* has supported the discovery of plant signalling mechanisms, however, to produce transgene-free lines it is an extensive process of outcrossing. To mitigate this issue, the authors engineered the *Cas9* transcript to be able to move across a grafting junction. This was achieved by adding a tRNA-like sequence motif that stabilises and promote systemic movement. This construct was transform into *A. thaliana*, and the transgenic plant obtained was used as a rootstock for wild-type scions. From the wild-type scions of the grafted plants, they recover genome edited seeds. These were a product of the *Cas9* activity from rootstock transgenic transcripts, which moved in the wild-

type scion. Importantly, this result was also replicated in different species, which indicates that the mobilisation of a functional transcript is independent of the genotype. The first-generation progeny of the grafted plants was transgene-free and maintained the gene modifications. This study demonstrated that grafting can be used successfully to introduce gene editing mediated by a *CRISPR-Cas9* transgenic rootstock in to a wild-type genotype (Yang, Machin et al. 2023). However, this method is dependent upon developing transgenic rootstocks which are compatible with scions.

1.6.2 Transport mechanisms of mobile mRNAs and sRNAs in Plant Grafts

Much of our knowledge of RNA trafficking derives from viral infection and plant viroids studies - circular non-coding RNA species considered as plant pathogens (Capistrán-Barradas, Moreno-Casasola et al. 2006, Ding and Itaya 2007, Wang, Li et al. 2021). The mobility of exogenous viroid RNAs is facilitated by endogenous plant proteins in pear, as well as viroid hitch-hiking with endogenous organelle intracellular transfer (Gómez and Pallás 2004, Duan, Zhang et al. 2016, Luo, Huang et al. 2022). Similarly, the selective movement of viroids is dependent on the presence of specific pseudoknot/hairpin motifs and without them the intercellular transport is not possible (Qi, Peélissier et al. 2004, Zhong, Tao et al. 2007, Zhong, Archual et al. 2008, Takeda, Zirbel et al. 2018).

Using vascular exudates from Brassica species, endogenous RNAs were shown to be mainly transported by the phloem, rather than the xylem (Buhtz, Springer et al. 2008). Since, researchers have developed many a theory to describe whether RNA trafficking utilises passive or non-passive movement (Figure 1.9) and begs the question whether the spatial regulation of genes by sRNAs or

mRNAs goes further than what can be generated by transient gradients in the vascular system.

Passive RNA Transport

Molecules can move passively in the phloem taking advantage of integral turgor levels, which induces sap movement from source-to-sink (Münch 1930, Turgeon and Wolf 2009, De Schepper, De Swaef et al. 2013). Research suggests that the phloem appears to be the primary tissue to transport RNAs and can protect RNAs from degradation unlike the xylem sap which contains RNases (Sasaki, Chino et al. 1998, Doering-Saad, Newbury et al. 2002, Alvarez, Goodger et al. 2006, Gaupels, Buhtz et al. 2008, Bai, Liu et al. 2013, Knoblauch, Peters et al. 2018). Studies on passive mRNA movement suggest that their mobility is driven by local abundance – otherwise known as bulk flow (Thieme, Rojas-Triana et al. 2015, Calderwood, Kopriva et al. 2016). The majority of transcriptomic studies have supported source-to-sink movement, since most detect more RNAs moving from shoot-to-roots than from roots-to-shoots (Ruiz-Medrano, Xoconostle-Cázares et al. 1999, Omid, Keilin et al. 2007, Notaguchi, Higashiyama et al. 2015, Thieme, Rojas-Triana et al. 2015, Yang, Mao et al. 2015, Li, Wang et al. 2021). Movement via bulk flow theory supports the concept that mobile RNAs do not have specific targets or target locations and move in an indiscriminatory manner (Xia, Zheng et al. 2018). These studies were clear to note that not all RNAs were shown to be transported via the source-to-sink gradient, and that an active mechanism which utilises energy stores could be considered (Zhang, Sun et al. 2009, Thieme, Rojas-Triana et al. 2015, Zhang, Thieme et al. 2016, Garcia-Lozano, Dutta et al. 2020) (Figure 1.9). That said,

other investigations have demonstrated that even in high abundances a transcript may lack mobility (Kehr and Kragler 2018, Xia, Zheng et al. 2018).

Non-Passive RNA Transport

For some RNA transcripts movement across the graft junction has been demonstrated to be either bi-directional, in the root-to-shoot or into specific tissues which negates the suggested directionality in passive theories (Thieme, Rojas-Triana et al. 2015). Instead of a passive transport system, evidence has suggested that the mobility of RNAs could be dependent upon the support of faciliatory molecules and/or facilitated by structural features such as specific sequences or structural motifs (Figure 1.9).

RNA binding proteins (RBP) can act as chaperones to support RNA transport throughout the phloem (Figure 1.9) (Kempers and van Bel 1997, Imlau, Truernit et al. 1999, Stadler, Wright et al. 2005, Ostendorp, Pahlow et al. 2017, Yang, Perrera et al. 2019). These findings were largely inspired by the movement proteins (MPs) identified in RNA viruses which are known to interact with RNAs to promote intracellular mobility and the systemic spread of infection (Lucas 1995, Foster, Lough et al. 2002, Itaya, Ma et al. 2002, Gómez and Pallás 2004, Ham, Brandom et al. 2009, Hipper, Brault et al. 2013). The MPs support mobility by increasing the exclusion limit size of the plasmodesmata to allow the entry of larger molecules (Wolf, Lucas et al. 1989, Oparka, Prior et al. 1997). There have been strong arguments to suggest that plants have a similar natural mechanism to assist RNA mobility as mRNAs indeed can be usually too large for mobility. Several examples include KNOTTED1 (KN1) TF-mRNA–protein and PHLOEM PROTEIN 16 (PP16) RNA complexes which can alter the

plasmodesmata to increase permeability to facilitate movement between cells (Xoconostle-Cázares, Xiang et al. 1999, Kitagawa, Tran et al. 2023), as well as PHLOEM SMALL RNA-BINDING PROTEIN 1 (PSRP1) which binds to an RNA to form a ribonucleoprotein complex in the phloem sieve tube system to carry the RNA (Ham, Li et al. 2014).

Additionally, intrinsically disordered proteins have also been observed to act as faciliatory proteins in a similar manner to RBPs and MPs. For example, two orthologs from *A. thaliana* and *B. napus* of the phloem-associated RNA chaperone-like (PARCL) protein are both able to bind to a broad-spectrum of RNAs and demonstrated RNA-chaperone activity using in vitro assays (Ostendorp, Ostendorp et al. 2022). This mechanism is dependent upon the state of the prion-like domain (PLD) within the faciliatory proteins where modifications, such as phosphorylation, inhibit affects RNA binding activity and hence inhibit transport (Ostendorp, Ostendorp et al. 2022). These intrinsically disordered proteins have been shown to have a high degree of flexibility which is thought to enable a level of molecular memory which could support plant responses to external stimuli over generations (Cuevas-Velazquez and Dinneny 2018, Fang, Wang et al. 2019, Ostendorp, Ostendorp et al. 2022).

Specific sequence and structural motifs have been identified to assist mRNA transport, resulting in the discovery of hundreds of protein-RNA complexes. Linking back to the usage of RBPs, in pumpkin, it has been observed that the mRNAs trafficking via binding to an RBP required the presence of a specific polypyrimidine tract binding motif (Xoconostle-Cázares, Xiang et al. 1999). In a similar way the presence of transfer RNA like (tRNA-like) structure (TLS) motifs show to correlate with mRNA long-distance mobility (Zhang, Sun et al.

2009). This was demonstrated by fusing Cas9 and guide RNAs for *CRISPR* with TLS motifs which enabled the movement of these molecules across a graft junction to deliver stably inherited transgene-free alterations in the recipient tissue (Zhang, Zheng et al. 2016, Ellison, Nagalakshmi et al. 2020, Beernink, Lappe et al. 2022, Yang, Machin et al. 2023). A causative relationship was further demonstrated by showing that these structures are highly abundant in the phloem and eliminating TLS from RNA molecules prevented RNA mobility (Garcia-Lozano, Dutta et al. 2020, Yang, Machin et al. 2023). This evidence supports the hypothesis that RNAs have mechanisms for target-specific transportation to subcellular compartments and it has been suggests that these motifs act as a "postcode" to ship the molecules to a specific destination (Jeffery, Tomlinson et al. 1983, Crofts, Washida et al. 2004, Lécuyer, Yoshida et al. 2007, Lécuyer, Yoshida et al. 2009, Weis, Schleiff et al. 2013).

Secondary 5-methylcytosine (m5-C) modifications on the RNA transcript is another structural feature that can facilitate the transport of RNAs across a graft junction. This modification is found on mRNA, tRNA, ribosomal RNA and long-non-coding RNAs (lncRNAs) (Xu, Szekely et al. 2024). RNA methylation is a highly abundant modification that alters various plant processes by modifying mRNA processing and metabolism (Xu, Szekely et al. 2024). This modification was highly abundant in specific graft-mobile transcripts, including *HSC70.1* and *TCTP1 (Yang, Perrera et al. 2019)*. The methylation of cytosine residues on mRNA molecules, specifically at TLS site, is positively associated with mobility (Yang, Perrera et al. 2019). Whereby removal of the cytosine methylation on the mRNA molecular can negatively impact mobility. This was demonstrated by generating mutants which lacked cytosine-methyltransferase

enzymes which showed a genome-wide reduction in DNA methylation along with a decreased level of transcript mobility and some previously mobile transcript showed no mobility (Yang, Perrera et al. 2019). This study suggested that for at least a subset of mRNAs the sequence at the beginning of the molecule is required and sufficient to mediate mobility (Yang, Perrera et al. 2019). Alongside the evidence on protein-RNA interactions, it has become clear that the RNA-binding proteins recognise the RNA methylation but not that the methylation can also be recognised by demethylases which can remove the modification (Meyer and Jaffrey 2014, Xue, Zhao et al. 2020).

The evidence above is largely collated in relation to mRNA mobility because the nature of sRNA mobility has proven challenging to determine. Most sRNA transport has been studied in the context of understanding the dispersion of RNA silencing at a whole organism level, and few efforts have been directed to understanding the mechanism which is utilised under different spatial or temporal contexts. It has been shown that sRNA can move intercellularly via the plasmodesmata, but this cell-to-cell movement can be blocked when a gain-of-function mutation in callose synthase is introduces (Vatén, Dettmer et al. 2011). In addition, all major size classes of sRNAs (21, 22, and 24 nt) can systemically move over long-distances by utilising the phloem and mobility has been linked to the coordination of responses to abiotic and biotic stressors (Buhtz, Springer et al. 2008, Lin, Chiang et al. 2008, Ruiz-Ferrer and Voinnet 2009, Molnar, Melnyk et al. 2010, Zhang, Kollwig et al. 2014). For example, this role has been vastly demonstrated in relation to viral pathogen attacks and nutrient stress (Yoo, Kragler et al. 2004, Buhtz, Springer et al. 2008, Pant, Buhtz et al. 2008, Brosnan and Voinnet 2011, Melnyk, Molnar et al. 2011, Borges and

Martienssen 2015). This suggests that sRNA movement may utilise active processes or faciliatory mechanisms to move against the flow in the phloem. Like mRNA transport, specific proteins have been associated with cell-to-cell sRNA trafficking across the plasmodesmata such as Phloem SMALL RNA BINDING PROTEIN1 (CmPSRP1) located in pumpkin, and similar binding proteins have been found in cucumber and lupin (*Lupinus albus*) (Yoo, Kragler et al. 2004). In this model, the CmPSRP1 protein binds to 25-nt single-stranded sRNAs and enables trafficking by altering the plasmodesmata size exclusion limit (Yoo, Kragler et al. 2004). Complementing these findings, it was later found sRNAs can be denied entry into a cell even after moving across multiple others (Skopelitis, Hill et al. 2018, Devers, Brosnan et al. 2023). This selectivity is likely derived from the presence or absence of specific AGO proteins (Devers, Brosnan et al. 2023) which have been demonstrated to cause selective depletion of sRNA abundance resulting in distinct silencing patterns across cells and tissues (Devers, Brosnan et al. 2020). Similarly, utilising the information collected from studies on RNAi involvement in viral attacks, other mobility factors can be polarised at specific cell-cell interfaces and act as "gate-keepers" to control sRNA trafficking, (Skopelitis, Hill et al. 2018). Specifically, BAM1/2 receptor-like kinases have been located in close proximity to the plasmodesmata and proposed to act as "gate-keepers" (Fernandez-Calvino, Faulkner et al. 2011, Stahl and Faulkner 2016, Rosas-Diaz, Zhang et al. 2018). Since these findings, researchers have also identified the importance of microtubules in the non-cell autonomous action of sRNAs, whereby they prevent the loading of sRNAs into AGO1 proteins within the nucleus which allows the sRNA to leave the cell (Fan, Zhang et al. 2022).

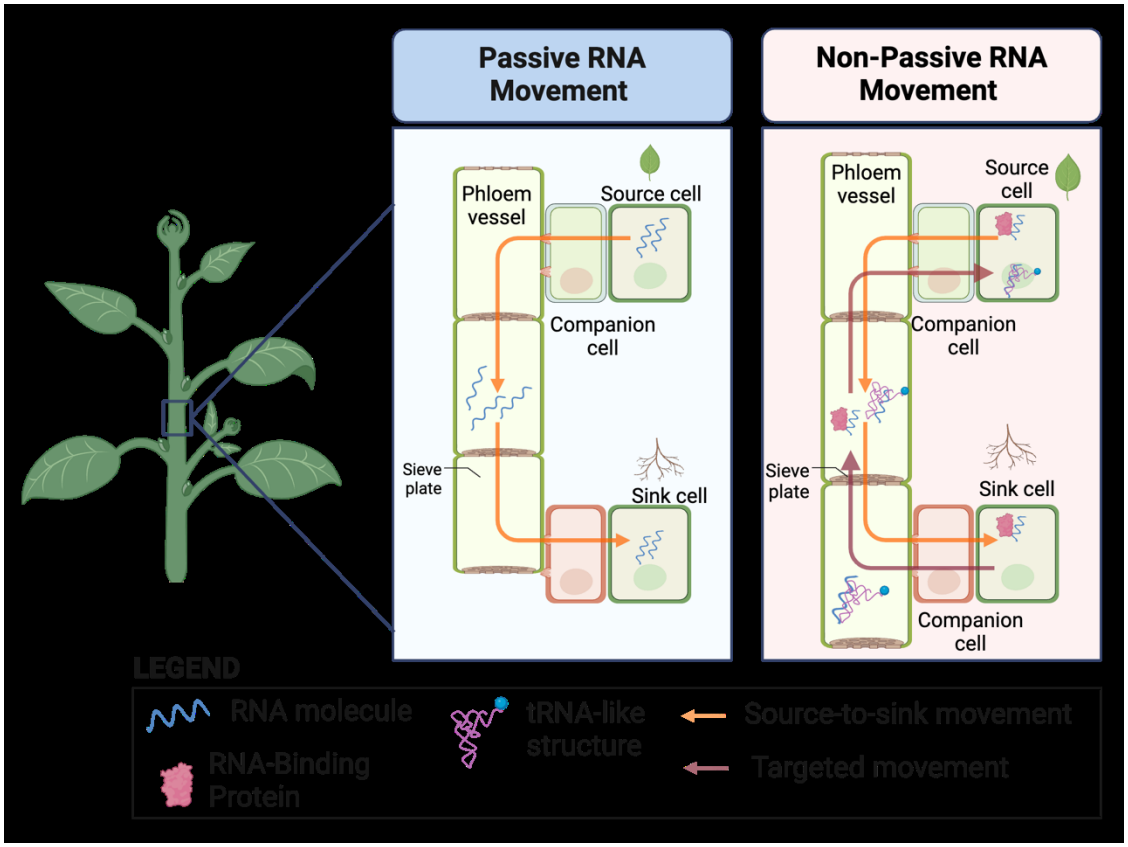


Figure 1.9. Diagram summarising the potential mechanism long-distance RNA transport in plants. RNAs can move via both passive and non-passive mechanisms. Passive movement utilises bulk flow system which transport substrates from source-to-sink, such as photosynthates. Non-passive mechanisms allow RNAs to both bi-directionally against the sap flow in the phloem. This mechanism utilises proteins and tRNA-like motifs. Created using BioRender.com.

1.6.3 Measuring the sRNA and mRNA mobilomes

To measure the RNA mobilome, the most common approaches use NGS technologies, such as messenger RNA sequencing (mRNAseq) and small RNA sequencing (sRNAseq) (Heeney and Frank 2023, Jeynes-Cupper and Catoni 2023). RNA sequencing technologies involve four key steps to quantify RNA in a biological sample: RNA isolation, conversion of RNA to cDNA, library preparation and sequencing using a NGS platform. There are two major considerations to identify putative mobile RNA molecules: 1.) the biological experimental design. 2.) the bioinformatical pipeline.

In the laboratory, several molecular laboratory techniques can be used as systems to detect trans-species or mobile RNAs. Some common techniques include RT-qPCR, Northern blotting and microarrays (Kim, LeBlanc et al. 2014, Notaguchi, Higashiyama et al. 2015, Thieme, Rojas-Triana et al. 2015, Zhang, Thieme et al. 2016, Xia, Zheng et al. 2018, Liu, Xiang et al. 2020, Wang, Wang et al. 2020, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022). However, these methods have both advantages and disadvantages. Firstly, RT-qPCR is a speedy, cost-efficient, and sensitive approach for the quantitation of mRNA expression. Specifically, it allows for its detection at very low levels which is very suitable for the detection of mobile mRNAs which are expected to be at low levels in recipient tissues. However, it could be challenging to normalise the expression of the mobile mRNA expression against the reference genes if the expression levels differ across the samples which might be expected in this design. In comparison, both Northern blotting and microarrays can be used for the detection of mobile sRNAs and mRNA. They are highly versatile as they can simultaneously analyse multiple targets, provide information of the size of the transcripts, and can illustrate semi-quantitative results with regards to the expression levels. However, Northern blotting can be limiting as it struggles to detect sRNA molecules with a low abundance which is particular problematic as mobile transcripts are not expected to be present in high abundance within the recipient tissue (Martinho and Lopez-Gomollon 2023). All three methods have a common disadvantage – they require designing either probes or primers to identify specific or putative targets. The design of probes or primers are based on the nucleotide sequence of the targets, hence, limiting the ability of these methods to detect novel transcripts. In addition, it is unclear how the production of sRNAs shifts and fluctuates over time and how this may affect

the validation of results. For instance, in studies where a miRNA produced by a transgene has been observed to be mobile it shows a linear decrease in miRNA abundance within the sink tissue as the grafted plant matures (Kasai, Bai et al. 2016). Therefore, these methods are typically employed to validate results from sequencing data. That said, trans-species mobile RNAs could have high sequence homology with non-mobile transcripts in the sample, hence, the design of primers or probes requires finetuning to minimise background noise.

The Illumina sequencing platform is a popular technology to extract the genetic information stored within nucleic acid samples to enable researchers to analyse genetic variation between conditions. The popularity of this approach is evident in its application in the analysis of RNAs in phloem exudates in both cucurbits and brassica species (Buhtz, Springer et al. 2008), and is due to its high-throughput, accurate and cost-efficient nature. The output of Illumina sequencing is represented as raw sequencing data in the form of a FASTQ file and serves as the foundation for downstream bioinformatic analysis. In a typically RNA expression analysis, these sequencing reads would be cleaned, aligned to a reference genome that represents their origin, and quantified to determine the abundance of each gene or transcript. In a circumstance where we a sample contains RNAs from the origins and trans-species RNAs, such as in heterografting experiments, the approach will aim to identify which RNAs originates from each of the multiple genomes (Figure 1.10). In this respect, the most used bioinformatic approaches are based on the alignment on a genotype of reference and post-alignment screening of genetic difference to identify RNAs which better match for the genotype of the grafted partner. This has been encapsulated into two different approaches to discriminate trans-species RNA:

1.) Sequential mapping: samples are mapped onto one genotype and then onto another.
2.) Differences in structural variation: samples are mapped onto a single genome followed by the selection of genetic variation single-nucleotide polymorphisms (SNPs) between the genotypes.

Overall, discriminating putative trans-species/mobile RNAs is heavily dependent on many factors including the bioinformatical pipeline, the similarity between the genomes of interest, the sequencing platform, and the experimental design. Choosing one of the described approaches has generally been based on the genetic relatedness of the scion and rootstock, where more closely related genotypes employ the use of an SNPs in their approach (Kim, LeBlanc et al. 2014, Notaguchi, Higashiyama et al. 2015, Thieme, Rojas-Triana et al. 2015, Zhang, Zheng et al. 2016, Xia, Zheng et al. 2018, Liu, Xiang et al. 2020, Wang, Wang et al. 2020, Danecek 2021, Rubio, Stammitti et al. 2022). This is because the sequential mapping approaches typically aligns reads firstly to the genome of tissue origin and then retains only the unmapped reads for downstream analysis (Figure 1.10). When the genotypes of interest are closely related, the sequence variation will be very low and hence this approach could discard a high abundance of data due to its inability to discriminate and identify the sequence variation and it can be challenging to distinguish SNPs from sequencing errors. These two approaches summarise the many differing methods utilised in experimental studies, yet, these appear to have a number of limitations which could contribute to the overestimation of putative mobile RNAs with high false positives (Heeney and Frank 2023). This includes the

ineffective use of well-established alignment algorithms, relatively high dependency on arbitrary thresholds to determine mapped and unmapped sequencing reads, and the use of additional statistical tests to discriminate genetic difference from sequencing noise in post alignment analysis. The alignment of samples onto individual genomes to decimate trans-species RNAs negates the design of mapping algorithms. The mapping algorithms are designed to find the most suitable alignment in the provided reference. Hence, the described methods do not consider that a specific sequence may match outside of the individual genome provided. Instead, for all reads, the best alignment will be restricted to the provided genome depending on the arbitrary set quality thresholds, regardless of whether they are better suited to a different genome. The adjustment to alignment parameters, including quality thresholds, are applied to all sequencing reads rather than considering the actual difference that a trans-species/mobile RNA could have compared to the genome used for mapping. Hence, the usage of these methods is expected to generate a high number of false positive. Therefore, when RNAs from multiple origins are involved, the independent mapping approaches of the sample on separated genomes is not an efficient solution. Thus, without all the genomic information at the time of alignment, the algorithm cannot possibly confer the statistically best location across the multiple genomes to place the reads (Kim, LeBlanc et al. 2014, Notaguchi, Higashiyama et al. 2015, Thieme, Rojas-Triana et al. 2015, Zhang, Thieme et al. 2016, Xia, Zheng et al. 2018, Liu, Xiang et al. 2020, Wang, Wang et al. 2020, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022).

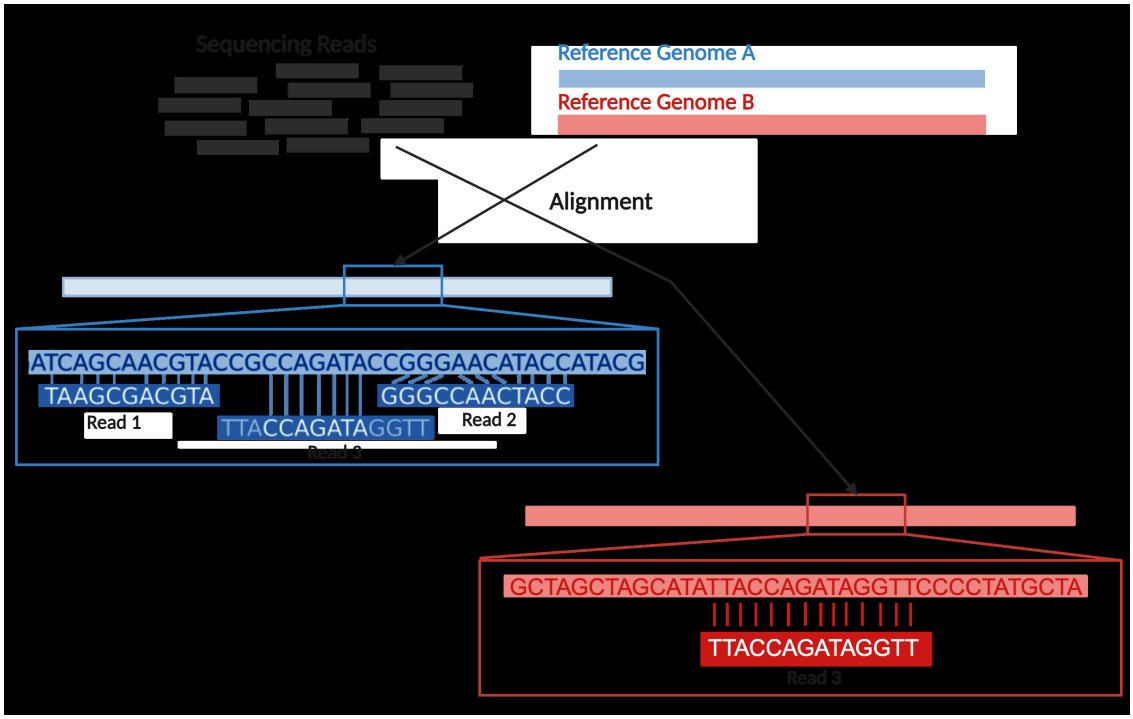


Figure 1.10. Diagram to illustrate the alignment of reads to two individual reference genomes. A set of sequencing reads can be aligned to each genome reference. Reads 1 and 2 map identically to Reference Genome A but Read 3 aligns with fewer mismatches to Reference Genome B than Reference Genome A. Created using BioRender.com.

The type of experimental design and sequencing technology can affect the efficacy of the described methods. The experimental design may choose to locate either sRNAs or mRNAs, and hence utilise either sRNAseq or mRNAseq. A major difference between sRNAseq and mRNAseq are the nucleotide lengths of sequencing reads, where sRNAseq reads are usually within the range of 18-30 nucleotides long while mRNAseq reads are much longer and can be many hundreds of nucleotides. A source of data noise can arise from the misalignment of RNA transcripts to a genome reference. This makes it critical that approaches consider nucleotides mismatches during alignment. One possible solution to improve the placement of mRNA reads between multiple genomes could be to use long-read sequencing, such as Oxford Nanopore or PacBio sequencing technologies. These technologies can generate reads that span the length of a given transcript, rather than relying on short read lengths

to make up each transcript. This reduces bias in the sequencing processes and a more comprehensive view of the RNA population. In a similar manner, the quality of the sample processing before and during sequencing could impact the recovered trans-species/mobile RNAs. Any errors or mistakes can lead to misinterpretation of the sequencing results facilitating the false identification of sequence variations between genotypes. For example, this can be introduced due to sample contamination. This can occur either during sample preparation or library construction, hence, careful handling and quality control measures should be adhered to minimise the risk of contamination. In addition, despite the accuracy of illumine sequencing, errors may occur. Sequencing errors are more likely to occur in regions with high GC content, near or within homopolymers or repeating regions, and if any sequenced read containing sufficient polymorphisms, it could be potentially recovered as a mobile RNA unit.

Above we have described the two bioinformatic frameworks used to identify trans-species RNAs. Most heterografting studies leverage these frameworks but, in each instance, adopt a unique methodological approach. This lack of uniformity due to the absence of a standardised approach poses challenges for maintaining consistency, generating comprehensive findings and drawing biological insights from each study and from the collective body of literature on studies exploring the impact of mobile RNAs on plant phenotypes. This inconsistency in research finding has been noted in a recent review on mRNA mobilome by Heeney and Frank (2023). When several studies find disparaging results, it can hinder the validation of results and slow down the progress of scientific knowledge. The variation in methodology brings to question whether

the differences stem from biological variations or methodological discrepancies and whether the reliability of the biological conclusions are undermines. There are several other possible explanations including experimental procedures, the number of biological replicates, and when exploring similarities between grafting experiments which utilise different plant species there is little overlap with orthologs (Guan, Yan et al. 2016, Xia, Zheng et al. 2018, Liu, Xiang et al. 2020, Kehr, Morris et al. 2022). Similarly, other factors such as sampling time and maturity of plant or tissue could influence the variations in production and abundance of RNA transcripts. For instance, difference could be observed from the molecular process of mRNA transcription, sRNA production and level of transcript translocation to distinct tissues which may vary across a day or over the course of a plant's life cycle, particular in response to change in developmental states (Munsky, Neuert et al. 2012, Sanchez and Golding 2013, Morris 2018, Tutucci, Livingston et al. 2018, Kehr, Morris et al. 2022). Overall, the absence of a standardised bioinformatic approach for the identification of trans-species RNAs has several damaging implications; it can damage the reliability and robustness of individual studies and stunt scientific progress. Hence, standardisation would enhance comparability, reliability, and reproducibility, supporting the development of more comprehensive insights into RNA mobility and the mobilome in plants.

1.6.4 Detecting the action of mobile RNAs in recipient tissues

How can we predict and validate the molecular action of mobile RNAs? For sRNA workflows, there are several high-quality target prediction tools, specifically designed for plants. These developments greatly assist researchers as these algorithms consider many factors to identify possible gene targets and

utilise an optimised system typically via an online interface to a remote server which reduces processing time and usage restrictions on local systems. It is essential to recognise that a single sRNA could have multiple targets, and this targeting is based on several requirements. Firstly, this includes the sequence complementarity between the sRNA and the mRNA target - this is thought to be the most effective way to identify potential target genes. There are specific regions where complementarity is thought to be more important and the mismatches in some regions provide helpful indications about the affinity towards a target locus. In conjunction with complementarity, scoring schemas has been widely employed in tools to quantify the complementary-sequence match pattern. To further support sRNA target gene prediction, the sRNA datasets can be overlapped with further NGS analysis. Researchers might expect that at predicted target sites they observe alteration in DNA methylation and/or alterations in gene expression patterns depending on the type of sRNA. Hence, transcriptomic analysis and genome-wide DNA methylation analysis can be undertaken to validate these expectations and reinforce the potential functional implications of the sRNA mobilome on grafting-induced traits. The integrative analysis has been demonstrated in several studies (Lewsey, Hardcastle et al. 2016, Ren, Xu et al. 2018, Li, Wang et al. 2021). For example, in the pilot study which proved that sRNAs could travel across the graft junction and regulate genome-wide DNA methylation in recipient tissues (Lewsey, Hardcastle et al. 2016).

Current laboratory and bioinformatic methodologies can detect putative mobile mRNA, however, detecting the mode of action is slightly more elusive. It has been largely assumed and theorised that the mobile mRNA is translated into a

protein at the recipient tissue to the influence gene regulation, such as TFs. That said, this is just a theory as this mechanism has not yet been directly demonstrated (Heeney and Frank 2023). In this field, it has been a challenge to uncouple and identify whether the protein produced by the mobile mRNA was produced within the recipient tissues or whether the protein moved into the recipient tissue alongside the mRNA. Previous studies were not able to distinguish the difference (Zhang, Thieme et al. 2016, Yang, Perrera et al. 2019). Of the two modes, the later has been demonstrated in cucumber grafts, where the CmPP16 protein was shown to bind to its own mRNA to form a ribonucleoprotein complex to facilitate their cell-cell and long-distance movement (Xoconostle-Cázares, Xiang et al. 1999). For the former, indirect studies may provide a good indication of the mechanism. In one study on plant-parasite interactions they illustrated the movement and translation of a GUS mRNAs from plant tissues into the parasite where the GUS enzymatic activity can be observed (Park, Shimizu et al. 2021). Alternatively, mass spectrometry has been used as a technique to quantify protein sequences related to putative mobile mRNAs (Thieme, Rojas-Triana et al. 2015). Consequently, to overcome this barrier research could utilise the up-and-coming TRAP-seq (translating ribosome affinity purification followed by RNA sequencing) technology which can enable the spatial characterisation of actively translated proteins (Dermit, Dodel et al. 2017, Heeney and Frank 2023). TRAP-seq has already been employed in a number of plant studies as a way to obtain the translatome profile, for example, to identify phloem-specific RNA produced during infection (Collum, Stone et al. 2020). In a similar manner, it has been discussed that the movement of mRNA could be visualised with imaging using approaches and techniques which have been developed in recent years (Heeney

and Frank 2023). Such approaches can help distinguish the path of mobile mRNA as well as the location of translation. Yet, they have not been utilised within this specific field of research. This restriction is likely rooted in the protocols which typically don't offer mRNA tracking over long distances (Heeney and Frank 2023).

Since the mRNA and its protein have been located within a recipient tissue, regardless of the location in which the protein was translated, then trans-species units may have an impact on gene regulation. That said, determining where the protein is produced can influence the potential of this communication system. If indeed the protein is produced after the mRNA has arrived at its destination, then the signal may have the ability to intensify its message to coordinate action where a single transcript could be translated into several different proteins to target gene families. Moreover, due to the sequence-variations between the genotypes in the graft systems, the acquisition of mRNAs similar to the native mRNA but with small sequence variations could contribute to the amplification of traits contributing to survival under stress or to grafting-induce vigour (Heeney and Frank 2023, Jiang, Neti et al. 2023).

1.7 Aims and Objectives

It remains unclear how specific grafting combinations induce changes to crop vigour under non-stress conditions. So far, the evidence points to the involvement of systemic signalling from the rootstock that drives the molecular alterations in the transcriptome and epigenome. Understanding the underpinning molecular mechanisms would increase our understanding of the connect between the allocation of photosynthates, systemic signalling and epigenetics, and inform breeding programs for both rootstocks and varieties.

This work aims to address the role of mobile RNAs as systemic signalling molecules and their role in grafting-induced traits in Solanaceous crops. Hence, the key objects were to:

1. Determine an efficient bioinformatic approach to detect the transmission of RNAs across a graft junction using NGS data.
2. Determine the physiological phenotype that occurs between interspecific grafting of tomato and eggplant, as well as in tomato intraspecific grafting.
3. Determine whether graft-mobile RNAs could be associated the observed phenotypes.

Declaration

Declaration of published works in Chapter 2

A significant proportion of Chapter 2 has been published as a paper under review which is available as a preprint (https://doi.org/10.1101/2024.08.19.608270). The authors of this work declare that the contents of this thesis belong to Katherine Jeynes-Cupper, whom is the first author of these publications. The senior author is Dr. Marco Catoni who contributed to the works by providing critical analyses of methodologies and media and contributed to writing and editing the manuscripts.

Katherine Jeynes-Cupper

Dr. Marco Catoni

CHAPTER 2. *mobileRNA*: A NEW TOOL FOR EFFICIENT ANALYSIS OF RNA EXPRESSION IN MULTIPLE GENOMES

2.1 Introduction

Plant grafting is a technique utilised in horticulture and research to join multiple plants together. This typically involves two plants where one contributes the shoot, referred to as the "scion", and a second contributes the lower stem and root system lending to the name "rootstock" (Goldschmidt 2014, Gaion, Braz et al. 2018). Grafting has been extensively implemented to cultivate crops since it can introduce or improve desirable traits, such as environmental stress tolerance, pathogen resistance and improved crop vigour (Gaion, Braz et al. 2018). Whereas in research its implementation has been two-fold, either to understand how grafting initiates these desirable traits or as a tool in scientific discovery (Melnyk 2017, Heeney and Frank 2023). Grafting offers a valuable tool as it allows for a systemic connection to be created between two distinct genotypes which has allowed researchers to track the movement of mobile hormones, RNA and proteins and to discover their roles in signalling pathways. In recent years, researchers have utilised grafting alongside traditional laboratory experiments and modern techniques to track the non-autonomous movement of RNAs between the roots and shoots via the phloem and reveal their roles in genetic and epigenetic regulation (Molnar, Melnyk et al. 2010, Mahajan, Bhogale et al. 2012, Notaguchi, Higashiyama et al. 2015, Lewsey, Hardcastle et al. 2016, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022). For example, mobile RNAs have been

associated with changes to physiological and developmental processes such as leaf development, root growth, potato tuberization and resistance to environmental stress (Molnar, Melnyk et al. 2010, Mahajan, Bhogale et al. 2012, Notaguchi, Higashiyama et al. 2015, Lewsey, Hardcastle et al. 2016, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022).

High throughput genomic analysis with NGS technologies are used to systemically study mobile RNAs in heterografted plants and provide quantitative insights on mobile RNAs based on sequence polymorphisms (Deshpande, Chhugani et al. 2023). mRNAseq has become the method of choice to quantify the expression of mobile transcripts, while sRNAseq is employed to quantify mobile sRNA accumulation (Li 2018). These approaches rely on the extraction of RNA from plant tissue samples, converting RNA to cDNA and the sequencing library preparation to be processed into NGS. Where possible, sequencing reads are aligned to a reference genome assembly and RNA expression levels can be quantified for downstream analysis (Deshpande, Chhugani et al. 2023). There are several studies that document how reference-based alignment outperforms reference-free approaches, and the growing use of reference-based alignment can be attributed to the increased availability of open-source assembled genomes and the advancement of tools with highly efficient alignment algorithms (Langmead, Trapnell et al. 2009, Kim, Paggi et al. 2019). These tools offer a strong balance between speed and accuracy to maximise efficiency, and among them the most advanced tools consider the likelihood of sequencing errors or library preparation error generated during reverse transcription. Equally, these algorithms also consider the possibility of variation between the sequencing reads and the reference genome due to the presence of

structural variations, such as single nucleotide polymorphisms (SNPs) (Kim 2019). To do so, these approaches assume that the large majority of the sequenced reads are assembled from the provided reference genome and determines the most suitable location in the genome to place a sequenced read based on the user defined alignment quality thresholds (Jeynes-Cupper and Catoni 2024). This is ideal for standard RNAseq experiments where a single genome is considered, however in samples where genomic sequences originate from multiple organisms, as is the case for heterografts, the output can be unpredictable.

Devising an appropriate method to detect mobile RNAs has been one of the key challenges in grafting studies and has resulted in an abundance of different bioinformatic methodologies. That being said, these pipelines commonly employ an approach of independent single-reference alignment and either recover unmapped reads or utilise downstream variant calling methods as well as additional statistical testing to place reads to their most likely genomic origin (Notaguchi, Higashiyama et al. 2015, Xia, Zheng et al. 2018, Wang, Wang et al. 2020, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022). These practises aim to distinguish and remove data noise from genuine genetic polymorphisms between two genotypes. However, errors such as mis-aligned reads may occur more frequently due to the lack of complete genomic information at the alignment step when aligned to each genome individually.

Here, we introduce an original and alternative method to investigate long-distance RNA movement with plant grafting. This method aims to help support the standardisation of analysis methodologies in this research avenue. The method performs simultaneous alignment of RNA sequencing reads to multiple

reference genomes to access all possible alignment locations across the two genomes. The methods ability to place reads to their genomic origin was tested using simulated datasets generated using biological samples and the results were benchmarked against previous methods. The results demonstrated that the method could place reads to their genome of origin more accurately with substantially less background data noise. The greatest influence on the expected confidence in the discrimination of the placed reads is the similarity of the genomes used as references. To encourage reproducibility and accessibility of the method to general biologists, we incorporated the methodology into an *R* package for RNAseq or sRNAseq analysis. This *R* package is referred to as *mobileRNA* and is available in through Bioconductor (Jeynes-Cupper and Catoni 2023).

2.2 Methods & Materials

Description of *mobileRNA* pipeline

The method comprises of a pre-processing and analysis pipeline to quantify the expression and abundance of mobile RNAs from sRNAseq or mRNAseq data from heterografting experiments. The pre-processing steps utilises pr-existing alignment tools, including Bowtie and HISAT2, using R as an interface to the command line (Langmead and Salzberg 2012, Kim, Langmead et al. 2015). The pipeline greatly benefits from users utilising bio-replicates within their analysis, which helps improve confidence. When multiple genomes are involves, they are merged to support the alignment step. This utilises the mapping tool's algorithm to place reads in the best location across more than one genome as an alternative

to aligning sequentially to single references as traditionally done. The methodology implements two workflows:

1. "Mobile RNA Analysis" implements simultaneous alignment to multiple genome and downstream analysis to detect the expression of mobile RNA from more than one genome in RNAseq or sRNAseq dataset in *R*. For example, graft-mobile RNAs traveling from the rootstock-to-scion in an inter-specific heterograft.
2. "Core RNA Analysis" implements a traditional reference-based analysis of RNAseq or sRNAseq dataset in *R* and assumes the use of a single genotype.

The pipeline requires as input cleaned sequencing reads from either sRNA or mRNA sequencing in FASTQ format for two conditions, control and treatment samples. It is recommended to utilise control replicates, however, it is not essential. Plus, the single or multiple genome assemblies in FASTA format and the corresponding genome annotations in GFF format, if available (Figure 2.1). The pipeline is embedded in the Bioconductor/R package, *mobileRNA* (available at https://bioconductor.org/packages/mobileRNA).

Merging of reference genomes or annotations, read alignment and raw count.

To leverage alignment algorithms in mapping tools to discriminate the genomic origin of sequencing reads across multiple genomes, *mobileRNA* generated a new merged reference genome. For the multiple genomes to be distinguishable within the merged reference, a unique prefix is added to each pseudomolecule

(chromosome/contig/scaffold) that represents the respective individual genome. A merged annotation file was also generated by combining the individual annotation files for each genome in a similar approach which ensured the unique prefixes matches. The individual genome references were supplied by public repositories (Table 2.1).

The alignment step for mRNA sequencing reads is performed by HISAT (default settings) (Kim, Langmead et al. 2015), retaining only uniquely mapped reads and discarding multi-mapped reads. The raw count estimation is performed HTSeq (Anders, Pyl et al. 2015) (Figure 2.1). The alignment step for sRNA reads is performed using Bowtie (Langmead, Trapnell et al. 2009) and similarly retains only the uniquely mapped reads and discarding multi-mapped reads. The sRNA cluster analysis was undertaken by ShortStack (Axtell 2013) which is initially ran to generate an annotation file for each sample that denotes *de novo* sRNA clusters. The sample annotation files from all samples are merged into a single file in *R* with the *GenomicRange* package (Lawrence, Huber et al. 2013). Then finally, the quantification of read coverage across *de novo* sRNA clusters are performed by ShortStack (Axtell 2013).

Table 2.1.The genomes utilised across the analysis. The table displays the source and version of the genome assembly and annotation were extracted from for analysis.

Organism	Culivar/Accession	Common Name	Genome Assembly & Annotaion	Citation	Size (Mb)
Solanum melongena	Pan-genome	Eggplant	Solanum melongena Version 4.1	Barchi L et al. 2021	1,180.0
Solanumn lycopersicum	Heinz	Tomato	Solanum lycopersicum Heinz Version 4.0	Hosmani P et al., 2019	795.6
Arabidopsis thaliana	Columbia (Col-0)	Thale cress	TAIR10	Lamesch P et al., 2012	121.7
Arabidopsis thaliana	Columbia (Col-0)	Thale cress	TAIR10	Lamesch P et al., 2012	121.7
Arabidopsis thaliana	Landsberg (Ler-0)	Thale cress	De novo Ler-0 Version 2	Jiao W et al., 2019	122.3
Arabidopsis thaliana	C24	Thale cress	De novo C24 Version 2	Jiao W et al., 2019	121.3

To detect mobile RNA in intraspecific grafts, previous methods utilised SNP information as opposed to a reference-based approach. Here, we produce and access the use of a SNP based approached for Arabidopsis intraspecific grafts. SNP-injected genomes references were generated using GATK (version 4.2.0) (Van der Auwera and O'Connor 2020) to inject SNPs for the Ler-0 and C24 accessions into the Col-0 *de novo* genome assembly, respectively.

Genome mappability and index calculation

Genome mappability is a measure that estimates the level of repetitiveness within a genome (Derrien et al. 2012) and can be used to evaluate how unique or repetitive a DNA region of interest is in comparison to the complete genome (Catoni et al. 2017). Genome mappability is represented at single-nucleotide resolution across the genome and is a score from 0 to 1, where 1 represents a unique region while 0 represents a region with hypothetically infinite repeats. GenMap (1.3.0) was used to calculate the mappability at a single nucleotide

resolution (-K 30) (Pockrandt, Alzamel et al. 2020) for each genome. To attain the mappability across coding regions, first the average mappability was calculated across each exon using BEDtools (bedtools map -c 4 -o mean) (Quinlan and Hall 2010). Then, the average mappability across all exons for a gene were weighted against their total nucleotide length. To derive a quantitative value to compare individual and merged genomes within an analysis we introduce an arbitrary genome mappability index that represents the proportion of a genome that has a mappability score above a 0.5 threshold.

Quantitative analysis and differential expression

Raw counts of mRNA transcripts or sRNA clusters are imported into R as a single data frame object containing all samples. Quantitative data, including Fragments Per Kilobase of transcript per Million (FPKM) for genes, or Reads Per Million (RPM) in each sRNA cluster, are automatically calculated. If the experimental design includes control and treatment conditions (e.g. self-grafted control plants and hetero-grafted plants), differential expression analysis can be performed with either *edgeR* (Robinson, McCarthy, & Smyth, 2010) or *DESeq2* (Love, Huber, & Anders, 2014) R packages, which are both integrated into the *mobileRNA* pipeline. For either statistical test, the *P*-values are adjusted for multiple testing using Benjamini and Hochberg's method (Benjamini Y, 1995) to control the false discovery rate (FDR).

Dicer call

For the analysis of sRNAseq datasets, ShortStack has identified *de novo* sRNA clusters and denotes their features. For each sRNA cluster, ShortStack deduces a

putative Dicer enzyme deriving the sRNAs, referred to as the dicercall, which has a biological significance (Shahid and Axtell 2014). *mobileRNA* uses this information to predict a "consensus" dicercall class for each sRNA cluster by evaluating the individual dicercall values in each sample or specific samples for each sRNA cluster and selects the most abundant dicercall. In the case of a tie, the "consensus" dicercall is set as unclassified, however, the system prioritises a valid dicercall over an unclassified result.

Mobile RNA analysis

mobileRNA selects the mobile RNAs by utilising the raw counts obtained from the alignment and clustering steps. In this way, the approach exploits the decision by the algorithm in the mapping tool that has discriminate for each read the best placement on the two genomes based on the alignment parameters set by the user. The read raw counts for gene annotated features (for mRNAseq) or for the sRNA clusters that were aligned to the distant genome reference (Genome B) are expected to represent graft-mobile RNAs. *mobileRNA* offers additional filtering steps, as following:

1) When self-graft control samples are available, these are used to eliminate additional false positives by removing mobile RNAs that contain counts in these samples.
2) When multiple biological replicates are available, a threshold can be applied to considers the number of heterograft replicates which contained reads.
3) Additionally, candidates can be filtered based on a minimum coverage requirement. This is not a default filtering step since there is an

assumption that graft-mobile RNAs may exhibit relatively low coverage in comparison to other RNA populations.

Output results

mobileRNA generates as output a structured repository of information in the form of a data frame with rows representing either sRNA clusters or mRNA transcripts. There is the option to convert the data frame into a *SummarizedExperiment* object. For the sRNA analysis, the columns include information on the genomic location, pseudomolecule, dicercall, consensus dicercall, the number of replicates contributing to the consensus dicercall, statistical expression values including log fold change, p-value, adjusted p-value only if the self-graft control condition is available, as well as, RNA sequence, consensus RNA sequence and RPM. For the mRNA transcripts, the columns include information on the genomic location, pseudomolecule, gene name, the number of replicates contributing to a read count, Fragments per kilobase of transcript per million mapped reads (FPKM), statistical expression values including log fold change, p-value and adjusted p-value if there are self-graft control samples available.

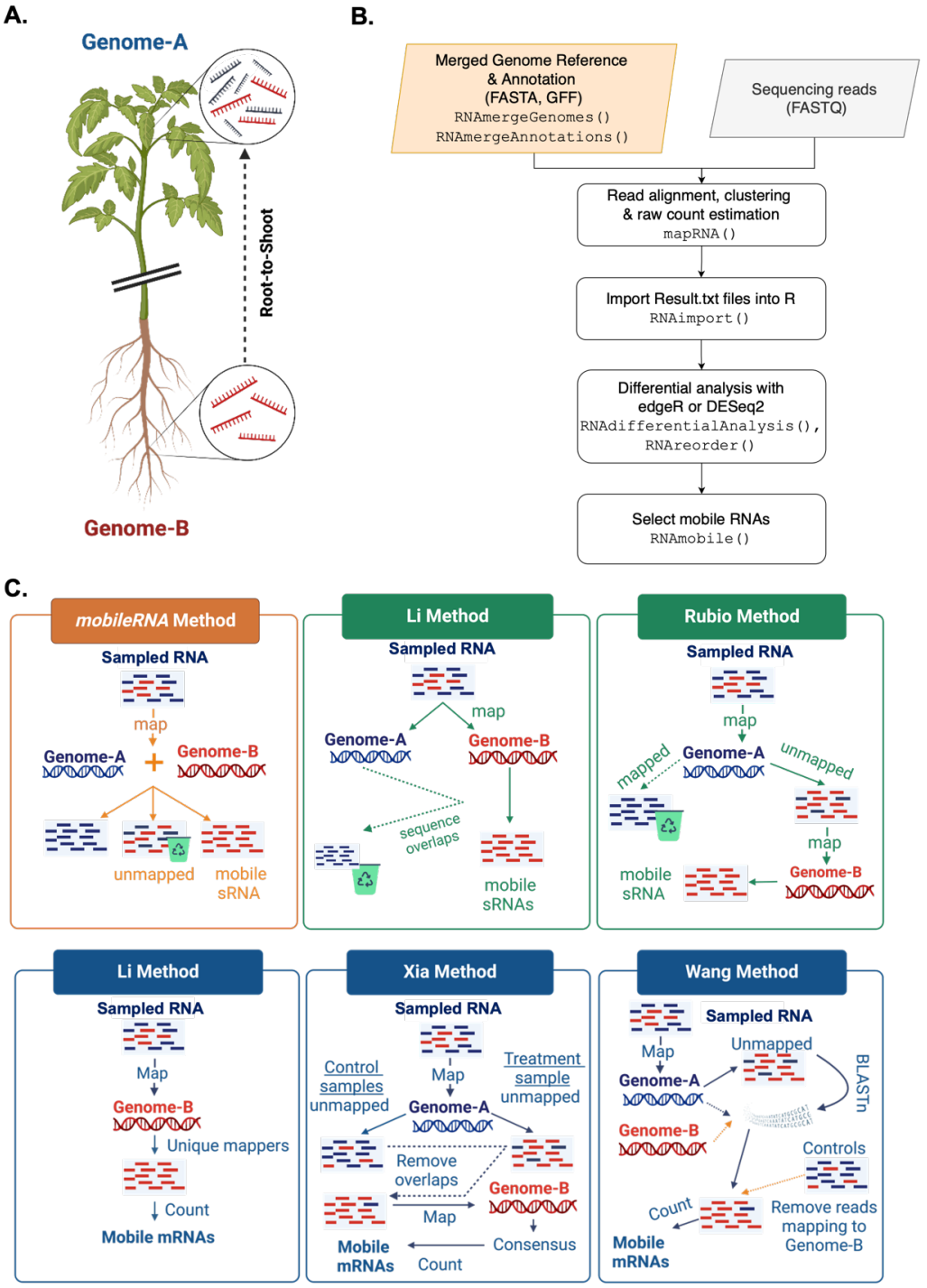


Figure 2.1. The *mobileRNA* approach in comparison to previous methods. A) Plant grafting example illustrating mobile RNA movement in the root-to-shoot direction whereby the scion tissue contains RNAs produced by Genome A (blue) and mobile RNAs from Genome B (red). B) A simplified *mobileRNA* workflow. A full description and source code is available on the Bioconductor repository (available at https://bioconductor.org/packages/mobileRNA). C) Schematics of the *mobileRNA* pipeline in comparison to the re-implemented pipelines utilised for benchmarking whereby the blue and red lines illustrate sequencing reads from the Genome A and Genome B, respectively. Re-implemented pipelines including Li and Rubio methods for sRNA analysis (Li, Wang et al. 2021, Rubio, Stammitti et al. 2022), and the Li, Xia and Wang methods for mRNA analysis (Xia, Zheng et al. 2018, Wang, Wang et al. 2020, Li, Wang et al. 2021). Created using BioRender.com.

Visualising data & additional features for assisting functional analysis

The *mobileRNA* package utilised established methods to visualise data and undertake exploratory data analysis for the purposes of quality control. The exploratory data analysis utilises multidimensional scaling to illustrate the relationships between samples, including the use of principal component analysis (PCA) using the *R* package *DESeq2* (Love, Huber, & Anders, 2014) and visualising the distribution of the dicercall classes for sRNA clusters within a sample or the consensus dicercall across the experimental design. The results can further be visualised using a heatmap that employs hierarchical clustering of normalized RPM/FPKM values transformed logarithmically, commonly referred to as "rlog" values. Or, by plotting the distribution of genomic features which overlap with sRNA clusters.

Re-implementation of known bioinformatic pipelines for mobile RNA identification

We re-implemented previous genomic methodologies that were used in previously published research papers that aimed to identify mobile mRNAs or sRNAs in plant heterografts. This was employed to benchmark the *mobileRNA* approach; each was interpreted as well as described and for simplicity, each method has been named after the first author's name. The methods although different to one another commonly align sequencing reads to each genome separately and then undertake downstream screening for genetic variants.

For the analysis of graft-mobile sRNAs, we re-implement two previous pipelines using Bowtie and ShortStack universally. The Li method was taken from a study that grafted common bean (*Phaseolus vulgaris*) and soybean (*Glycine max*),

however, this study was limited by one replicate per condition (Li, Wang et al. 2021). The Li method aligned a sample to each genome separately followed by the selection of reads which were aligned to the distant genome and were unmapped to the sampled tissue genome (Figure 2.1.C). The Rubio method was taken from a study that grafted grapevine species and first mapped reads to the tissue sampled genome before selecting only unmapped reads and aligning these to the distant genome (Rubio, Stammitti et al. 2022) (Figure 2.1.C).

To identify graft-mobile mRNAs, the *mobileRNA* approach was benchmarked against three previous methods referred to as the Li method (mRNA) (Li, Wang et al. 2021), Xia method (Xia, Zheng et al. 2018), and Wang method (Wang, Wang et al. 2020) (Figure 2.3). The Li method (Li, Wang et al. 2021) used STAR to align cleaned reads to the distant genome (Dobin, Davis et al. 2013) and retained transcripts that only had uniquely mapped reads. The normalised abundance was estimated as CPM (counts per million) using BEDtools (Quinlan and Hall 2010). The Xia method (Xia, Zheng et al. 2018) used HISAT to align reads (Kim, Langmead et al. 2015) with default settings to the sampled tissue genome. Only the unmapped reads are maintained and any reads from the heterograft samples which perfectly match with the self-grafted control are discarded (Quinlan and Hall 2010). The remaining reads are mapped to the distant genome and raw feature counts are estimated using HTSeq (--order=pos -a=0 --stranded=no --mode=union --nonunique=all --type=mRNA) (Anders, Pyl et al. 2015). Features with counts in at least 2/3 of samples were considered as mobile mRNA transcripts. Lastly, the Wang method (Wang, Wang et al. 2020) uses Bowtie2 to align reads to the sampled genome (sensitive-local mode: -D 15 -R 2 -N 0 -L 20 -i S, 1, 0.75) (Langmead and Salzberg 2012), and retains only the

unmapped reads (Danecek 2021). BLASTn was used to place unmapped reads against both the sampled and distant genomes, independently (Altschul, Gish et al. 1990) (-max_target_seqs 3 -e value 1e-5 -outfmt 6 -num_threads 8). False positives were removed based on reads from self-graft controls that aligned to the distant genome. Raw feature counts were estimated with the remaining reads using HTSeq and were considered mobile (Anders, Pyl et al. 2015) (Figure 2.1C).

Generating simulated sequencing datasets

To generate the simulated sRNA datasets, we retrieved sRNAseq datasets obtained from tomato, eggplant and Arabidopsis (Col-0, Ler-0 and C24 accessions) from the public Sequence Read Database (SRA) repository. Samples were selected based on pairing that are known to be possible to graft which included the combinations of eggplant and tomato, or among different *Arabidopsis thaliana* accessions (Col-0, C24 and Ler-0) (as detailed in Supplementary Table 2.1). The simulated datasets aimed to replicate heterografted samples as closely as possible, including the assumption that mobile RNA abundance is expected to be relatively low in comparison to the total pool of RNA transcripts, as well as the assumption that we expect the abundance of mobile RNAs to be lower than the abundance of non-mobile transcripts (Notaguchi, Wolf et al. 2012, Notaguchi, Higashiyama et al. 2015, Yang, Mao et al. 2015, Wang, Wang et al. 2020).

To create the blended sRNA datasets, we first undertook traditional analysis of the biological samples chosen to represent the distant genome. Raw reads were trimmed using trimmomatic (Bolger, Lohse et al. 2014) followed by unique alignment with Bowtie to the distant genome reference (bowtie -p 6 -v 0 -a -m 1)

(Langmead, Trapnell et al. 2009). Based on the simulated combination, reads were either aligned to the *Solanum lycopersicon* (Tomato) Version 4 assembly (Hosmani, Flores-Gonzalez et al. 2019) from Sol Genomics Network (https://solgenomics.net/), *A. thaliana* Landsberg (Ler-0) ecotype assembly version 2 (Jiao and Schneeberger 2019) or *A. thaliana* C24 ecotype assembly version 2 (Jiao and Schneeberger 2019) both from "The Arabidopsis Information Resource" (https://www.arabidopsis.org/). Following alignment, ShortStack (V4.0.2) (Axtell 2013) was utilised to perform sRNA cluster analysis (--threads 6 --pad 200 --mincov 0.5 --nohp). We subset the sRNA clusters to maintain only those with a predicted dicercall between 21-24 nt and a non-zero raw count. From this population, we randomly selected 150 sRNA clusters and extracted the associated reads from the alignment file using SAMtools (Danecek 2021). The extracted reads were converted from BAM to FASTQ format using BEDtools (Quinlan and Hall 2010) and injected into the samples of the species used to simulate the sampled genome (Supplementary Table 2.2). The blended sRNAseq datasets generated with this method were referred to as "Random-Format". To introduce more control over the expression level of simulated mobile sRNAs, we utilised another method referred to as "Tier-format". This involved injecting a total of 150 sRNA clusters from three groups of 50 loci associated to different levels of coverage; 1. respectively a low, 2. average (mean) and 3. high (> ~5x mean quartile) read coverage in the original alignment (Supplementary Table 2.3).

The distribution of simulated reads is illustrated in Figure 2.2 which shows that between the Random and Tier formats there is a similar distribution of simulated reads for each dataset, but typically the Tier format has a marginally wider distribution (Figure 2.2A). The distribution of sRNA lengths in nucleotides is not

mirrored between the Random and Tier formats. The Tier format has a more uniformed distribution of sRNA sizes across the datasets than the Random format (Figure 2.2B).

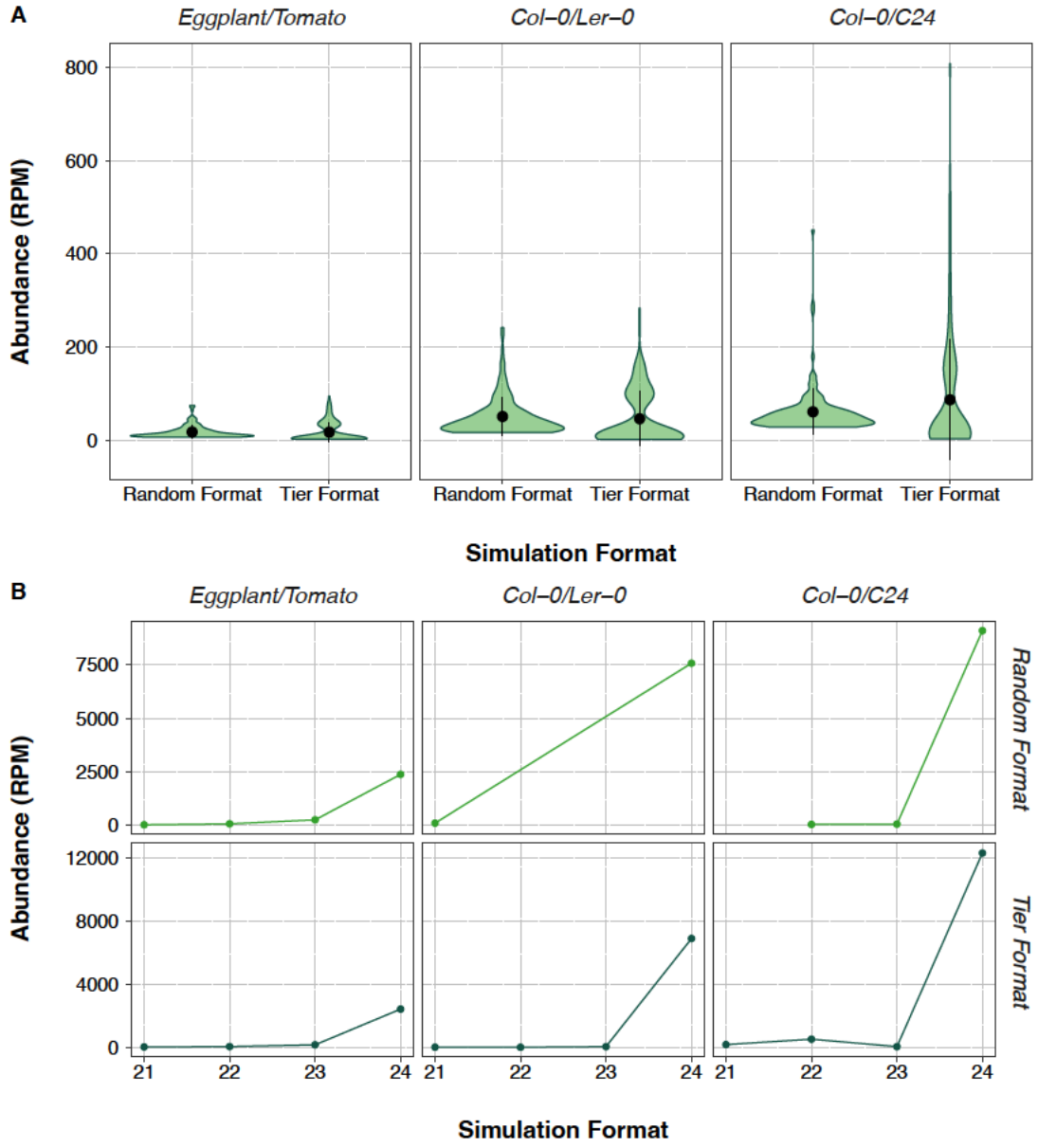


Figure 2.2. Distribution of simulated mobile small RNAs (sRNAs) in each blended dataset, including relative abundance and nucleotide length (nt) across the Random and Tier formats. For more information on the methods for generation of simulated see described in Methods section. A) Violin plot showing distribution of the relative abundance in Reads Per Million (RPM) of simulated graft-mobile sRNAs. B). Line graph to show the distribution in relative abundance in RPM of the nucleotide lengths (nt) of simulated graft-mobile sRNA clusters.

Based on design, the spiked reads never exceed more than 0.25% of the total reads in the simulated sRNA datasets (Supplementary Table 2.2). Theoretically, we expect that in a grafting experiment aiming to located long-distance signalling mobile RNAs that only a small fraction of the total RNA population within the destination tissue are derived from a distant organ (Buhtz, Pieritz et al. 2010, Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Liang, White et al. 2012, Thieme, Rojas-Triana et al. 2015, Liu and Chen 2018). Yet, the limited knowledge in this area has required this work to draw inference from both theoretical and experimental resources. Transgenic lines with sRNA constructs have been employed in plant grafting experiments to demonstrate sRNA mobility and action in recipient tissues. These studies quantified the abundance of the mobile transgenic siRNAs at 3- and 7-weeks post-grafting at 0.00109% and 0.000886% of the total read population, respectively (Kasai, Bai et al. 2016). However in grapevine heterografts, 0.5% of all reads across three heterografts were associated to mobile root-to-shoot sRNAs and 1.9% were associated with mobile shoot-to-root sRNAs (Rubio, Stammitti et al. 2022). Whereas, based on the proportions of sRNAs rather than the reads, common bean and soybean grafting determined that mobile sRNAs could accounted for 27.5% of all sRNA across replicates (Li, Wang et al. 2021). On the other hand, in mRNA mobilisation studies have recorded the abundance of identified mobile mRNAs. For instance, in watermelon-bottle guard grafts it shows that most putative mobile mRNAs are from low-expressed transcripts with an FPKM less than 1 (Wang, Wang et al. 2020). Similarly, in *N. benthamiana*/tomato grafting demonstrated that the abundance of around half of the mobile transcripts were ranked lower than 30,00th within the entire leaf transcriptome (Xia, Zheng et al. 2018).

To produce the simulated mRNA datasets, the R package *polyester* was implemented (Frazee, Jaffe et al. 2024). This tool allowed us to produce sets of synthetic raw RNAseq reads for each analysis what were associated to 150 randomly selected genes from the reference annotation of the distant genome (Supplementary Table 2.4). The baseline mean number of reads per transcript was defined by the transcript length with a coverage of 20 and 100 bp read length. Although the simulated mobile transcripts will not be present in the control samples, we randomly simulated different levels of expression for each transcript based on the multiplication of base line reads by either a value of 1, 5, or 10 (Frazee, Jaffe et al. 2024). Although random, the expression levels were evenly distributed across the transcripts with approximately 50 transcripts per expression value. The synthetic reads were spiked into RNAseq datasets containing biological samples of the genotype chosen as the sampled genome (Supplementary Table 2.4). To simulate heterografting, each dataset was injected with a varying number of the synthetic reads: 1000 (1k), 5000 (5k), 10,000 (10k) or 50,000 (50k) (Figure 2.3). This generated two heterograft combinations for testing with five blended datasets with different amounts of reads that represent the simulated mobile RNAs. The percentage of synthetic read in each blended dataset ranged from circa 0.006% for datasets with 1000 spiked reads to 0.293% for datasets with 50,000 spiked reads in comparison to the total sequenced reads which was on average between 3-13 million (Supplementary Table 2.4). The simulated self-grafted control samples were the same real datasets used for generating the blended data but without the spiked reads.

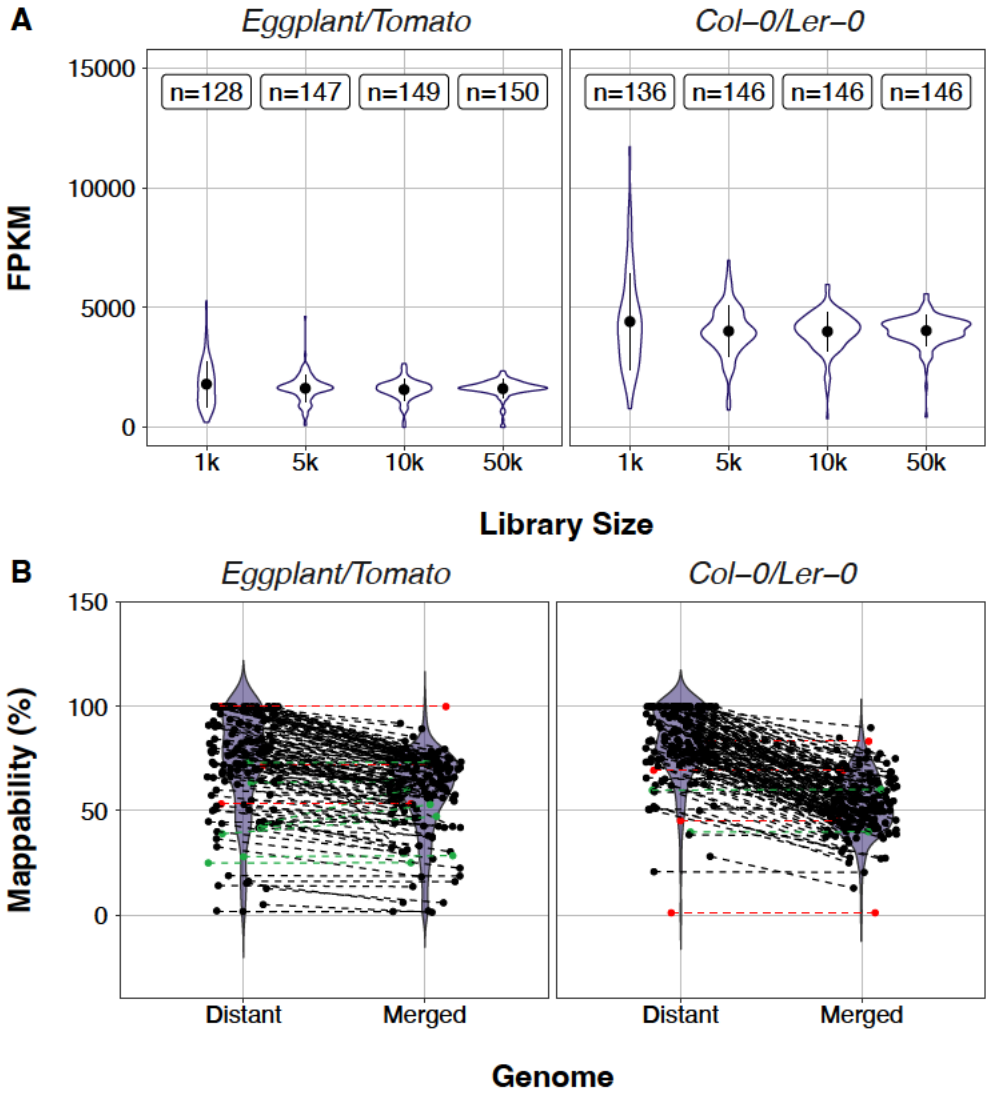


Figure 2.3. The distribution of simulated messenger RNAs (mRNAs) reads injected in each blended dataset. Two heterograft comparisons were examined, Eggplant/Tomato and Arabidopsis thaliana Col-0/Ler-0. A pool of simulated reads was generated (see methods) were each dataset and a library size of 1k, 5k, 10k, and 50k reads were selected at random. A) Violin plot showing distribution of simulated mobile mRNA transcripts as Fragments Per Kilobase of transcript per Million (FPKM) within each dataset. The text annotation represents the number of simulate transcripts in the distribution. B). Violin plot showing the genome mappability for simulated mobile mRNA transcripts in the distant genome and in the merged genome. Each point is a mobile mRNA transcript, where dash lines connect the genome mappability of the transcript between each genome. The dash line colour represents the change in mappability from the distant genome in comparison to the merged genome, whereby black represents a decrease in mappability, green represents an increase and red represents no change.

Across each library size in a mRNA dataset the distribution of simulated reads was comparable (Figure 2.3). The mean FPKM of simulated reads in the Eggplant/Tomato dataset was almost half that of the mean FPKM values in Col-0/Ler-0 dataset (Figure 2.3). The genome mappability of the simulated graft-mobile mRNAs were compared between the distant genome and the merged genome (distant genome plus the sampled genome). As expected, most transcripts demonstrated a reduced mappability (i.e. reduced uniqueness). This separation is clearly demonstrated in the Col-0/Ler-0 dataset because the individual ecotypes are highly similar since coding regions are separated by several SNPs. In a few instances, the uniqueness of a mRNA transcripts was improved in the merged genome (Figure 2.3).

2.3 Results

Alignment with a merged genome for efficient mobile RNA identification

To identify mobile RNAs, bioinformatic approaches rely on the use of structural polymorphisms between two genotypes. The *mobileRNA* approach leverages the design and efficiency of alignment algorithms to place reads to locations across multiple genomes and ultimately discriminate RNAs produced by the sampled genome verses the distant genome (Figure 2.1A-B). The approach aims to avoid complex post-alignment comparisons that are utilised in previous methods, hence, our approach implements an alignment step that aligns reads to both the distant and sampled genome simultaneously (Notaguchi, Higashiyama et al. 2015, Xia, Zheng et al. 2018, Wang, Wang et al. 2020, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022). This is achieved using a merged

genome reference at the alignment step, whereby all genomes of interest are individually labelled and compiled into a single file (Figure 2.1.B). Following alignment, multi-mapped reads are discarded leaving only uniquely mapped reads. These reads are used to determine the raw counts for either mRNA transcripts or sRNA clusters that have the potential to be mobile.

To evaluate the *mobileRNA* approach we generated simulated datasets that aimed to replicate combinations known to be graft compatible. To simulate an interspecific grafting combination, utilised tomato and eggplant. To simulated intraspecific grafts, we utilised three different ecotypes from *Arabidopsis thaliana* merging Columbia (Col-0) with either Landsberg (Ler-0) or C24. All the ecotypes have *de novo* reference assemblies readily available (Schneeberger, Ossowski et al. 2011, Jiao and Schneeberger 2020).

When genome references are merged and utilised for alignment, we expect a reduced mapping efficiency due to the presence of homology between the sequences of the two genomes. To measure this effect, we calculated the genome mappability score for annotated coding regions in each of the individual and merged genomes in the analyses (Figure 2.4). Previous analyses have utilised SNP data to differentiate and discriminate read placements between the distant and sampled genotypes in intraspecific grafts. Hence, for the Ler-0 and the C24 Arabidopsis accessions we calculated the mappability scores for their *de novo* assemblies and the reference generated by injecting SNPs into the Col-0 reference assembly. As we expected, we observed a lower mappability score in all combinations of merged genomes in comparison to their respective individual genome references (Figure 2.4). In the

Eggplant/Tomato combination the mappability score faced a 15% reduction in the merged genome compared to the corresponding individual genomes (Figure 2.4). Similarly, a 40% reduction was observed across all Arabidopsis merged combinations. We observed the proportion of coding regions with a mappability score above 0.5 to drop from 70% and 77% in eggplant and tomato references to 66% in the merged Eggplant/Tomato genome. In the *de novo* Arabidopsis assemblies, the average mappability was 34% in the Col-0/Ler-0 and 35% in Col0/C24 merged references whereas in the SNP injected references, these values dropped respectively to 18% and 14%. Based on these results, we find that an interspecific grafting example will likely provide a stronger discrimination of RNA molecules. The results reveal that the *de novo* assembled references for Arabidopsis ecotypes have the potential to align close to double the number of coding regions as a SNP injected reference, hence, for onwards analysis only the *de novo* assembled references were utilised for the following analyses.

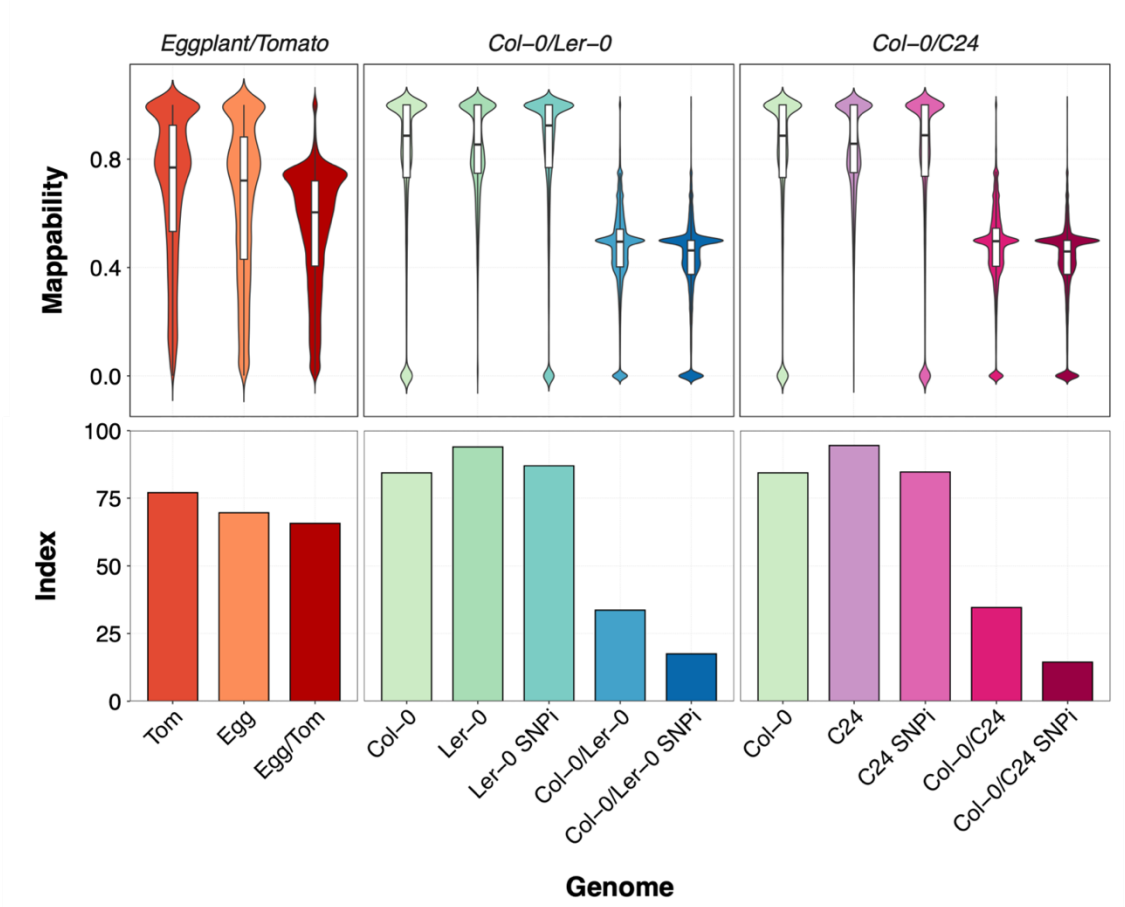


Figure 2.4.The genome mappability scores for each individual and merged genome reference utilised in the comparisons. For more information on each genome, see methods. The genome mappability value is represented from 0-1 where 0 represents a highly repetitive region and 1 signifies a highly unique region. The genome mappability is calculated across the genome, and the plot illustrated the distribution of mappability across coding regions of the genome. The abbreviated, "Tom" refer to "Tomato", "Egg" refers to "Eggplant" and "SNPi" refers to a reference generated by injecting single nucleotide polymorphisms (SNPs) into the Col-0 genome reference. The Index (%) represents the proportion of the genomes coding regions that are above a mappability threshold of 0.5.

Benchmarking *mobileRNA* with blended RNA datasets

To benchmark genomic pipelines, simulated synthetic datasets are often employed. With these datasets we can control variables that are usually unknown in real biological data. However, the artificial nature of simulated data can often lack a true reflection of real biological contexts. To maintain a greater degree of biological context in the simulated data, we generated blended RNAseq and sRNAseq datasets to benchmark the performance of *mobileRNA*. The blended

datasets were designed to simulate the systemic movement of RNAs heterografting experiments. This was achieved by using real biological data sets whereby simulated RNA reads, accounting for approximately 150 mobile RNAs, were generated from biological samples and spiked into additional biological samples (Lähnemann, Köster et al. 2020). Using this approach, we maintained complete control of real positives and promoted benchmarking of the rates of false negative and false positive.

Analysis of Simulated sRNA Data

The performance of the *mobileRNA* pipeline was benchmarked against re-implemented methods. For sRNAseq, these included two previously used methods, namely the Li (sRNA) and the Rubio methods. The performance of each analytical method was assessed by comparing the levels of true positives, to false negatives and false positives. A true positive was a simulated mobile sRNA that was correctly identified, whereas a false positive was an incorrectly identified mobile sRNAs and a false negative were those simulated mobile sRNAs which were not identified (Figure 2.5). The *mobileRNA* pipeline retrieved approximately 97%, 60% and 24% true positives in the Eggplant/Tomato, Col-0/C24 and Col-0/Ler-0 combinations, respectively (Figure 2.5, Supplementary Table 2.6). This demonstrates that the performance of *mobileRNA* correlates with the genetic similarity of the genotypes (Schneeberger, Ossowski et al. 2011, Jiao and Schneeberger 2020). The false positive rates demonstrate that *mobileRNA* has a remarkable performance in all simulations where it recovers less than 1%. By contrast, the re-implemented methods including, Li and Rubio methods, recovered around 99% and 48% false positives in the Eggplant/Tomato combination, respectively. Similarly,

both the Li and Rubio methods retrieves over 98% of false positives in the *Arabidopsis* simulations. These results reveal the *mobileRNA* approach through using a merged genome for alignment can improve detection of mobile sRNA and considerably reduce the amount of background noise (Figure 2.5).

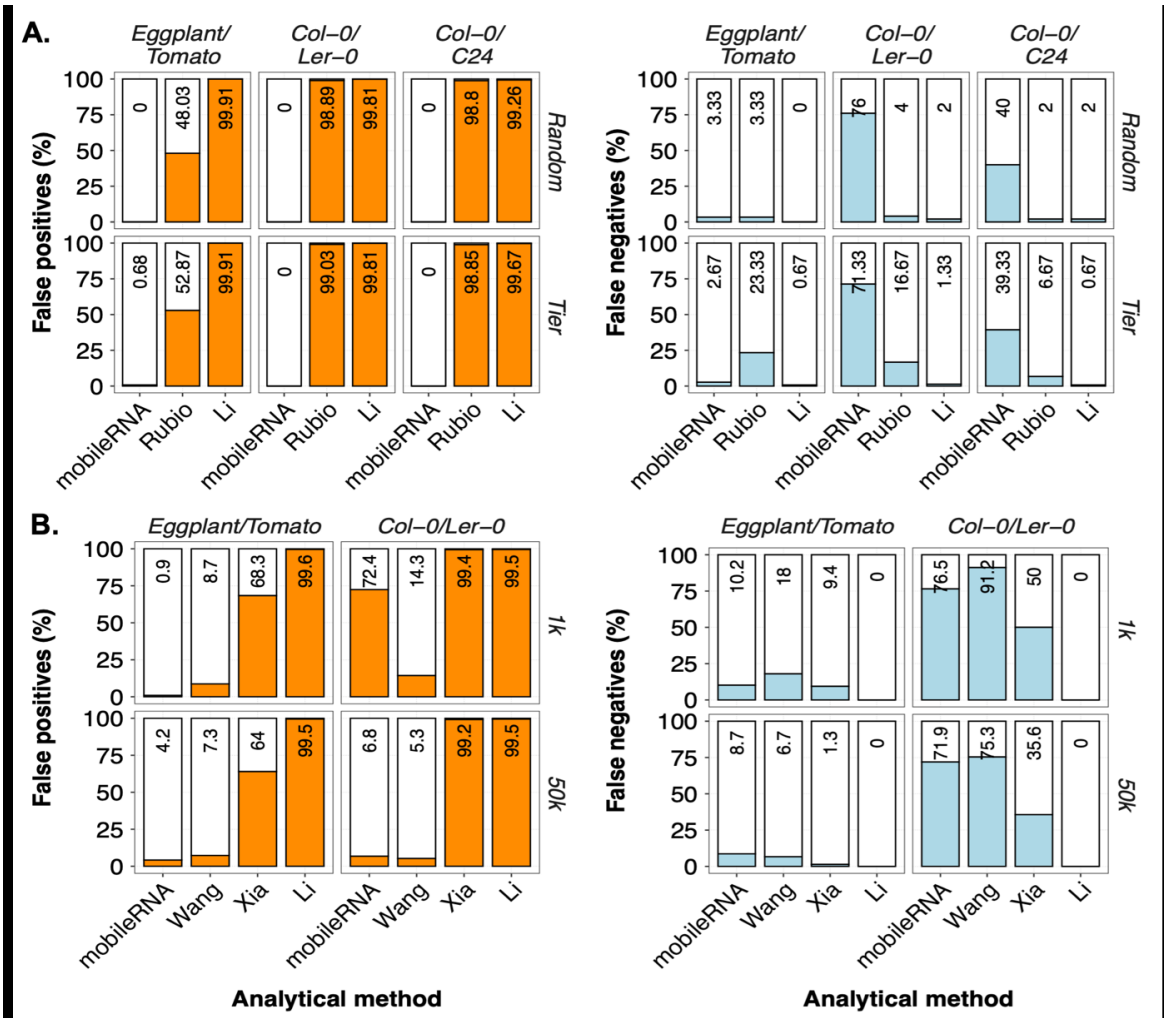


Figure 2.5. Comparative analysis of mobile small RNAs (sRNAs) and messenger RNAs (mRNAs) in the simulated datasets. A) For each sRNA simulated experiment analysed by *mobileRNA* and the re-implemented methods, the bar plots represent the proportion of false positives to the true positives, and proportion of false negative which is expressed as percentage of the total spiked sRNAs. B) For each mRNA simulated experiment analysed by *mobileRNA* and the re-implemented methods, the bar plots represent the proportion of false positives to the true positives, and proportion of false negative which is expressed as percentage of the total spiked transcripts.

To assess the effect of sRNA expression level, we designed blended datasets based on the Tier Format to compare to the random format (see method). The results from the Tier Format showed that the *mobileRNA* method's ability to detect mobile sRNAs was not affected by their abundance (Figure 2.6). Whereas the re-implemented methods demonstrated that the rates of false negatives were largely associated with sRNAs that had a low abundance (Figure 2.6). This indicates that the detection of mobile sRNAs can be influenced by their abundance.

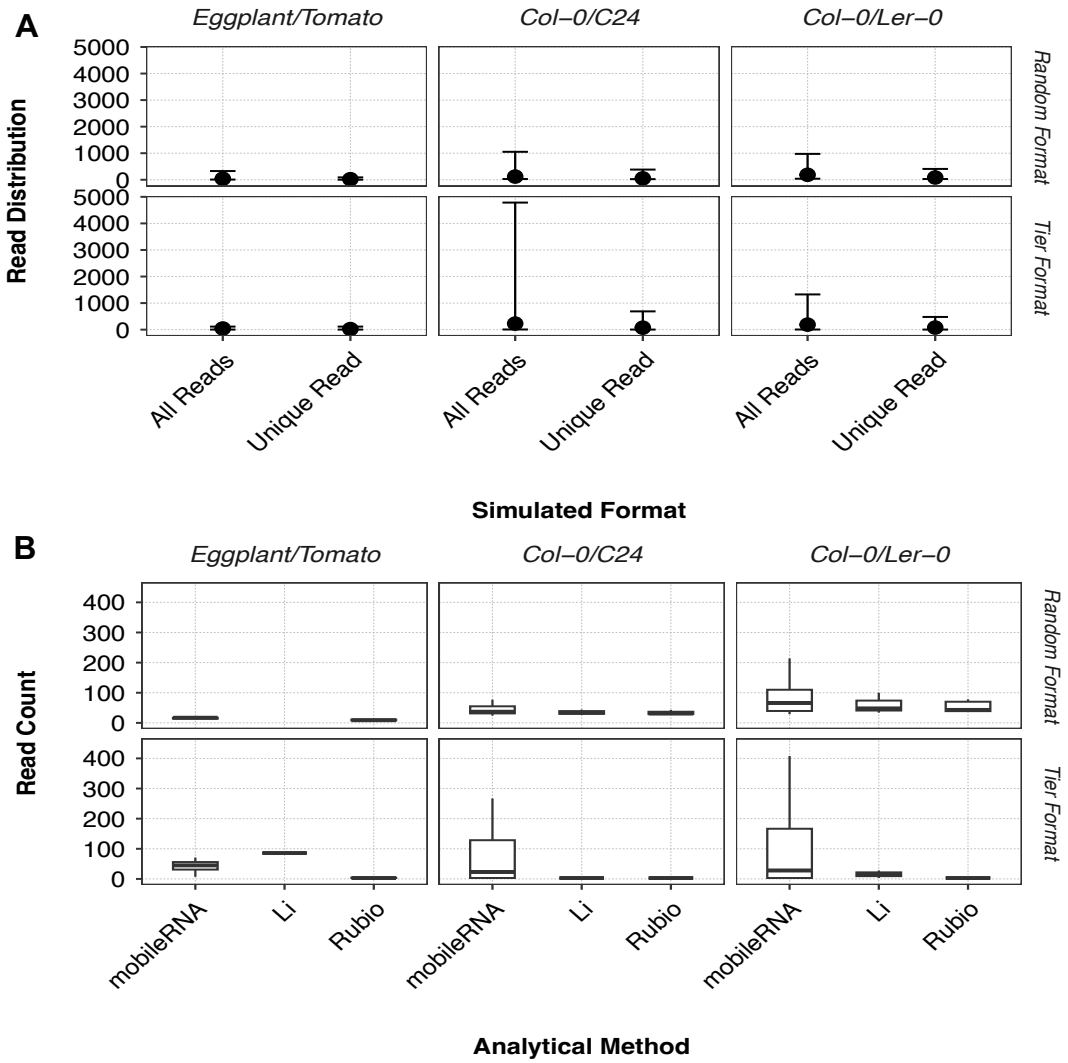


Figure 2.6. Distribution of simulated small RNA (sRNA) sequencing reads associated with false negatives. A). The distribution in raw read counts associated with simulated sRNA clusters in each dataset. B). The distribution in raw read counts of simulated mobile sRNAs that were identified as false negatives, i.e. not identified in each analysis.

Analysis of simulated mRNA datasets

To access the *mobileRNA* method's performance and ability to distinguish mobile mRNA transcripts, blended RNAseq datasets were generated for Eggplant/Tomato and Arabidopsis Col-0/Ler-0 heterografting comparisons. All mRNA transcripts are transcribed from gene coding regions in the genome and have a much greater nucleotide length in comparison to sRNAs. Due to their large size, transport of mRNAs between cells and tissues can be more challenging than sRNAs due to size exclusion (Heeney and Frank 2023). Therefore, we expect that the abundance of mobile mRNAs in distant organs will be lower than that of the average gene expression level (Heeney and Frank 2023). Taking this into consideration, we designed blended datasets that accounted for this assumption by varying the library size of injected reads that were associated with mobile transcript. This ranged from 1k, 5k, 10k, and 50k reads, which corresponded to between 0.002% - 0.451% of the total sequencing reads in the blended datasets (Supplementary Table 2.4).

Each simulated dataset was analysed with the *mobileRNA* method and the re-implemented methods which were based on individual genome alignment and included the Wang, Xia and Li methods. To assess the output of each method we visualised the true positives against the incorrectly identified mobile mRNAs (false positives) and assessed the proportion of simulated mobile mRNAs which were not located by the method (false negatives) (Figure 2.5). We observed that the rate of false positives marginally decreases as we increase the abundance of mobile mRNA transcripts. In particular, the *mobileRNA* method performed exceedingly well across all datasets with a false positive rate below 5%. The Wang

method is the most comparable to *mobileRNA* while the Xia and Li methods have a false negative rate over 16x that of the *mobileRNA* approach.

Across genomics, we are also concerned about transcript quantitative abundance alongside transcript presence. In heterografting analysis, a great deal of background data noise can be generated which could mask or falsely estimate the true accumulation of mobile transcripts. Therefore, for each dataset we estimated the expression of the simulated mobile transcripts identified by each analytical method. The expression level (FPKM) was calculated but utilising gene sets original RNAseq library sizes and compared to their designed expression levels – which is referred to as the expected expression levels (Figure 2.7). Outstandingly, *mobileRNA* displayed a very high correlation between the observed and expected transcript expression levels across all combinations (Eggplant/Tomato R2 = 0.59; Col-0/Ler-0 R2 = 0.012). While the re-implemented analytical methods showed poorer correlations, typically underestimating the transcripts abundance (Eggplant/Tomato R2 < 0.35; Col-0/Ler-0 R2 < 0.0.00043) (Figure 2.7). Based on these results we have drawn the conclusion that aligning RNA reads from heterograft samples to a merged genome reference not only drastically reduced the noise produced by the presence of false positives but also generates a more confident estimation of the real RNA accumulation in the destination plant tissue.

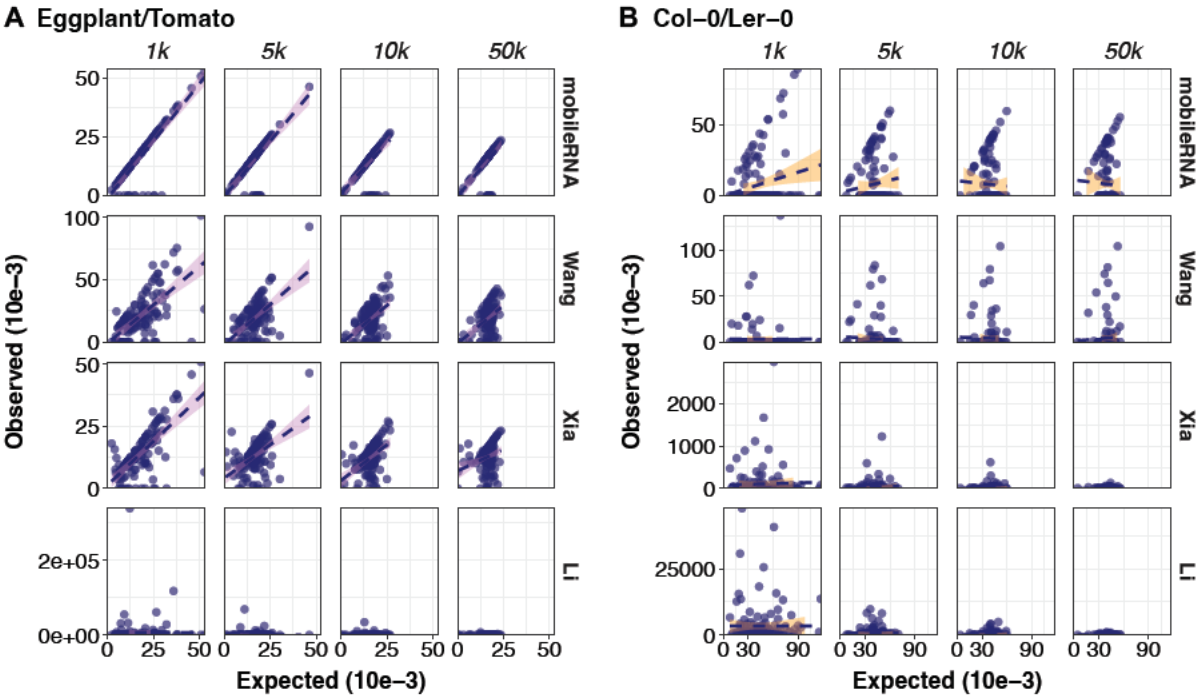


Figure 2.7. Scatter plots of the expected verses observed RNA transcript abundance in Fragments per kilobase of transcript per million mapped reads (FPKM). Each point represents 1 of the approximately 150 simulated mRNA transcripts. Each library size was assessed including 1k, 5k, 10k, 50k, against the mobileRNA approach and the reimplemented approached namely Wang, Xia and Li (Xia, Zheng et al. 2018, Wang, Wang et al. 2020, Li, Wang et al. 2021). A) Scatter plots from the Eggplant/Tomato heterograft combination. B) Scatter plot from the Arabidopsis Col-0/Ler-0 combination.

2.4 Discussion

The *mobileRNA* approach offers a streamline pipeline to efficiently detect the presence and expression of mobile RNAs in heterografting studies. With the implementation of blended datasets created from real experimental samples, we have demonstrated that *mobileRNA* outperforms previous methods by considerably reducing data noise generated by false positives and by generating more accurate estimations of transcript abundance. Consequently, this approach offers users greater confidence in their ability to detected mobile RNAs as putative mobile signals. This has important implications to research

since it enables researchers to draw stronger biological inferences. With that, we propose that *mobileRNA* could be a promising tool to detect mobile RNAs in heterografting studies and has the potential to be applied to other experimental situations to detect the expression of multiple genomes within a sample.

Previously, the detection of graft-mobile RNAs has been linked with a high levels of background data noise (Paajanen, Tomkins et al. 2024). Traditionally, researchers first utilised a genomic approach before undertaking experimental validation approaches in the laboratory, however, validation typically only confirms the presence of a small fraction of the putative mobile RNAs (Notaguchi, Higashiyama et al. 2015, Kehr, Morris et al. 2022). The issues surrounding the state of previously identified mobile mRNA transcripts has been highlighted in a recent study, and insist that more rigorous approaches are necessary to mobile RNA detection (Paajanen, Tomkins et al. 2024). Through the re-analysis of previously published datasets from grafting experiments the study points out how the vast amounts of data noise, either technological or biological, have contributed to the transcripts that we believe to be mobile in plant systems (Paajanen, Tomkins et al. 2024). In our study, we have designed the *mobileRNA* approach and evaluated its performances against other methods for detecting mobile RNAs in grafting systems. Here, we have demonstrated that the *mobileRNA* approach outperforms other methods for both the detection of graft-mobile sRNAs and mRNA by considerably reducing data noise and improving the estimation of transcript abundance in distant tissues. The increased confidence in the detection of these mobile RNAs supports researchers to draw conclusive biological implications.

The success of *mobileRNA* has been attributed to supplying the alignment algorithms with the genomic information from all genomes of interest within a merged genome. Alignment algorithms have been specifically designed to compare and match sequences to a reference sequence based on their features such as polymorphisms or structural variants. Here, we have exploited this ability by simply supply the tools with all the genomic information to allow the algorithms to make the most informed decisions. To date, there are no references to the use of a merged genome used to detect mobile endogenous RNAs in grafting studies, however, a merged genome has been used before in other contexts, including hybrid plant studies (Lopez-Gomollon, Müller et al. 2022). In recent years, pangenomes have been development and there usages replicate what we wanted to achieve with a merged genome in this work. A pangenome is a genome reference assembly that contains genomic sequences from more than one strain or accession or ecotype within a species (Bayer, Golicz et al. 2020). In genomic analysis a pangenome is beneficial when there is a high degree of genetic diversity within a species, thus, enables the alignment algorithms to more efficiently capture the genetic profile and variation within a sample. Similarly, the genomic sequences of microorganisms are typically merged into a single database that is used in metagenomic studies to identify multiple organisms within a sample to allow researchers to capture the full diversity within the community (Blanco-Míguez, Beghini et al. 2023, Nam, Do et al. 2023). In this work, we demonstrate that the application of a merged genome is also applicable when the contribution is unequal between the genome, whereby the mobile RNAs only contributed to a fraction of the total RNA population.

Limitations associated with mobileRNA

The development of *mobileRNA* aims to improve upon existing bioinformatic methodologies utilised within the field, but it is not without its own limitations. Firstly, the similarity of the genomes within the heterografted system plays the largest role in our ability to detect putative mobile molecules via existing methods, including *mobileRNA*. Here we demonstrated that the ability to detect mobile RNAs decreases as the two genomes become more similar, for instance in intraspecific grafts. This results in an under-estimation of the possible mobile RNAs. Henceforth, we advise user to undertake genome mappability analysis and calculate the index to estimate the proportion of detectable mobile RNAs (Pockrandt, Alzamel et al. 2020).

Our results further support recent finding that propose that long read-assisted *de novo* assemblies are better suited to the detection of mobile RNAs than the use of SNPs alone (Paajanen, Tomkins et al. 2024). This advocates that the quality of the reference genome also plays a vital role in mobile RNA detection and highlights how draft, or incomplete genome references may hinder research objectives. Furthermore, the lack of functional gene characterisations makes it challenging to theorise the role of putative mobile mRNAs.

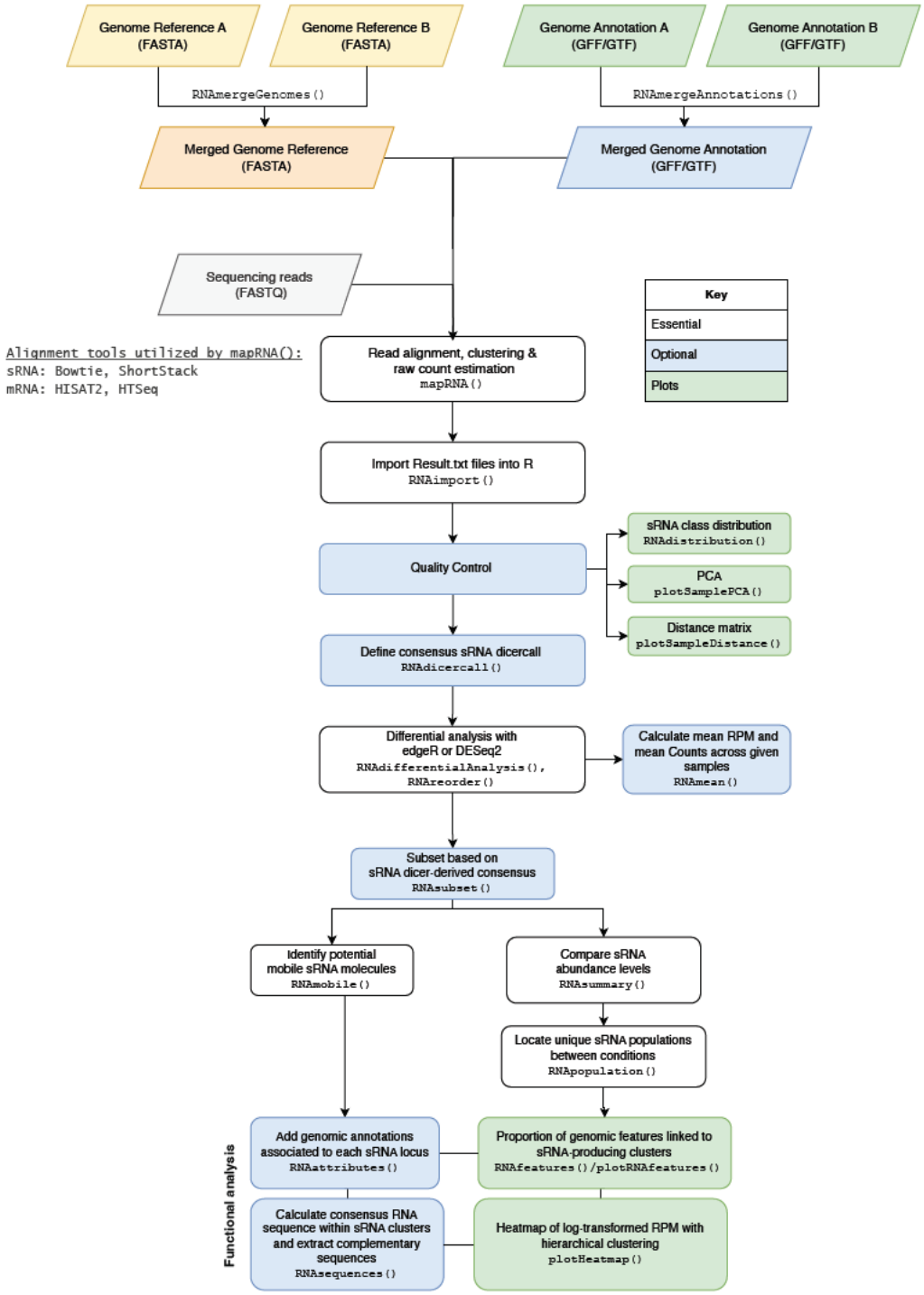
Lastly, many plant sRNAs originate from repetitive regions, including TEs (Vaucheret and Voinnet 2024) and are primarily involved in the RdDM pathway which mediates *de novo* DNA methylation (Vaucheret and Voinnet 2024). The repetitive nature of these short read sequences prevents their detection via existing methods, including *mobileRNA*. A high proportion of reads associated with these sRNAs will likely align ambiguous to sequences in one or multiple

genomes. Consequently, making it impossible to determine their true origin. To avoid misinterpretation, the *mobileRNA* approach discards ambiguously aligned reads, thus, rendering *mobileRNA* unable to efficiently and unambiguously detect mobile RNAs with highly repetitive sequences. This limitation underscores a broader concern whereby mobile RNA populations are biased and skewed towards those lacking extremely repetitive regions.

Conclusion

To conclude, although indeed this method has its limitations it offers a significant improvement on existing bioinformatic pipelines used to detect mobile RNAs in plant heterografting systems. Our results demonstrated a high detection efficiency and lower rates of background data noise. The *mobileRNA* approach has been incorporated into an easy-to-use R package to support the deployment of the method across the field.

2.5 Supplementary Figures & Tables



Supplementary Figure 2.1. Advanced pipeline for *mobileRNA*. The genome references for the scion and rootstock (represented as Genome Reference A and B) are merged to form a merged genome reference supplied to the alignment tool. Following alignment of the RNA sequencing reads they undergo clustering or raw count estimation. Results are imported into R for downstream analysis.

Supplementary Table 2.1. Summery metrics of biological samples used to generate the blended datasets. Information includes data type, genotype, tissue, its representation in the blended data, the number of raw and cleaned reads, plus, citation and accession number from the NCBI Sequence Read Archive (SRA).

Sequencing type	Dataset	Replicates	Species	Accession/Variety	Simulated genotype	Tissue	Raw reads	Clean reads	Raw data accession	Citation
sRNAseq	Tomato/Eggplant	Eggplant_1	*Solanum melongena*	Line S63	Tissue (collection)	Anther	15,431,011	10,432,197	SRR17301403	Li B et al., 2022
		Eggplant_2	*Solanum melongena*	Line S63	Tissue (collection)	Anther	11,725,861	8,127,789	SRR17312491	Li B et al., 2022
		Eggplant_3	*Solanum melongena*	Line S63	Tissue (collection)	Anther	13,799,582	10,451,052	SRR17312490	Li B et al., 2022
		Tomato	*Solanum lycopersium*	BGV007023	Distant	Leaf	3,951,725	3,828,653	SRR16077825	Qing Y et al., 2022
	Col-0/Ler-0	Col-0_1	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	15,832,411	15,832,411	SRR8723396	Blein T et al., 2020
		Col-0_2	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	11,546,857	11,546,857	SRR8723397	Blein T et al., 2020
		Col-0_3	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	13,258,374	13,258,374	SRR8723398	Blein T et al., 2020
		Ler-0	*Arabidopsis thaliana*	Landsberg erecta	Distant	Root	23,009,703	23,009,703	SRR8723405	Blein T et al., 2020
	Col-0/C24	Col-0_1	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Leaf	15,644,139	13,059,905	SRR21197493	Yang F et al., 2023
		Col-0_2	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Leaf	16,023,144	13,296,185	SRR21197492	Yang F et al., 2023
		Col-0_3	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Leaf	15,982,248	13,396,813	SRR21197491	Yang F et al., 2023
		C24	*Arabidopsis thaliana*	C24	Distant	Leaf	31,572,522	30,057,858	SRR11521543	Zhou H et al., 2020
mRNAseq	Tomato/Eggplant	Eggplant 1	*Solanum melongena*	Ecavi	Tissue (collection)	Leaf	53,624,938	53,624,938	SRR10060529	Villanueva G et al., 2023
		Eggplant 2	*Solanum melongena*	Ecavi	Tissue (collection)	Leaf	50,214,317	50,214,317	SRR10060530	Villanueva G et al., 2023
	Col-0/Ler-0	Col-0_1	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	13,982,591	13,982,591	SRR23623443	PRJNA938935 NCBI database (www.ncbi.nlm.nih.gov)
		Col-0_2	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	11,038,436	11,038,436	SRR23623442	PRJNA938935 NCBI database (www.ncbi.nlm.nih.gov)
		Col-0_3	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	13,485,527	13,485,527	SRR23623441	PRJNA938935 NCBI database (www.ncbi.nlm.nih.gov)
	Col-0/C24	Col-0_1	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	13,982,591	13,982,591	SRR23623443	PRJNA938935 NCBI database (www.ncbi.nlm.nih.gov)
		Col-0_2	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	11,038,436	11,038,436	SRR23623442	PRJNA938935 NCBI database (www.ncbi.nlm.nih.gov)
		Col-0_3	*Arabidopsis thaliana*	Columbia	Tissue (collection)	Root	13,485,527	13,485,527	SRR23623441	PRJNA938935 NCBI database (www.ncbi.nlm.nih.gov)

Supplementary Figure 2.2. Summary statistics of blended small RNA sequencing (sRNAseq) samples representing the heterograft in the combination. Simulated reads generated by either the Random or Tier format (see methods) were injected into biological samples. Injected reads were associated to sRNAs from the 'Distant' genome to represent as mobile.

Simulation Format	Simulated dataset	Simulated replicates	Tissue genotype	Distant genotype	Cleaned origin reads	Spiked reads	Total reads	% Spiked reads of total
Random Format	Eggplant/Tomato	EggplantTomato_1	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	10,432,197	5,928	10,438,125	0.057
		EggplantTomato_2	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	8,127,789	5,928	8,133,717	0.073
		EggplantTomato_3	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	10,451,052	5,928	10,456,980	0.057
	Col-0/Ler-0	Col0Ler0_1	Columbia (Arabidopsis thaliana)	Landsberg (Arabidopsis thaliana)	15,832,411	28,106	15,860,517	0.177
		Col0Ler0_2	Columbia (Arabidopsis thaliana)	Landsberg (Arabidopsis thaliana)	11,546,857	28,106	11,574,963	0.243
		Col0Ler0_3	Columbia (Arabidopsis thaliana)	Landsberg (Arabidopsis thaliana)	13,258,374	28,106	13,286,480	0.212
	Col-0/C24	Col0C24_1	Columbia (Arabidopsis thaliana)	C24 (Arabidopsis thaliana)	13,059,905	9,248	13,069,153	0.071
		Col0C24_2	Columbia (Arabidopsis thaliana)	C24 (Arabidopsis thaliana)	13,296,185	9,248	13,305,433	0.070
		Col0C24_3	Columbia (Arabidopsis thaliana)	C24 (Arabidopsis thaliana)	13,396,813	9,248	13,406,061	0.069
Tier Format	Eggplant/Tomato	EggplantTomato_1	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	10,432,197	6,474	10,438,671	0.062
		EggplantTomato_2	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	8,127,789	6,474	8,134,263	0.080
		EggplantTomato_3	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	10,451,052	6,474	10,457,526	0.062
	Col-0/Ler-0	Col0Ler0_1	Columbia (Arabidopsis thaliana)	Landsberg (Arabidopsis thaliana)	15,832,411	28,251	15,860,662	0.178
		Col0Ler0_2	Columbia (Arabidopsis thaliana)	Landsberg (Arabidopsis thaliana)	11,546,857	28,251	11,575,108	0.244
		Col0Ler0_3	Columbia (Arabidopsis thaliana)	Landsberg (Arabidopsis thaliana)	13,258,374	28,251	13,286,625	0.213
	Col-0/C24	Col0C24_1	Columbia (Arabidopsis thaliana)	C24 (Arabidopsis thaliana)	13,059,905	6,236	13,066,141	0.048
		Col0C24_2	Columbia (Arabidopsis thaliana)	C24 (Arabidopsis thaliana)	13,296,185	6,236	13,302,421	0.047
		Col0C24_3	Columbia (Arabidopsis thaliana)	C24 (Arabidopsis thaliana)	13,396,813	6,236	13,403,049	0.047

Supplementary Table 2.2. The parameters for selecting the simulated mobile sRNAs from biological samples. The coverage selection represents the coverage value or range (RPM) utilised to select simulated sRNAs. “Ave. % of spiked reads” represents the average across samples in the condition of the reads associated to the simulated sRNA injected into the blended sRNAseq samples.

Simulation Format	Simulated dataset	Tissue genotype	Distant genotype	Ave. % of spiked reads	Coverage selection	Low coverage selection	Mean coverage selection	High coverage selection
Random Format	Eggplant/Tomato	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	0.0621	>7	-	-	-
	Col-0/Ler-0	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype(Arabidopsis thaliana)	0.2105	>28	-	-	-
	Col-0/C24	Columbia ecotype (Arabidopsis thaliana)	C24 ecotype (Arabidopsis thaliana)	0.0698	>14	-	-	-
Tier Format	Eggplant/Tomato	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	0.0678	-	3	7	>35
	Col-0/Ler-0	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype(Arabidopsis thaliana)	0.2116	-	3	27-28	>140
	Col-0/C24	Columbia ecotype (Arabidopsis thaliana)	C24 ecotype (Arabidopsis thaliana)	0.0470	-	3,4,5	14-15	>30

Supplementary Table 2.3. Summary statistics of blended messenger RNA sequencing (mRNAseq) samples representing the heterografts in the combination. The R package polyester (Frazee, Jaffe et al. 2024) was used to produced synthetic RNAseq reads from the "Distant" genome in the combination.

Simulation format	Simulated dataset	Simulated replicates	Tissue genotype	Distant genotype	Cleaned origin reads	Spiked reads	Total reads	% Spiked reads of total
1k	Eggplant/Tomato	EggplantTomato_1	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	53,624,938	1,000	53,625,938	0.002
		EggplantTomato_2	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	50,214,317	1,000	50,215,317	0.002
	Col-0/Ler-0	Col0Ler0_1	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,982,591	1,000	13,983,591	0.007
		Col0Ler0_2	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	11,038,436	1,000	11,039,436	0.009
		Col0Ler0_3	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,485,527	1,000	13,486,527	0.007
5k	Eggplant/Tomato	EggplantTomato_1	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	53,624,938	5,000	53,629,938	0.009
		EggplantTomato_2	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	50,214,317	5,000	50,219,317	0.010
	Col-0/Ler-0	Col0Ler0_1	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,982,591	5,000	13,987,591	0.036
		Col0Ler0_2	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	11,038,436	5,000	11,043,436	0.045
		Col0Ler0_3	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,485,527	5,000	13,490,527	0.037
10k	Eggplant/Tomato	EggplantTomato_1	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	53,624,938	10,000	53,634,938	0.019
		EggplantTomato_2	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	50,214,317	10,000	50,224,317	0.020
	Col-0/Ler-0	Col0Ler0_1	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,982,591	10,000	13,992,591	0.071
		Col0Ler0_2	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	11,038,436	10,000	11,048,436	0.091
		Col0Ler0_3	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,485,527	10,000	13,495,527	0.074
50k	Eggplant/Tomato	EggplantTomato_1	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	53,624,938	50,000	53,674,938	0.093
		EggplantTomato_2	Eggplant (Solanum melongena)	Tomato (Solanum lycopersicum)	50,214,317	50,000	50,264,317	0.099
	Col-0/Ler-0	Col0Ler0_1	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,982,591	50,000	14,032,591	0.356
		Col0Ler0_2	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	11,038,436	50,000	11,088,436	0.451
		Col0Ler0_3	Columbia ecotype (Arabidopsis thaliana)	Landsberg ecotype (Arabidopsis thaliana)	13,485,527	50,000	13,535,527	0.369

Supplementary Table 2.4. Performance metrics for binary classification of blended mRNA datasets. The blended datasets were analysed by four methods: *mobileRNA*, Xia, Li, and Wang (described in Methods section). For each library size in a dataset, the table shows the recall, precision and F-score for each analytic method. Recall denotes the proportion of true positive mobile RNAs compared to the false negatives, and precision reflects the proportion of the total predicted mobile RNAs which were positively identified. The F-score is a measure of predictive performance that compares recall and precision. Values are rounded to two decimal places.

Simulated Dataset	Analytical Method	Simulation Format	Recall	Precision	F-score
Eggplant/Tomato	mobileRNA	1k	0.90	0.99	0.94
		5k	0.92	0.99	0.95
		10k	0.91	0.99	0.95
		50k	0.91	0.96	0.94
	Wang	1k	0.82	0.91	0.86
		5k	0.90	0.93	0.91
		10k	0.93	0.93	0.93
		50k	0.93	0.93	0.93
	Xia	1k	0.91	0.32	0.47
		5k	0.97	0.36	0.53
		10k	0.97	0.36	0.53
		50k	0.99	0.36	0.53
	Li	1k	1.00	0.00	0.01
		5k	1.00	0.01	0.01
		10k	1.00	0.01	0.01
		50k	1.00	0.01	0.01
Col-0/Ler-0	mobileRNA	1k	0.24	0.28	0.25
		5k	0.27	0.98	0.42
		10k	0.27	0.98	0.43
		50k	0.28	0.93	0.43
	Wang	1k	0.09	0.86	0.16
		5k	0.16	0.92	0.28
		10k	0.19	0.93	0.32
		50k	0.25	0.95	0.39
	Xia	1k	0.50	0.01	0.01
		5k	0.53	0.01	0.01
		10k	0.58	0.01	0.02
		50k	0.64	0.01	0.02
	Li	1k	1.00	0.01	0.01
		5k	1.00	0.01	0.01
		10k	1.00	0.01	0.01
		50k	1.00	0.01	0.01

Supplementary Table 2.5. Performance metrics for binary classification of blended sRNA datasets. The blended datasets were analysed by four methods: *mobileRNA*, Rubio, and Li (described in Methods section). For each simulation format in a dataset, the table shows the recall, precision and F-score for each analytic method. Recall denotes the proportion of true positive mobile RNAs compared to the false negatives, and precision reflects the proportion of the total predicted mobile RNAs which were positively identified. The F-score is a measure of predictive performance that compares recall and precision. Values are rounded to two decimal places.

Simulated Dataset	Analytical Method	Simulation Format	Recall	Precision	F-score
Eggplant/Tomato	mobileRNA	Random Format	0.97	1.00	0.98
		Tier Format	0.97	0.99	0.98
	Rubio	Random Format	0.97	0.52	0.68
		Tier Format	0.77	0.47	0.58
	Li	Random Format	1.00	0.00	0.00
		Tier Format	0.99	0.00	0.00
Col-0/Ler-0	mobileRNA	Random Format	0.24	1.00	0.39
		Tier Format	0.29	1.00	0.45
	Rubio	Random Format	0.96	0.01	0.02
		Tier Format	0.83	0.01	0.02
	Li	Random Format	0.98	0.00	0.00
		Tier Format	0.99	0.00	0.00
Col-0/C24	mobileRNA	Random Format	0.60	1.00	0.75
		Tier Format	0.61	1.00	0.76
	Rubio	Random Format	0.98	0.01	0.02
		Tier Format	0.93	0.01	0.02
	Li	Random Format	0.98	0.01	0.01
		Tier Format	0.99	0.00	0.01

CHAPTER 3: RE-ANALYSIS OF BIOLOGICAL DATASETS USING *mobileRNA*.

3.1 Introduction

In plants, the systemic movement of RNAs (mobile RNAs) has been coupled to the regulation of plant development and responses to environmental stimuli (Atkins, Hull et al. 1991, Zhang, Kollwig et al. 2014, Borges and Martienssen 2015, Li and Zhao 2021, Rubio, Stammitti et al. 2022, Cheng, Xu et al. 2023). Their role as non-autonomous systemic signals has been characterised in diverse physiological processes such as flowering, potato tuberization (Banerjee, Chatterjee et al. 2006, Bhogale, Mahajan et al. 2014, Ghate, Sharma et al. 2017), changes to leaf morphology (Kim, Canio et al. 2001), root development (Omid, Keilin et al. 2007, Notaguchi, Wolf et al. 2012) and environmental stress tolerance (Haywood, Yu et al. 2005, Wang, Liu et al. 2012, Davoudi, Song et al. 2022). Determining the molecular mechanisms that enable the transport of RNAs, determining which can move and where they can go, is key to understanding the role of RNAs in systemic signalling.

To study RNA signalling, researchers have utilised plant grafting. This approach can join multiple genotypes into a single plant that enables researchers to distinguish the genomic origin of RNAs (Jeynes-Cupper and Catoni 2023). Since grafting itself can introduce new or improved traits, this practise has been globally employed to promote the horticulture of perennial and herbaceous plants (Gaion, Braz et al. 2018, Habibi, Liu et al. 2022).

Consequently, researchers and breeders alike have been keen to understand the root of grafting-induced traits, and indeed many are associated to the rootstock's intrinsic traits (such as pre-existing resistance to a pathogen) (Jeynes-Cupper and Catoni 2023). However, some traits cannot be as simply explained and the involvement of RNAs has been suggested in many studies (Cerruti, Gisbert et al. 2021, Jeynes-Cupper and Catoni 2023). Therefore, grafting offers a platform to additionally investigate the roles of RNAs in the regulation of physiological processes (Kehr and Kragler 2018, Kehr, Morris et al. 2022). With this technique, RNAs have been demonstrated to move bi-directionally across the graft junction and introduce transcriptomic and epigenomic variation (Molnar, Melnyk et al. 2010, Lewsey, Hardcastle et al. 2016, Heeney and Frank 2023).

To characterise the mobile RNAs and their biological roles, we first need to identify which RNAs are mobile, from where and to they travel to, and under what conditions are they mobile. By identifying putative mobile RNAs we can also begin to characterise features connected to their mobility, such as molecular modifications or structural features. In line with objectives, researchers have utilised genomic analysis including mRNAseq or sRNAseq for genome-wide identification (Mahajan, Bhogale et al. 2012, Notaguchi, Higashiyama et al. 2015, Xia, Zheng et al. 2018, Wang, Wang et al. 2020, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022, Paajanen, Tomkins et al. 2024). In addition, researchers have found an association between the presence of tRNA-like structures, cytosine methylation and the mobilisation of mRNA molecules (Zhang, Sun et al. 2009, Zhang, Thieme et al. 2016, Xue, Zhao et al. 2020).

Although these previous findings have shed valuable insights in the molecular mechanisms underpinning RNA movement, they emphasize that further uncharacterised mechanisms are likely involved. Due to the availability of resources and recent advancements in analytical techniques, it could be valuable to re-analyse these datasets to identify changes that could have been masked by additional background data noise by previous analysis methods. Nevertheless, previous re-analyses of published datasets have found it challenging to identify predictive features associated to RNA mobility (Fu, Xu et al. 2024, Paajanen, Tomkins et al. 2024). Despite the availability of datasets, there is immense variability between experiments, showing little overlap between their results. It has been suggested that this result is a consequence of the deployed bioinformatic pipelines which each use different criteria to select for mobile candidates (Paajanen, Tomkins et al. 2024). Together with the results in Chapter 2, we must assume that previous studies likely over-estimated the number of mobile RNAs due to the presence of data noise. Here, we re-analyse published sRNA and mRNA heterografting datasets from genetically diverse families using *mobileRNA*. This work sought to compare the results to the previously published results to identify mobile RNAs and their biological roles which previously could have been masked by background data noise. This work also aimed to further validate *mobileRNA*'s capacity in real-world scenarios. Our results show that the chosen analysis method plays a central role in the outcome and without reported phenotypical changes associated with the grafting, it is challenging to confer the biological importance of the mobile molecules.

3.2 Materials and Method

Here, published biological sequencing datasets from four plant grafting experiments to identify putative graft-mobile RNAs were re-analysed using the *mobileRNA* approach (Figure 3.1). originally, each utilised a different bioinformatic pipeline to detect their graft-mobile RNAs and they embody a good representation of the current literature. Across the literature, the bioinformatic pipelines commonly align RNA sequencing reads to each genotype in the grafting system separately. This is then followed by downstream filtering of genetic variants. To add further complications, some studies lack a comparison to biological controls which prevents the mitigation of false positives. The following datasets were re-analysed to provide a deeper assessment of the *mobileRNA* methodology:

I. *Vitaceae* – Grapevine:

   This study generated heterografts where *Vitis vinifera* cv. Cabernet Sauvignon was the scion and *Vitis riparia* cv. Gloire de Montpellier was the rootstock. These were compared to *V. vinifer*a cv. Cabernet Sauvignon self-grafts. This study investigated mobile sRNAs in both directions through the sampling of root and shoot tissues (Rubio, Stammitti et al. 2022).

II. *Fabaceae* – Bean:

   This bean grafting experiment used common bean (*Phaseolus vulgaris* cv. Jiulibai) and soybean (*Glycine max* cv. Williams 82) plants. Here, we used

the mobile mRNA data to investigated mobility in both directions using tissues sampled from the root and shoot (Li, Wang et al. 2021).

III. *Brassicaceae* - Brassica:

The brassica grafting study combined *Nicotiana benthamiana* as a scion with *Arabidopsis thaliana* rootstock to identify root-to-shoot mobile mRNA transcripts (Notaguchi, Higashiyama et al. 2015). This includes shoot samples from two replicates per condition.

IV. *Solanaceae* – Solanaceous:

The solanaceous grafting study combined *N. benthamiana* as a scion with tomato (*Solanum lycopersium*) as a rootstock to detect shoot-to-root mobile mRNA transcripts (Xia, Zheng et al. 2018). This included three root samples from heterografts, with no controls.

Merged Genomes

To facilitate the simultaneous alignment of sequencing reads to both the scion and rootstock genotype in the *mobileRNA* approach, a merged genome reference was generated for each dataset. Before combining the individual genome references into a single file (FASTA), a unique prefix is added to each pseudomolecule (chromosome/contig/scaffold) in each reference to maintain them distinguishable in the downstream analysis. In a similar manner, a merged genome annotation file is generated for each dataset by concatenating the individual annotation files. For instance, for the grapevine dataset the *V. vinifera* and *V. riparia* were merged. The genomes utilised in this analysis included:

- *V.vinifera* cv. Cabernet Sauvignon (PN40024.v4) (French 2007)

- *V.riparia* cv. Gloire de Montpellier (EGFV_Vit.rip_1.0, GCF_004353265.1) (Girollet, Rubio et al. 2019)
- *P.vulgaris* cv. G19833 (PhaVulg1_0, GCF_000499845.1) (Schmutz, McClean et al. 2014)
- *G.max* cv. Williams 82 (Glycine_max_v4.0) (Schmutz, Cannon et al. 2010)
- *A. thaliana* cv. Columbia (Col-0) (TAIR10) (Lamesch, Berardini et al. 2012)
- *N.benthamiana* (draft genome v2.6.1) (Bombarely, Rosli et al. 2012)
- *S.lycopersicum* (Version 4) (Hosmani, Flores-Gonzalez et al. 2019)
- *N.benthamiana* (draft genome v1.0.1) – specifically for the Solanaceous dataset (Bombarely, Rosli et al. 2012)

Genome mappability and index calculation

The genome mappability estimates the degree of repetitiveness of a genome (Derrien et al. 2012), and allows users to evaluate how unique or repetitive a DNA regions is in a given genome. Mappability is expressed, at every genomic location, with a score from 0 to 1, where 1 is represents a unique region and 0 represents a hypothetical infinitely repeated region. We used GenMap (1.3.0) (Pockrandt, Alzamel et al. 2020) to compute the mappability at single nucleotide resolution (-K 30) for each of the genome used, taken alone or in combination in pairs (merged genomes). The mean mappability value across each exonic region was determined using BEDtools (bedtools map -c 4 -o mean) (Quinlan and Hall 2010). For each gene, a single mean was obtained by averaging the value of each exon weighted on they nucleotide length. These averaged values have been used to estimate gene repetitiveness in single or merged genomes. The genome

mappability index represents the proportion of the merged genome that is above a mappability threshold of 0.5.

sRNAseq analysis

To make a comparison between the mobileRNA output and previously published results, the datasets were processes following the same parameters utilised in the publication. The raw sRNA sequencing reads from the Grapevine dataset were cleaned and trimmed using Trim Galore (version 0.6.5) to remove adaptor sequences, low quality reads and eliminate reads shorter than 16 nucleotides or longer than 30 nucleotides (Krueger F 2021). Sequencing reads from the Bean dataset did not require trimming. Reads were aligned to their respective merged genome using Bowtie (-p 6 -v 0 -a -m 1) (Version 1.3.1) and sorted using SAMtools (Version 1.17) (Langmead, Trapnell et al. 2009, Danecek 2021). ShortStack (Version 4.02) was utilised to undertake *de novo* sRNA clustering and parameters were set, where possible, to match the parameters utilised in published works for each dataset (Axtell 2013, Shahid and Axtell 2014). ShortStack identifies sRNA clusters (sometimes referred to as sRNA-producing loci) by building "islands" which are genomic locations defined by the minimum alignment depth/coverage and the required distance between "islands". The minimum reads coverage is defined by the `mincov` parameter (default is 1 RPM), and similarly the `pad` parameter defines the continuous regions with depth exceeding the `mincov` value, whereby initial peaks will be merged if they are within this distance of one another (default is 200). ShortStack also allows a user to define the minimum (`dicermin` parameter) and maximum (`dicermax ` parameter) size range of valid sRNAs which allows users to discriminate between the dicer-derived sRNA loci (--dicermin 21 –

dicermax 24) (Axtell 2013, Shahid and Axtell 2014). For the Grapevine dataset, sRNA clusters were selected between nucleotides of 20-24 and clusters were defined by a minimum coverage of 5 RPM and with a 100-nucleotide distance between "islands" (--dicermin 20 --dicermax 24 --pad 100 --mincov 5). For the Bean dataset, default parameters were utilised alongside a minimum coverage of 0.5 RPM to define sRNA cluster loci (--mincov 0.5). For each dataset, a sRNA loci file was generated which contained all *de novo* sRNA clusters identified across the sample replicates. Analysis with ShortStack was repeated utilising the sRNA loci file to define the sRNA clusters in each sample. Results were imported into R and downstream analysis was undertaken using the Bioconductor/R package, *mobileRNA* (Jeynes-Cupper and Catoni 2023). Target prediction analysis with psRNATarget (Dai, Zhuang et al. 2018) was undertaken using the consensus sequences. This was followed with gene ontology (GO) enrichment analysis using a custom script.

mRNAseq analysis

The raw mRNA sequencing reads were trimmed using fastp (Chen 2023) (version 0.11.9) using default settings to remove low quality reads. Cleaned reads were aligned to their respective merged genome using HISAT2 (Kim, Paggi et al. 2019) with default settings. Aligned reads were filtered to select only those which aligned to a single location, discarding reads which aligned to multiple locations. This was accomplished by utilising the "NH:i:1" flag. Filtered reads were sorted using SAMtools (Danecek 2021). Raw counts for mRNA transcripts were surmised by HTSeq (Putri, Anders et al. 2022) (--order=pos -a=0 --stranded=no --mode=union --nonunique=none --type=mRNA --idattr=ID). Downstream analysis of raw count files was undertaken using the

Bioconductor/R package, *mobileRNA* (Jeynes-Cupper and Catoni 2023). The analysis calculated FPKM and mRNA transcripts with a raw count value of zero were discarded from the analysis. The putative graft-mobile mRNAs were selected for using default settings; those with reads only located within heterograft samples and absent within control samples. Functional enrichment of mobile transcripts was undertaken using ShinyGO (Ge, Jung et al. 2020) and protein-interaction analysis with STRINGdb (Szklarczyk, Kirsch et al. 2023).

Here, we utilised RNAmotif to detect the presence of TLS motifs in the re-analysed datasets, using default settings and the existing tRNA descriptors (Macke, Ecker et al. 2001). In order to enable the detection of TLS motifs in the 5′ and 3′ untranslated regions we added 50 "N" at the start and end of each input cDNA sequence (Zhang, Thieme et al. 2016). Moreover, we employed RNAFold (Hofacker 2003, Lorenz, Bernhart et al. 2011), tRNAscan-SE (Chan and Lowe 2019) and ARAGORN (Laslett and Canback 2004) to identified whether the mobile transcripts were tRNA genes. Read coverage was calculated using BEDtools (Version 2.29.2) (Quinlan and Hall 2010). The list of putative mobile mRNA identified by *mobileRNA* was compared to the published results of each dataset.

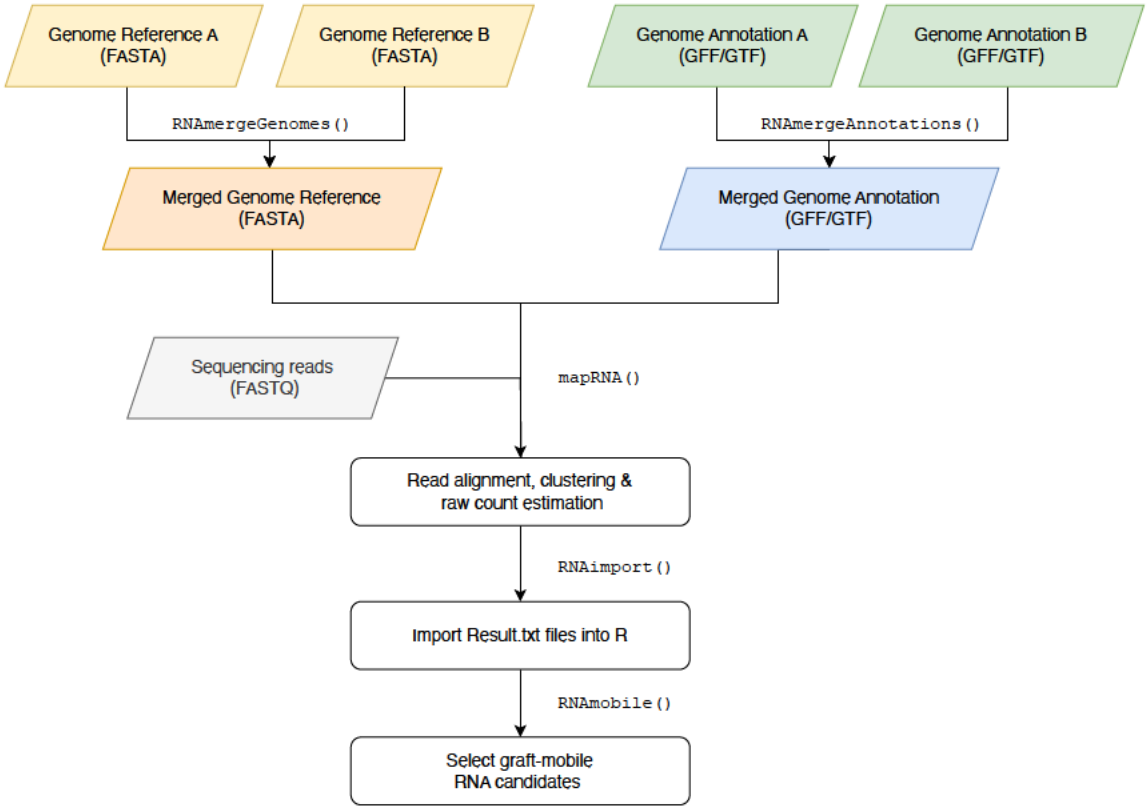


Figure 3.1. Schematic diagram of the mobileRNA pipeline to identify putative graft-mobile RNA candidates from Next-Generation Sequencing (NGS) data, including sRNA and mRNA sequencing data. *mobileRNA* leverages a merged genome to simultaneously align sequencing reads to multiple genomes. The results are represented as plain text files (.txt) and imported into R to generate a dataframe. Additional information is calculated during the organisation, such as Fragments Per Kilobase of transcript per Million mapped reads (FPKM) values. mobileRNA selected the graft-mobile RNA candidates by selecting RNAs associated with the distant genome and utilises the control replicates to mitigate alignment errors.

3.3 Results & Discussion

3.3.1 Analysis of sRNA mobility in the Grapevine dataset

The Grapevine grafting study investigated the heterografting between *V. vinifera* and *V. riparia*. The study produced three *V. vinifera* self-grafts and three heterograft where *V. vinifera* represented the scion and *V. riparia* represented the rootstock (Figure 3.2). Previous studies have stated this the heterografting

combination confers low levels of scion vigour by the end of the growth cycle (Cookson and Ollat 2013), as well as enhanced stem biomass and reduced trunk biomass (Cookson and Ollat 2013). To access the results produced from the re-analysis of the grapevine data, it was essential to compare our results to the previously published results. Unfortunately, the grapevine study did not report information for all identified mobile sRNAs, instead, the study only supplied information on 24-nt root-to-shoot sRNAs or root-to-shoot sRNAs which overlapped with genomic features.

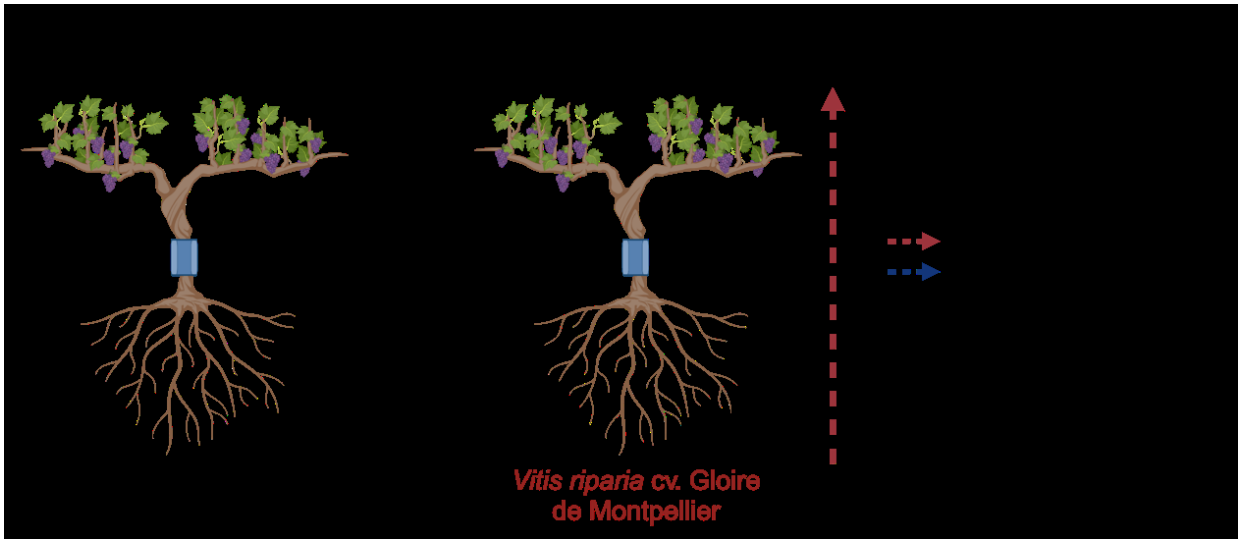


Figure 3.2. Experimental design of the data utilised from the grapevine study. The grapevine datasets from Rubio, Stammitti et al. (2022) compared the scions of V. vinifera self-grafted plants to V. vinifera scions grafted onto V. riparia to identify root-to-shoot mobile small RNAs. Created using BioRender.com.

To estimate the effect of homology between the grapevine species utilised in the grafting experiment, the genome mappability scores were estimated for each individual genome and the merged genome (Figure 3.3). The scores revealed that singularly the two grapevine genomes contain a significant proportion of unique coding regions, with a median mappability score of approximatively 0.75. However, when combined, they only contain 26.4% of coding regions with a high level of uniqueness (>0.5 mappability) (Figure 3.3), indicating that the

two grapevine genomes share close homology. These results are further demonstrated when we access the alignment statistics, as we observed that 95-97% of reads were either unmapped or discarded due to multiple alignments (Supplementary Table 3.1). Consequently, *mobileRNA* may underestimate the number of mobile RNAs, because they lack structural polymorphisms between the genomes.

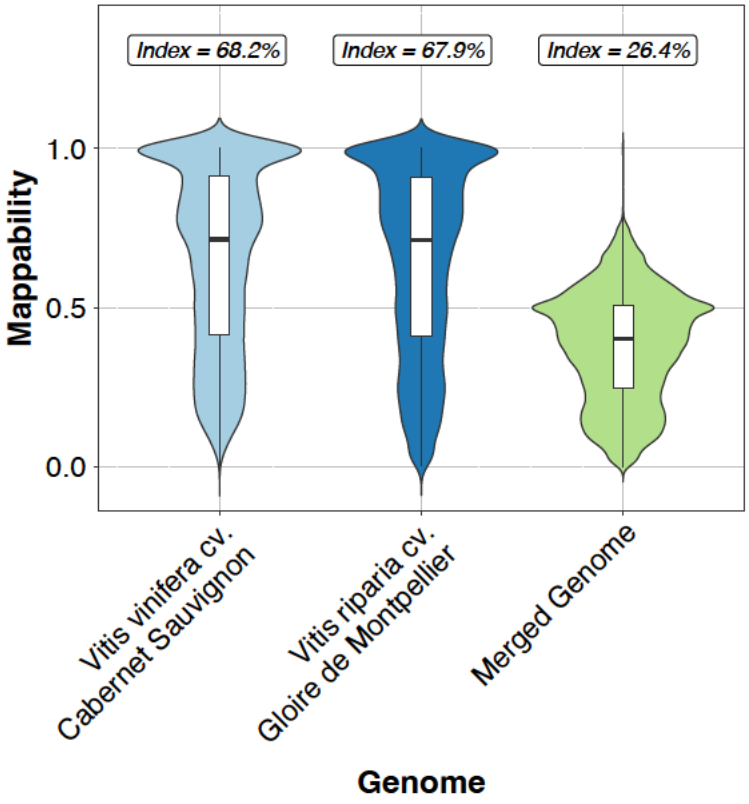


Figure 3.3. The genome mappability across exonic regions for individual and merged genome reference utilised in the grapevine data analysis. The genome mappability is from 0-1 where 0 represents a highly repetitive region and 1 signifies a highly unique region.The V. vinifera PN40024.v4 genome (Taxonomy ID 29760) is a diploid genome with 19 haploid chromosomes with an estimated genome size of around 500 Mb, 35,134 coding genes and 41,097 gene transcripts (French 2007). The V. riparia genome is a diploid genome with 19 haploid chromosomes with an estimated genome size of around 500.1 Mb and 30,745 coding genes (Girollet, Rubio et al. 2019).

We first analysed the sRNA populations in the *V. vinifera* scions grafted onto *V. riparia* rootstocks. In the scion we detected 2,904 sRNAs produced by the *V.*

vinifera scion and a total of 7 root-to-shoot mobile sRNAs produced by the *V. riparia* rootstock. This is approximately 97% fewer mobile sRNAs than stated in the published results (Figure 3.4.A). Conversely, we analysed the sRNA populations in the *V. riparia* rootstock tissues. Here, we detected 1,142 sRNAs which were natively produced by the rootstock and 167 mobile sRNAs produced by the *V. vinifera* scions travelling in the shoot-to-root direction. This is around 94% fewer than the reported mobile sRNAs in the study. The published study identified more sRNAs that were moving from the root into the shoots, which was similarly found with *mobileRNA*. Furthermore, we compared the distribution in nucleotide length of detected mobile sRNAs (Figure 3.4.A). Although the *mobileRNA* approach detected significantly fewer mobile molecules, it however did illustrate a similar trend in sRNA lengths to the published results whereby peaks in 21-nt and 24-nt sRNAs were observed.

The distribution of the mobile sRNAs across the genome was assessed in the published study. They surmised that most 21-nt sRNA clusters were associated with gene bodies while 24-nt siRNAs were associated with 2kb promoter regions (Rubio, Stammitti et al. 2022). The genes associated with shoot-to-root 21-nt sRNAs were enriched in processes related to stress response, signal transduction, cell communication and lipid metabolism. In comparison, the root-to-shoot 21-nt sRNAs signal transduction, malate transport and superoxide metabolic processes. Whereas genes associated to the promoters associated with the 24-nt siRNAs were not enriched in any processes (Rubio, Stammitti et al. 2022). In our analysis, three of the seven root-to-shoot graft-mobile sRNAs overlapped with annotated genes. Specifically, one overlapped with a non-exonic gene region and the 2 kb promoter, the second overlapped with only

non-exonic regions and the third sRNA cluster overlapped with the gene exons. These three genes were associated with the regulation of developmental processes and nucleotide-excision repair (Figure 3.5.B). Whereas the shoot-to-root sRNAs produced by the *V. vinifera* genome appears to be synthesis from regions including rRNAs, promoters, genes, five-prime UTRs and exons (Figure 3.5.B). Functional enrichment was undertaken on the genes and 1 kb promoter regions that overlapped with the sRNA-producing loci (i.e. sRNA clusters), there was an enrichment in tRNA-type intron splice site recognition and cleavage, as well as, rhythmic processes, carbon utilisation and the exonucleolytic trimming to generate mature 3' untranslated end of 5.8S rRNA.

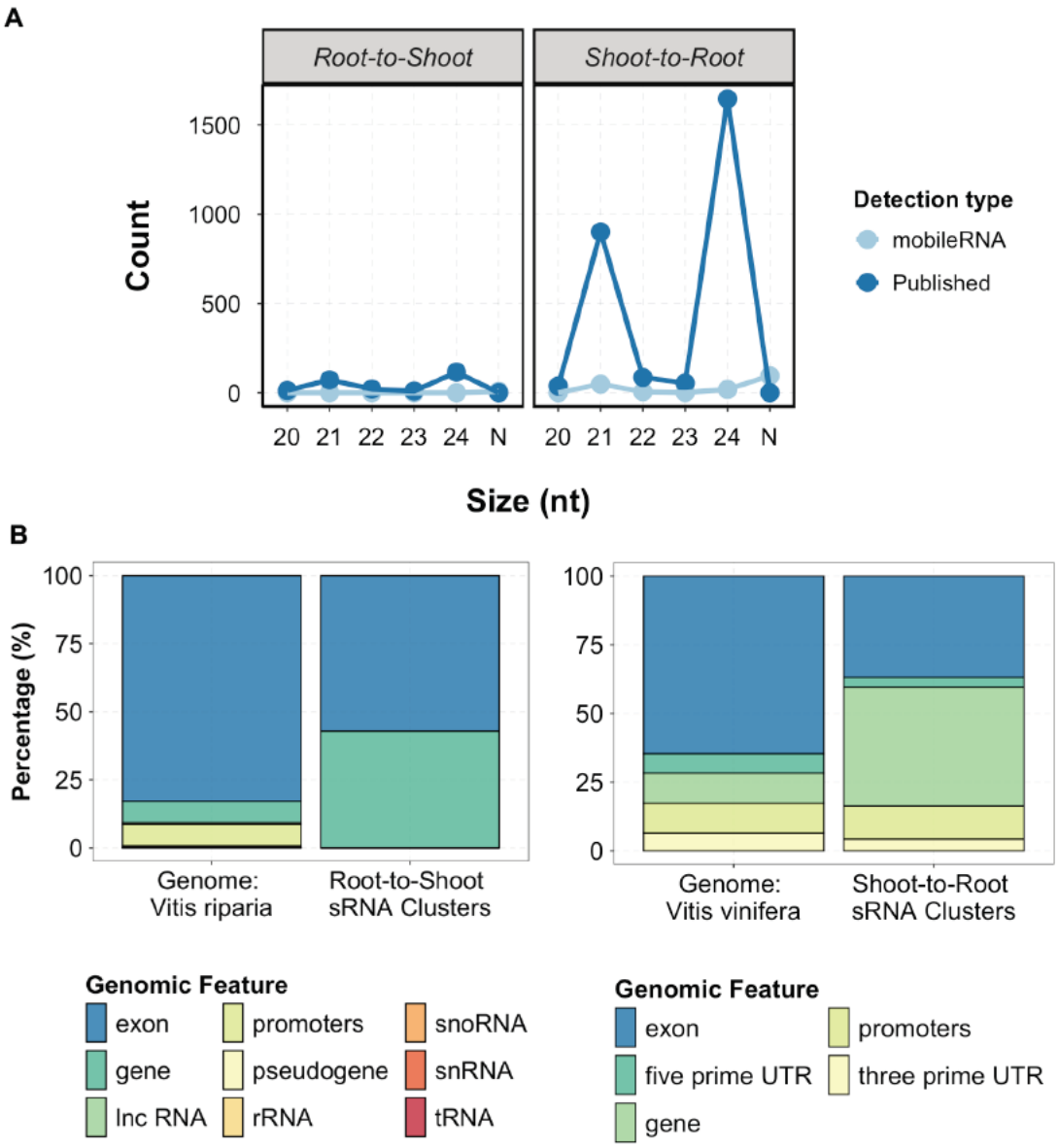


Figure 3.4. Comparison of mobile small RNAs (sRNAs) detected by *mobileRNA* to previous results. The grapevine datasets from Rubio, Stammitti et al. (2022) was re-analysed using *mobileRNA*. The results compared to the published results. Note that the total database of characterised sRNAs identified in the published results were not publicly available. A). The distribution of putative graft-mobile sRNAs in nucleotide (nt) length isolated in each published dataset using the mobileRNA approach. For the comparison, the parameters for the mobileRNA approach were adjusted to select sRNAs in the same sizes ranges as those in the published results. B) The distribution of genomic features in each genome (*V. riparia*, *V. vinifera*) compared to the distribution of sRNA producing-loci that overlap with genomic features for root-to-shoot and shoot-to-root sRNAs.

Plant sRNAs play a key role in the regulation gene expression to control proper plant growth and development. Target prediction analysis can be utilised to identify such targets by identifying complementary matches between sRNAs and targets. Using the tool psRNATarget (Dai, Zhuang et al. 2018), gene targets in the *V. vinifera* genome were predicted for the root-to-shoot *V. riparia* sRNAs - 85% had a valid sequence. Based on the 2017 schema, the top five targets were identified for each sRNA, which generated 26 possible targets. Many transcripts included different gene isoforms and were targeted by a particular sRNA. GO enrichment analysis of gene targets was undertaken to identify functional enrichments (Figure 3.5). No GO terms were found to be statistically significant due to the low number of gene target transcripts in the analysis. Yet, the target transcripts were enriched in biological processes including protein phosphorylation and ubiquitination, metabolic processes and potassium ion transmembrane transport (Figure 3.6). This is unlike the published results that stated many of the target genes of the mobile 24-nt sRNA were related to stress responses (Rubio, Stammitti et al. 2022). As stated previously, this heterograft combination is known to alter the plant morphology, specifically the partitioning of biomass between the shoots and roots, including increased stem biomass and reduced trunk biomass (Cookson and Ollat 2013). The sRNA targeting of genes related to protein ubiquitination, protein phosphorylation, potassium ion transport, and metabolic processes could indeed drive the noted phenotypical changes. For example, protein phosphorylation is notable important in hormone signalling and hence disruptions or alterations to these pathways could result in a shift in biomass allocation (Zhang, Zhou et al. 2023). Such as changes to auxin or gibberellin signalling (Zhang, Zhou et al. 2023).

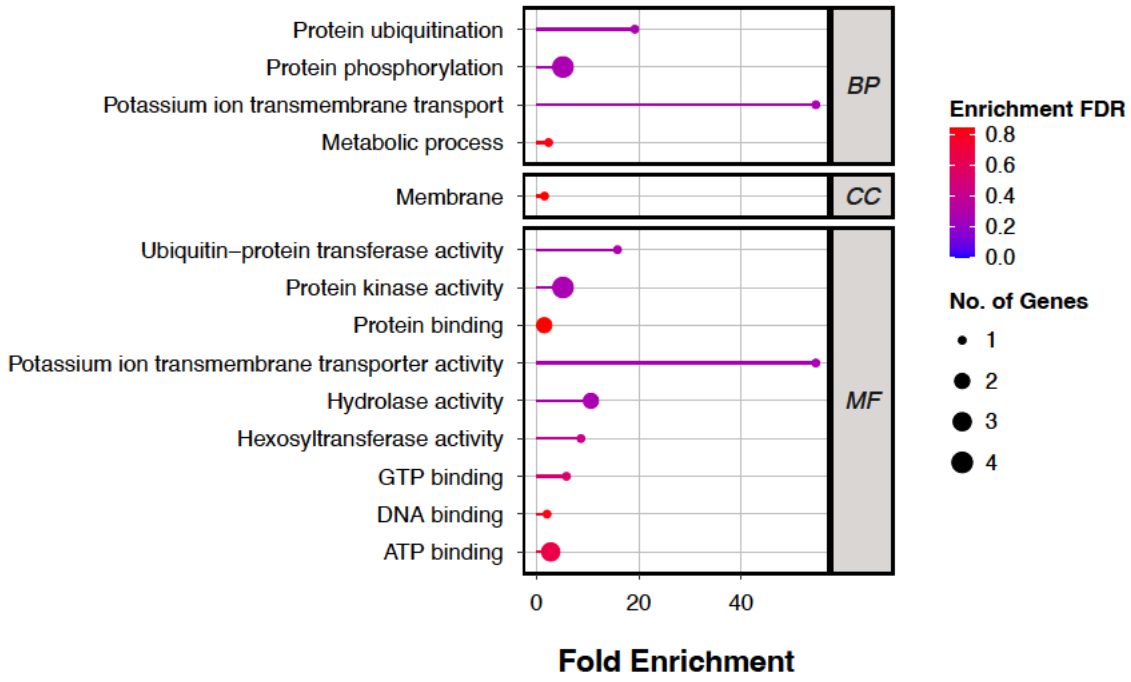


Figure 3.5. Target prediction analysis and Gene Ontology (GO) enrichment analysis of predicted targets of Root-to-Shoot mobile sRNAs in grapevine dataset. The grapevine datasets from Rubio, Stammitti et al. (2022) was re-analysed using the *mobileRNA* pipeline. Predicted mRNA targets in the *V. vinifera* genome for the root-to-shoot mobile sRNAs produced by the *V. riparia* genome. Target prediction analysis was undertaken using psRNATarget (No. top targets = 5, Expectation = 5, HSP size = 15) against the *V. viniferia* 457 V2.1 genome from JGI genomic project (Phytozome 13) (see https://phytozome-next.jgi.doe.gov/info/Vvinifera_v2_1) (French 2007).

3.3.2 Analysis of sRNA mobility in the Bean dataset

The bean grafting study explored the bi-directional movement of sRNAs produced by the soybean and common bean genomes (Figure 3.6). The soybean and common bean represent two distinct genomes originating from different species within the *Fabaceae* family. The sequence homology between the two genomes was estimated using genome mappability scoring to access the effect on our ability to detect mobile molecules. The assessment demonstrated that within coding regions, the soybean genome contains fewer unique sequences than the common bean genome. When combined into the merged genome, we see a drop in the proportion of unique regions where only 50% of the coding

regions demonstrate a high degree of uniqueness (Figure 3.7). The alignment efficiency demonstrate that around 65-70% of reads aligned to multiple regions in the merged genome (before being discarded) (Supplementary Table 3.2), indicating a moderate degree of homology among the two genomes. These results suggest that *mobileRNA* could more efficiently detect mobile RNA compared to the grapevine dataset.

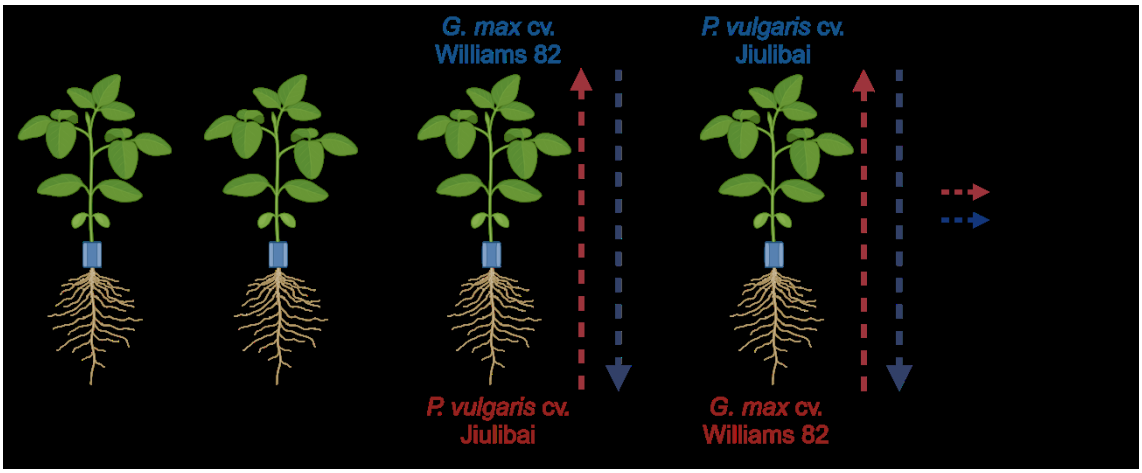


Figure 3.6.Experimental design of the data utilised from the bean study. The bean datasets from Li, Wang et al. (2021) investigated soybean (*Glycine max*) and common bean (*P. vulgaris*) mobile sRNAs that are produced either in the shoots, roots or both. The study compared mobile sRNAs populations through heterografting soybean and common bean whereby heterografts were produced for all possible combinations. The heterografted plants were compared to self-grafted plants. Tissue samples were collected for the leaves and roots for each combination, however, there were only one biological replicate per condition. Created using BioRender.com.

We identified 139,562 sRNAs which were produced in the scion of the Soybean and located 717 (0.5%) root-to-shoot mobile sRNAs produced by Common bean rootstock (Table 3.1). On the reverse, we identified 69,752 sRNAs which were produced in the Soybean rootstock and located 36,961 (53%) shoot-to-root mobile sRNAs produced by Common bean scion (Table 3.1). In comparison, the published results recorded 4 root-to-shoot and 7,607 shoot-to-root mobile Common bean sRNAs yet none of these overlapped with the published results

(Li, Wang et al. 2021). Note that from the reported results it remained unclear the number of non-mobile sRNA produced by the genotype of the destination tissue, hence, the proportion of sRNAs in respect to the non-mobile could not be distinguished (Li, Wang et al. 2021).

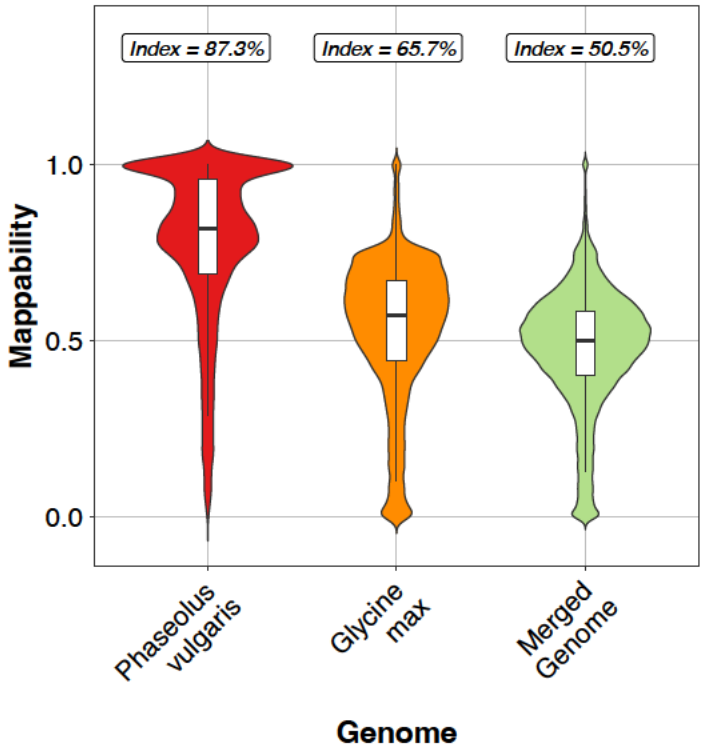


Figure 3.7.The genome mappability across exonic regions for individual and merged genome reference utilised in the bean data analysis. The genome mappability is from 0-1 where 0 represents a highly repetitive region and 1 signifies a highly unique region. The *P. vulgaris* genome is a diploid genome with 11 chromosomal pseudomolecules with an estimated genome size of around 587 Mb, 28,134 coding genes and 33,910 gene transcripts (Schmutz, McClean et al. 2014). The *G. max* genome is a diploid genome with 20 haploid chromosomes with an estimated genome size of around 978.4 Mb and 59,049 coding genes (Schmutz, Cannon et al. 2010).

The Bean data also allowed for the identification of mobile Soybean sRNAs. In this study, we identified 82,992 sRNAs which were produced in the scion of the Common bean and located 436 (0.5%) root-to-shoot mobile sRNAs produced by Soybean rootstock (Table 3.1). Similarly, on the reverse, we identified 19,658 sRNAs which were produced in the Common bean (*P. vulgaris*) rootstock and

located 57,156 (291%) shoot-to-root mobile sRNAs produced by Soybean scion (Table 3.1). In comparison, in the published records, they identified 2 root-to-shoot sRNA and 5,529 shoot-to-root sRNAs. There was no overlap in the soybean root-to-shoot mobile sRNAs characterised by *mobileRNA* in comparison to the published result, however 767 shoot-to-root mobile soybean sRNAs were common between the methods (Li, Wang et al. 2021). These results reveal that the *mobileRNA* approach detected more mobile sRNA, irrespective of the directionality, than the previous finds between soybean and common bean heterografts.

For a genomic analysis, it is standard practise to utilise, at the very least, two biological replicates per condition. However, in this dataset only one replicate per condition was provided. We surmise that the re-analysed results could be better defined with a greater sample size which would likely dismiss false positives, resulting in fewer mobile candidates.

The nucleotides length of sRNAs has been shown as an indicator of the functional role of the sRNA, as well as eluding the biosynthesis pathways that produced it. Here, we plotted the distribution of the detected mobile sRNAs characterised in the published and re-analysed results (Figure 3.8). In all instances, the *mobileRNA* approaches characterised a high proportion of the mobile sRNAs with an unclassified length, indicated by a DicerCall of "N". To characterise the most abundant sRNA length in a cluster, the *mobileRNA* method utilises ShortStack (Axtell 2013, Shahid and Axtell 2014). The creators of ShortStack describe this phenomenon in plant samples whereby typically a high proportion of sRNAs in samples will show an inconsistent size profile. This

phenomenon was described as a balance between potential contamination or the possibility that the sRNAs are in-fact a novel type (Axtell 2013, Shahid and Axtell 2014). The shoot-to-root mobile sRNAs demonstrated similar proportions of 21-23nt sRNAs with a peak in 24-nt sRNAs. This trend mirrors the previous findings (Figure 3.8). Based on previous studies, we expected to identify a greater proportion of 24-nt sRNAs in mobile populations, hence, these results show great promise (Lewsey, Hardcastle et al. 2016).

Table 3.1. Comparison of graft-mobile sRNAs characterised in the published study and using the mobileRNA approach. Here, the bean datasets were re-analysed using the mobileRNA pipeline and the results compared to the published results from Li, Wang et al. (2021). Table of results investigating root-to-shoot and short-to-root movement.

Sequencing type	Published dataset	Direction	Tissue genotype	Distant genotype	Published: No. of mobile RNAs	mobileRNA method: No. of mobile RNAs	Shared
sRNAseq	Bean	Root-to-Shoot	Glycine max cv. Williams 82	Phaseolus vulgaris cv. Jiulibai	4.00	717.00	0
	Bean	Root-to-Shoot	Phaseolus vulgaris cv. Jiulibai	Glycine max cv. Williams 82	2.00	436.00	0
	Bean	Shoot-to-Root	Glycine max cv. Williams 82	Phaseolus vulgaris cv. Jiulibai	7,607.00	36,961 00	0
	Bean	Shoot-to-Root	Phaseolus vulgaris cv. Jiulibai	Glycine max cv. Williams 82	5,529.00	57,156 00	767

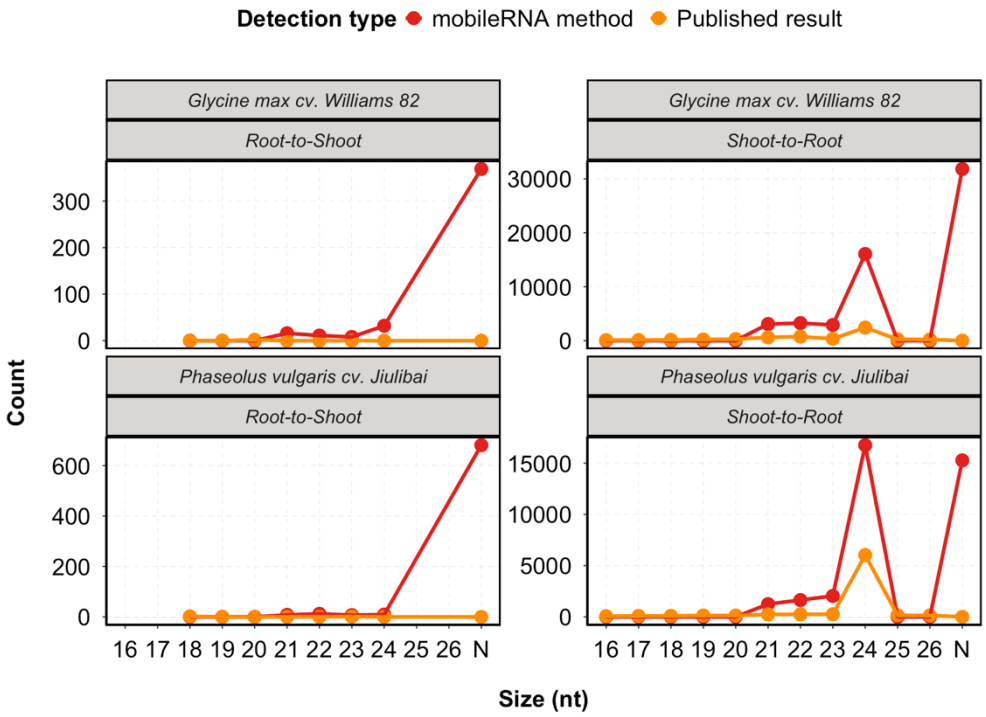


Figure 3.8.Comparison of graft-mobile sRNAs characterised in the published study and using the mobileRNA approach. Here, the bean datasets were re-analysed using the mobileRNA pipeline and the results compared to the published results from Li, Wang et al. (2021). Distribution of mobile small RNAs (sRNAs) in nucleotide (nt) length isolated in the bean dataset using the mobileRNA approach. For the comparison, the parameters for the mobileRNA approach were adjusted to select sRNAs in the same sizes ranges as those in the published results.

Following on, we investigated the possible functional implications of the soybean shoot-to-root sRNA clusters including the annotation of the sRNA-producing loci and target prediction analysis. Only the soybean shoot-to-root sRNA were investigated as this was the largest population and the only population with commonalities to the published results. The annotation of the sRNA-producing loci was investigated, and, of the 57,156 sRNA clusters, a high proportion were generated within exonic regions. Others were demonstrated to be synthesised from within promoters, pseudogenes and known long non-coding RNA regions (Figure 3.9). Specifically, there were 17,654 that were associated with a gene and/or its promoter of 1 kb (+/1). The GO enrichment

analysis identified 190 statistically significantly enriched terms, and of these 75 were for Biological Processes, and the top 10 were selected based on the enrichment false discovery rate (FDR). Genes which produced sRNA clusters were related to translation, signal transduction, intracellular protein transport and mRNA splicing. The publication from which the data stems did not state the genomic origin of sRNA clusters (Li, Wang et al. 2021).

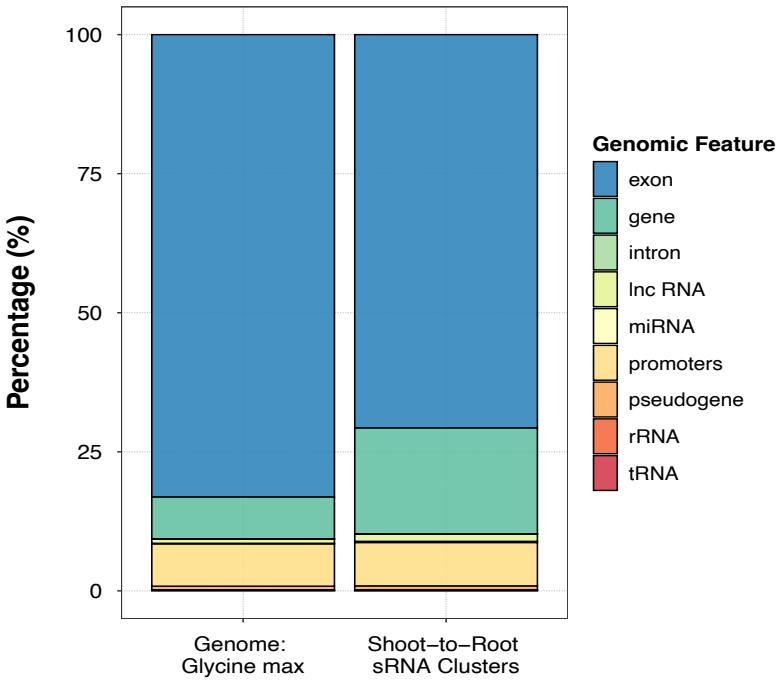


Figure 3.9. Distribution of shoot-to-root soybean mobile sRNAs detected by mobileRNA across genomic features. The bean datasets from Li, Wang et al. (2021) was re-analysed using the *mobileRNA* pipeline. The distribution of genomic features within the *Glycine max* genome and the distribution of features which overlap with the shoot-to-root mobile sRNA clusters produced by the *G.max* scion shown as a proportion.

Plant sRNAs have a key role in the regulation and control of gene expression through several pathways. Target prediction analysis can be utilised to identify target mRNA transcripts of the sRNAs of interest. The tool, psRNATarget, was employed to identify putative target transcripts in the destination tissue (*P. vulgaris*) of the graft-mobile shoot-to-root soybean (Dai, Zhuang et al. 2018). In

total, 36,413 valid sRNA sequences were extracted from the total population of 57,156 sRNAs. Based on the 2017 schema, the top three targets were identified for each sRNA, which generated 30,413 possible targets – many of which were targeted in multiple location by the same or multiple sRNAs. GO enrichment analysis of the target transcripts was undertaken to identify functional enrichments (Figure 3.10). The target transcripts were enriched in biological processes, the top three including phosphorelay signal transduction systems, carbohydrate metabolic processes and DNA repair (Figure 3.10). The publication from which the data stems utilised degradome-seq data to identify putative targets. Although a few specific targets are named in the results, the complete database is not available, hence, we are unable to compare functional results (Li, Wang et al. 2021). Similarly, the paper has no mention of a related grafting induced phenotype.

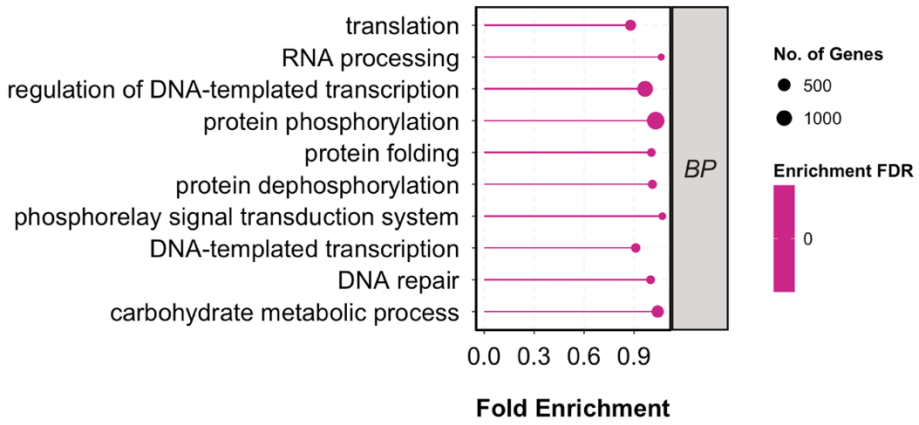


Figure 3.10. Enrichment analysis of predicted gene targets associated with shoot-to-root Soybean mobile sRNAs in bean dataset from Li, Wang et al. (2021). For the putative graft-mobile shoot-to-root sRNA clusters produced by the *G. max* genome, the consensus sRNA sequence was extracted and utilised to predicted mRNA targets in the *P. vulgaris* genome for mobile sRNAs. Target prediction analysis was undertaken using psRNATarget (No. top targets = 3, Expectation = 5) against the *P. vulgaris* 422 V2.1 genome from JGI genomic project (Phytozome 13) (see https://phytozome-next.jgi.doe.gov/info/Pvulgaris_v2_1) (Goodstein, Shu et al. 2012). GO term analysis was undertaken on targets using in house scripts. There were statistically significant enrichments in Biological Process (BP), Cellular Component (CC), and Molecular Function (MF) with a total of 75 BP, 49 CC and 66 MF enriched GO terms. The top 10 BP GO terms were selected to be plotted, based on the Enrichment False Discovery Rate (FDR).

3.3.3 Analysis of mRNA mobility in the Brassica dataset

mobileRNA was used to re-analyse mRNA sequencing data from a published study that previously aimed to identify root-to-shoot mobile mRNA transcripts in *N.benthamiana* and *A.thaliana* grafts (Figure 3.11). The dataset includes two *N. benthamiana* self-graft controls and two heterograft replicates which comprised of a *N. benthamiana* scion and an *A. thaliana* rootstock (Notaguchi, Higashiyama et al. 2015). This grafting study aimed to identify root-to-shoot mobile mRNA transcripts produce by the *A. thaliana* genome.

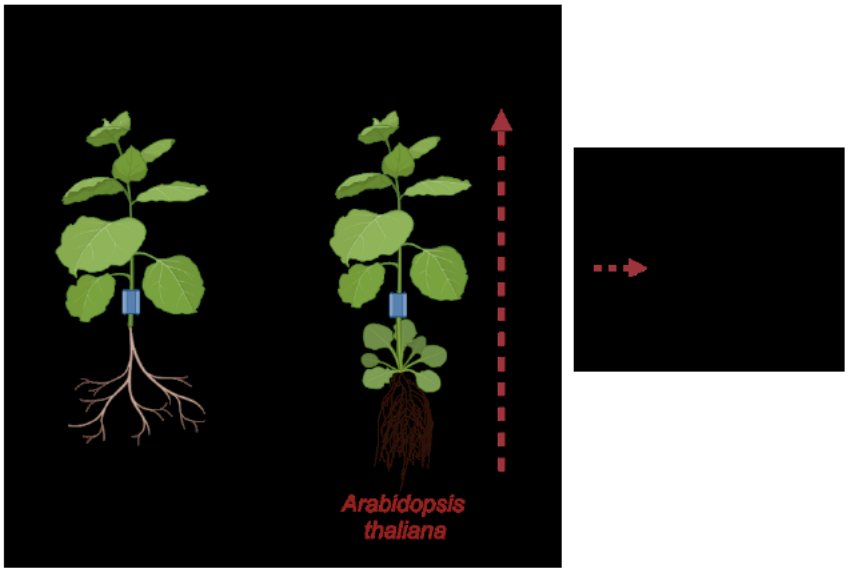


Figure 3.11. Experimental design of the data utilised from the brassica study. The brassica dataset from Notaguchi, Higashiyama et al. (2015) compared the scions of *Nicotiana benthamiana* self-grafted plants to *N. benthamiana* scions grafted onto *Arabidopsis thaliana* to identify root-to-shoot mobile messenger RNAs. Created using BioRender.com.

In the original analysis, the method detected 138 mobile transcripts and validated 17 transcripts from a random pool of 70 (Notaguchi, Higashiyama et al. 2015). This represents a rate of 24% of successfully identified putative mobile transcripts. The mobile transcripts included factors related to signalling pathways including transcription, receptor kinases, G proteins, and

stress/defence. In addition to transcript for cellular homeostasis and organelle-localised transcripts. GO term enrichment analysis with ShinyGO (Ge, Jung et al. 2020) of the 138 mobile mRNA transcripts identified the top 10 pathways related to biological processes (FDR < 0.05) included fluid transport, water transport, and purine nucleoside triphosphate metabolic processes (Figure 3.12). There was a strong enrichment in transcripts with a cellular component connection to the photosynthetic membrane, thylakoid and ribosome. The study did not identified enrichments in any specific motifs or structural features (Notaguchi, Higashiyama et al. 2015). The mobile transcripts were compared to a previous study by Deeken et al., 2008 that validated the presence of *Arabidopsis* transcripts in the phloem. Of the 138 transcripts, 56 overlapped with the 2,417 transcripts described by Deeken et al., 2008 (Deeken, Ache et al. 2008, Notaguchi, Higashiyama et al. 2015).

In comparison, *mobileRNA* identified the expression of 43,634 *N. benthamiana* transcripts in the scion, and 60 (0.14%) putative mobile transcripts produced by the *Arabidopsis* rootstock (Figure 3.12.A). GO term enrichment analysis found that the 60 mobile transcripts were enriched in processes relating to cellular respiration and specifically in NADH pathways for ATP synthesis and electron chain transport (Figure 3.12.A). Of these 60 mobile transcripts, 35 were listed in the Notaguchi, Higashiyama et al. (2015) study whereby the study attempted to validate 16 of the 35 and confirmed the movement of four transcripts (Figure 5C). This can be represented as 25%, a +1% improvement in comparison to the original analysis.

It was expected that a mobile transcript would contribute most of its coding sequence, hence, the read coverage across mobile transcripts was calculated for the 60 mobile mRNAs detected by *mobileRNA*. Of which, 39 transcripts (65%) had reads covering the entirety of the transcript, however, none of these 39 mobile transcripts were in either of the named studies. Structural features of mRNA transcripts have been associated with mobility including TLSs and cytosine methylation, yet the full extent of these features and others are yet to be fully characterised (Zhang, Sun et al. 2009, Zhang, Thieme et al. 2016, Xu, Szekely et al. 2024). The presence of TLS motifs in the 60 mobile transcripts detected by mobileRNA were analysed using RNAmotif (Macke, Ecker et al. 2001). There were four mobile transcripts (6.7%) that contained TLS motifs. These four transcripts were identified in the previous analysis, but not validated.

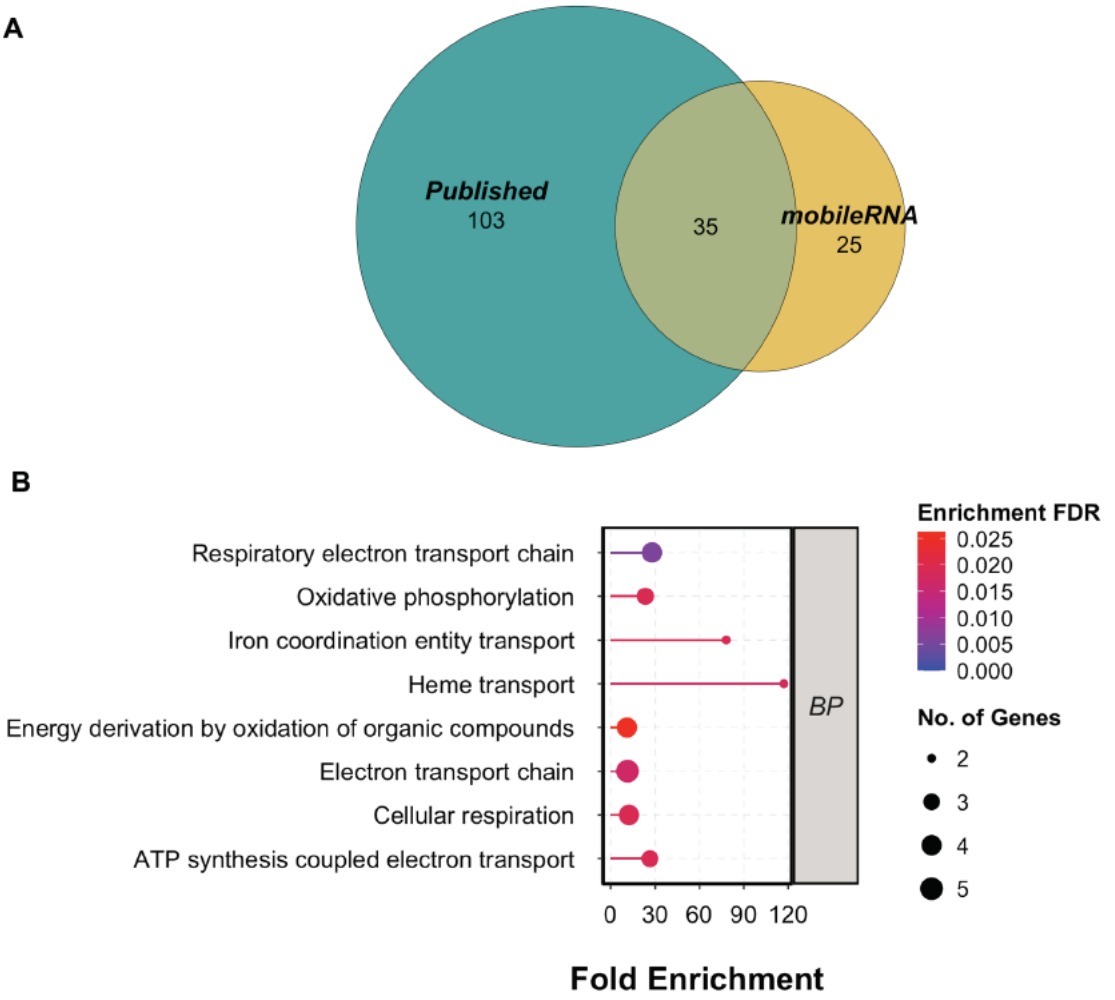


Figure 3.12. Comparison of root-to-shoot mobile mRNAs characterised in the re-analysis of published data using the mobileRNA method. The dataset from Notaguchi, Higashiyama et al. (2015) was re-analysed using the *mobileRNA* pipeline and the results were compared to the published results. A) Venn diagram representing the number of mRNAs transcripts characterised in the published study and the overlap with the total root-to-shoot mobile mRNAs detected by *mobileRNA*. B) Gene Ontology (GO) enrichment analysis of graft-mobile transcripts detected by *mobileRNA* using ShinyGO (Ge, Jung et al. 2020).

Similarly to the presence of TLS motifs, the proximity of tRNA genes has been associated with mobility (Zhang, Sun et al. 2009, Zhang, Thieme et al. 2016). In the *Arabidopsis* genome, we identified tRNA genes with ARAGON and assessed whether the candidate transcripts where within a 1 kb upstream/downstream region of tRNA genes. This analysis revealed that none of the candiates were in 1 kb proximity to tRNA genes. Lastly, we assessed whether mobile transcripts

were tRNA genes. Across the mobile transcripts identified by Notaguchi et al. 2015 only one (AT1G07940) contained a tRNA-like motif, whereas no transcripts identified by *mobileRNA* contained such motifs.

The detection of mobile RNAs in heterografts comprised of the *A. thaliana* and *N. benthamiana* has been assumed to be a highly effective method since the genomes are expected to share less homology than other combinations as these two genotypes are from different families (where most grafting combinations are between species of the same family) (Notaguchi, Higashiyama et al. 2015). As we expected, the *mobileRNA* approach detected fewer mobile mRNAs than previously described. The *mobileRNA* approach is sensitive to the similarity of the genomes comprised within the merged reference which is the largest factor determining whether the number of mobile molecules has been correctly estimated. To access the similarity of the *A. thaliana* and *N. benthamiana*, we utilised genome mappability scoring to access the uniqueness of all annotated coding regions and, specifically the mappability of the detect mobile molecules (Figure 3.13). The *A. thaliana* genome has been well-characterised and gene annotations have been routinely improved since *A. thaliana* is employed as the universal model for plant research. To date, the diploid *A. thaliana* genome (NCBI Taxonomy ID 3702) has been described to contain five chromosomes with an estimated genome size of around 135 Mb, containing approximately 27,655 coding genes and 54,013 gene transcripts (Lamesch, Berardini et al. 2012). In comparison, the *N. benthamiana* genome remains a draft (V2.6.1) containing 19 pseudomolecules and 17,620 small scaffolds, an estimated genome size of 3,030 Mb and 61,328 gene models (Bombarely, Rosli et al. 2012). This is roughly 22 times larger than the *A. thaliana* genome. Based on the genome mappability

analysis we can deduce that the *A. thaliana* genome contains a greater proportion of unique coding regions in comparison to the *N. benthamiana* genome. Furthermore, the findings support existing descriptions of the *N. benthamiana* genome that state that it contains a significant proportion of repetitive sequences (Bombarely, Rosli et al. 2012). When the *A. thaliana* and *N. benthamiana* genomes are merged, around 66% of the genomic sequences are unique with a mappability score above 0.5 (Figure 3.13.A). These results support our assumptions prior to analysis and demonstrate that *mobileRNA* will effectively distinguish a reflective population of mobile RNAs in the biological system.

Lastly, we plotted the distribution of detected mobile RNA transcripts characterised in the published results and the re-analysis based on their genome mappability scores. This analysis aimed to access the types of transcripts that each method was able to capture. Here, the *mobileRNA* approach characterised a more diverse population of transcripts (i.e. including transcripts with a low mappability) than the published results (Figure 3.13.B). This result was surprising to observe since the *mobileRNA* approach discards sequencing reads which mapped to multiple locations in the genome (i.e. repetitive sequences), and hence, we do not expect to distinguish repetitive regions either within an individual or merged genome. Therefore, we hypothesize that these transcripts were identifiable by the presence of short sequencing reads covering the regions containing SNPs within the repetitive transcripts.

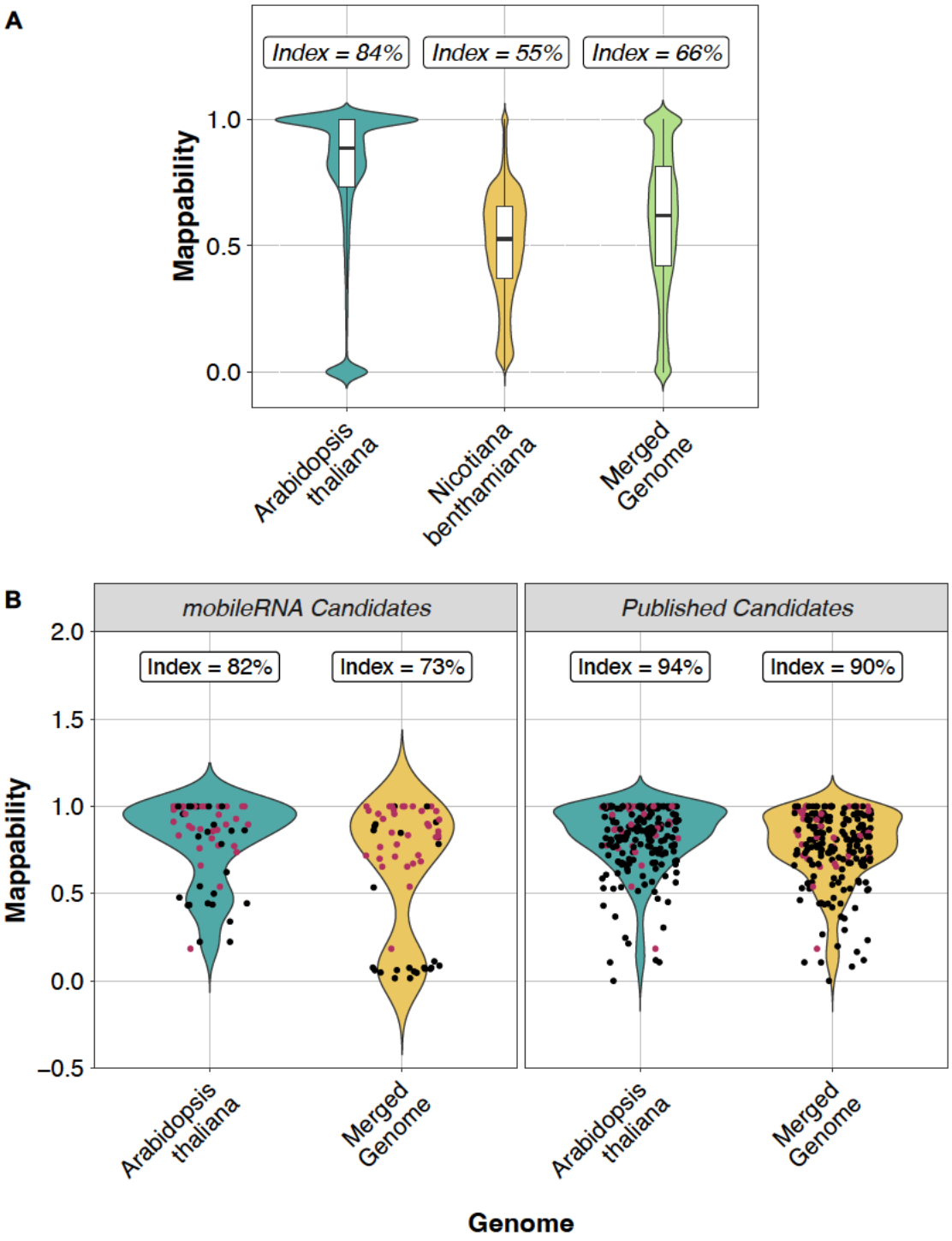


Figure 3.13. Comparisons of genome mappability of transcripts in genomes used in the re-analysis of Brassica dataset. Genome mappability is a measure of unique and repetitive regions within the genome, whereby unique regions have a value of 1 and repetitive regions have a value of 0. A) The mappability was calculated across the whole genome, and the distribution across coding regions is illustrated in the plot for the *Arabidopsis thaliana* genome, *Nicotiana benthamiana* genome and merged genome. B) Genome mappability of candidate mobile transcripts in the *Arabidopsis thaliana* genome and the merged genome. Candidate transcripts include the *mobileRNA* mobile transcripts (n=60) and the published mobile transcripts (n=138). Maroon points represent transcripts which were commonly identified, and black points represent all other transcripts.

3.3.4 Analysis of mRNA mobility in the Solanaceous dataset

mobileRNA was used to re-analyse a second published mRNA sequencing data. This dataset was taken from a study that utilised the grafting between *N. benthamiana* as the scion and tomato as the rootstock to identify shoot-to-root long distance transport of mobile mRNAs (Xia, Zheng et al. 2018) (Figure 3.14.A). Note that the study did not include self-graft controls and they did not observed any associated grafting traits (Xia, Zheng et al. 2018). In the study they identified 183 mobile *N. benthamiana* transcripts in the tomato rootstock with an enriched in biological functions related translation, transport and biosynthetic processes. They identified 14 RNAs (7.7%) contained TLS motifs (Guan, Yan et al. 2016).

In our re-analysis, we identified 2,524 mobile *N. benthamiana* mRNAs with 1,273 mRNA consistent across all three heterografted replicates (Figure 3.14.B). These transcripts were functionally enriched in calcium transmembrane transport, ATP metabolic processes and translational processes.

We identified a total of 41 (1.6%) mobile mRNAs which were previously characterised in the original study, and of these, 3 (7.3%) were previously defined to contain TLS motifs. Following this, we undertook an independent analysis to identified TLS motifs in the 2,524 mobile candidates using RNAmotif with default settings (Macke, Ecker et al. 2001). This analysis revealed 332 (13%) mRNA transcripts contained TLS motifs, and none of these transcripts were detected as mobile in the original study. This is almost double the proportion of candidates with TLS motifs than the previous results. To rule out the possibility that the mobile transcripts could be tRNA genes, we utilised ARAGON. This analysis identified tRNA genes associated with two mobile

mRNA transcripts (Niben101Scf00581g01016.1, Niben101Scf02525g01006.1) – these two transcripts were not detected in the original analysis. In the *N. benthamiana* genome, we identified tRNA genes with ARAGON and assessed whether the candidate transcripts where within a 1 kb upstream/downstream region of tRNA genes. This analysis revealed that none of the candiates were in 1 kb proximity to tRNA genes.

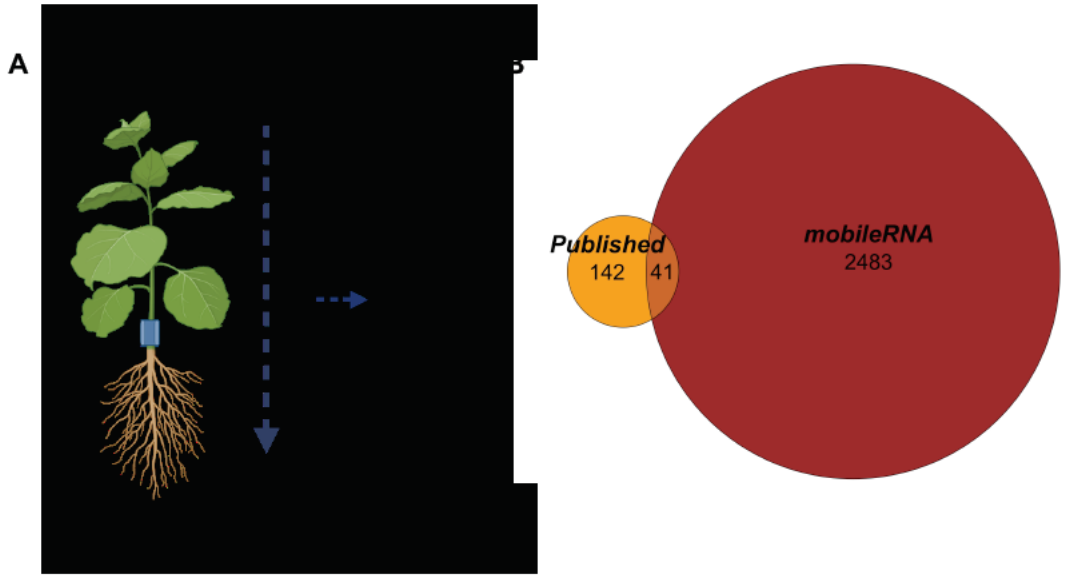


Figure 3.14.The re-analysis of data from the solanaceous study. The solanaceous datasets from Xia, Zheng et al. (2018) utilised heterografts with a *Nicotiana benthamiana* scion and a tomato (*Solanum lycopersicum*) rootstock to identify shoot-to-root mobile messenger RNAs. Created using BioRender.com.

Mobile transcripts are expected to have a coverage across the complete mRNA sequence (>70%), indeed we observed a consensus of 347 (13.7%) transcripts that met this expectation where 14 were those previously detected in the published results.

The *N. benthamiana* and *S. lycopersicum* genomes are renown to contains high regions of repetitiveness (Bombarely, Rosli et al. 2012, Hosmani, Flores-

Gonzalez et al. 2019). Here, we calculated the uniqueness (and thus receptiveness) of annotated coding regions in the *N. benthamiana* and *S. lycopersicum* genomes (Figure 3.15.A). This analysis demonstrated that 77% of the coding regions within the *S. lycopersicum* genome contained very few repetitive sequences, whereas in the *N. benthamiana* this proportion was around 58.9% in coding regions. To estimate the effect of combining these two genomes into a merged genome, the same analysis was repeated and determined that 50.8% of coding regions were unique. These two genomes are both from the *Solanaceae* family, and hence it is likely that the mappability score dropped to a greater degree than the merged genome of *N. benthamiana* and *A. thaliana* is due to the presence of conserved sequences within the family (Figure 3.13.A, 2.15A). Finally, based on these results we assessed the mappability scores of mobile mRNA transcripts detected in the published analyses in comparison to those detected by *mobileRNA* in the re-analysis (Figure 3.15.B). As we expected, the *mobileRNA* approach characterised mobile transcripts with less repetitive regions than the transcripts identified in the previous analysis. Interestingly, these transcripts reduced their mappability by around 50% in the merged genome in comparison to *N. benthamiana* (Figure 3.15.B). This suggests that there were sufficient uniquely aligning reads covering the transcript to report its presence. In comparison, only 8% of the transcripts located in the previous analysis contained unique regions in the *N. benthamiana* genome, which could be an indication that some of the transcripts are indeed noise (Figure 3.15.B).

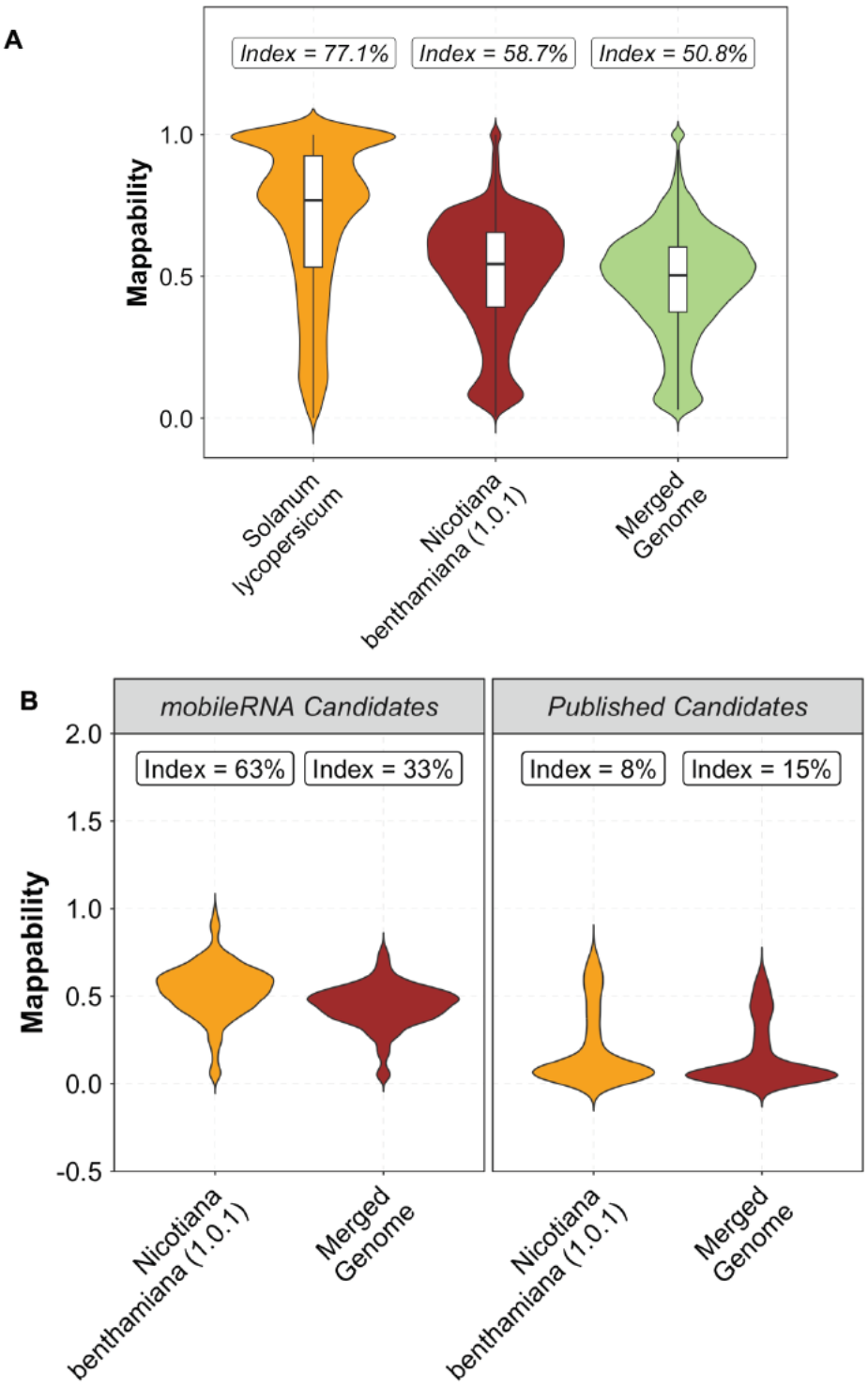


Figure 3.15. Comparisons of genome mappability of transcripts in genomes used in the re-analysis of *solanaceous* dataset. Genome mappability is a measure of unique and repetitive regions within the genome, whereby unique regions have a value of 1 and repetitive regions have a value of 0. A) The mappability was calculated across the whole genome, and the distribution across coding regions is illustrated in the plot for the *Solanum lycopersicum* (version 4) genome, *Nicotiana benthamiana* genome (version 1.0.1) and merged genome. B) Genome mappability of candidate mobile transcripts in the *Nicotiana benthamiana* genome and the merged genome. Candidate transcripts include the *mobileRNA* mobile transcripts (n=2,524) and the published mobile transcripts (n=183).

3.3.5 Comparison between datasets

Many heterografting datasets are now available that can be utilised for data mining. These resources offer an opportunity to identify common mobile RNAs across species or features associated with RNA mobility. These insights would provide a broader picture of RNA signalling mechanisms and enhance our confidence in engineering plants with favourable traits. Unfortunately, recent data-mining efforts have fallen short (Paajanen, Tomkins et al. 2024). This is largely due to technical issues, making it challenging to identify features that are associated with mobility (Paajanen, Tomkins et al. 2024). Here, we re-analysed four previously published datasets from interspecific grafting experiments. Here, we summarise the results from across the different species and identify commonalities such as structural features, origin or function among mobile sRNA/mRNAs.

Between the two mRNA datasets, we compared the detected mobile RNAs. Based on sequence homology using BLAST, we found no homologous mobile transcripts between the datasets. Moreover, there was little overlap between the functional enrichments in mobile transcripts detected between the two datasets. This is unsurprising considering that each dataset is investigating a different direction of movement. Lastly, we compared structural features including motifs, and GC content. We did not observe consistency of TLS motifs or similarly an enrichment in TLS motifs within mobile mRNAs between datasets. Even so, using enrichment sequence motif analysis with MEME suite (Bailey, Johnson et al. 2015) we identified similar motifs between the two datasets. Both datasets contained an enriched motif that had a close similarity to a BBR/BPC transcription factor family motif. Overall, the enriched motifs although different

show similar sequences including “TCTC” and “GAAGAA” (Supplementary Figure 3.1, Supplementary Figure 3.2). To access GC content, we calculated the GC-content percentage for each transcript. On average, we found that the transcripts from both datasets had a GC content of 41% (Brassica, Min = 32.57%, Mean = 41.38%, Max = 48.14%; Solanaceous, Min = 31.53%, Mean = 41.93%, Max = 59.18%). Considering that the gene GC-content in *Arabidopsis* ranges from 40–55% (Wang and Hickey 2007) and in *N. benthamiana* it ranges from 37.22% to 51.25% (Bombarely, Rosli et al. 2012), these transcripts are on the lower end of the GC-content spectrum.

In terms of mobile sRNAs, we detected root-to-shoot mobile molecules in grapevine grafts, as well as shoot-to-root soybean mobile molecules in bean grafts. Between the two datasets, there were no mobile sRNAs with the same RNA sequence, however, some sequences did show very close homology (+91%). Here, we were interested to investigate whether there was a consensus in the 5′-nucleotide terminal species across the mobile sRNAs since this features has been linked with the differential consumption of sRNAs during cell-to-cell movement (Devers, Brosnan et al. 2020). In the grapevine dataset, there was a larger proportion of mobile sRNAs (in both directions) with 5′-uracil (U) bases followed by 5′-adenine (A). Similar proportions were observed for the shoot-to-root soybean mobile sRNAs, however there were marginally more mobile sRNAs with 5′-adenine (A) than 5′-uracil (U). However, using MEME suite we were unable to identify any statistically enriched motifs within the mobile sRNAs for each dataset. Based on target prediction analysis, there was an enrichment in gene targets in both datasets involved in protein modification, specifically protein phosphorylation.

3.4 Conclusion

In plants, both mRNAs and sRNAs can act as long-distance signalling molecules. Determining RNAs which are moving, the molecular mechanisms permitting their mobility, and their destination is key to understanding plant systemic signalling pathways that control physiological processes. The movement of RNAs between distant tissues has been identified using genomic data and experimentally validated using techniques such as qPCR, Northern blotting, transgenics and RT-PCR of precursors (Yang, Sanchez et al. 2020, Kehr, Morris et al. 2022, Martinho and Lopez-Gomollon 2023). That being said, most RNA studies validate only a handful of the mobile RNAs, hence we cannot assume the rest are true mobile candidates (Notaguchi, Higashiyama et al. 2015, Kehr, Morris et al. 2022). Across these studies there is a lack of consistency in both experimental design and bioinformatic pipelines which begs the questions whether the experimental datasets contain high levels of uncharacterised data noise. The negative effects of unstandardised bioinformatic methods for mobile RNA identification have been reported in a recent study that looked to generated a database from published results of mobile mRNAs to support predictive modelling efforts (Paajanen, Tomkins et al. 2024). To combat this challenge, *mobileRNA* was developed to address these concerns.

Comparison of results to published findings

In this analysis, we re-analysed previous RNA-seq and sRNA-seq samples from inter-specific heterografting datasets using the *mobileRNA* approach. Our analysis highlights that although previous methods were thought to over-estimate the number of mobile RNAs the results highlight that in ~50% of our

cases they under-estimated their presence. Similarly to over-estimating, this has a significant effect on the outcomes, skewing our interpretation of the biological roles of mobile molecules. In datasets where their scion and rootstock genomes demonstrated high homology, such as in the grapevine dataset, we expect that the previous results would overestimate the number of mobile RNAs. In contrast, where their scion and rootstocks genomes where more unique, we expect that the previous methods might under-estimate the presence of mobile molecules. For instance, in the bean dataset the common bean and soybean genomes maintain 50% unique sequences between them. The method utilised in the previous analysis of the dataset aligned reads uniquely to each genome and then selected reads which were unique to only one. However, this technique is expected to be more stringent that the *mobileRNA* methods, since depending on the user-defined parameters, the alignment algorithm may force reads to align to a given genome, even if it is not strongly suited to that location.

In comparison to the previous methods, the results produced by *mobileRNA* differ. The interpretation of these findings remains a challenge for datasets which do not have associated phenotypical traits. This limitation underscores a wider issue whereby there lacks studies that investigate the relationship between graft-mobile RNAs and grafting-induced traits. However, based on the *mobileRNA* results we confer that the approach captures a broader variety of mobile mRNA transcripts, specifically those which contain both unique and repetitive sequences. In Chapter 2, we highlight that previous methods similarly discard multi-mapped reads and can struggle to capture the expression of transcripts with a low read depth. This attribute could explain

why transcripts containing repetitive sequences could be under-estimated within the detection of mobile mRNA molecules.

Comparison between datasets

Given the sessile nature of plants, they must coordinate complex responses to both developmental and environmental cues. RNAs, among others, are key signalling molecules that have been shown to have a non-cell autonomous role. Their role has been described in various processes, from the activation of defences against pathogens to floral development (Jorgensen, Atkinson et al. 1998, Waterhouse, Wang et al. 2001). So far, sRNA and mRNA biosynthesis pathways and their functional role have been well-described, however, the transport mechanisms that enable RNA signalling between cells and across tissues is still under debate. This debate arose from initial discoveries of RNA molecules within the phloem sap, which begged the question, how do plants control which RNAs can move between cells and over long distances (Sasaki, Chino et al. 1998, Xoconostle-Cázares, Xiang et al. 1999). In our analysis, the lack of consistent structural features between the mobile RNAs could have implications on our understanding of the evolution of mechanisms controlling RNA movement in plants. For instance, these results might suggest evolutionary plasticity whereby the mechanisms are highly adaptable and diverse across plant species – thus making it challenging to observe conserved features. Alternatively, the lack of conserved structural features could indicate that mobilisation of RNA signals is regulated at different organisation levels, including tissue-specific or response-specific (Lucas, Yoo et al. 2001). This could possibly encompass the idea that different RNAs might achieve mobility through various pathways. This is supported by current evidence which

indicates that RNA signalling utilises both passive and non-passive mechanism, as to assume only passive movement is to assume that an RNA signal does not has a specific target or role (Heeney and Frank 2023). Considering the vast number of processes RNA signalling is involved in, it thought that these RNAs have evolved specific features that are determinates of mobility and action. This includes structural features such as TLS motifs and "zip-code" motifs (Jeffery, Tomlinson et al. 1983, Xoconostle-Cázares, Xiang et al. 1999, Zhang, Thieme et al. 2016, Yang, Perrera et al. 2019). Thus, different RNAs could utilise several different mechanisms to achieve systemic mobilisation. This lends space for theories which support the idea of other factors, such as binding proteins, localised signals or epigenetic or chemical modifications that may influence mobility without requiring specific structural features as a prerequisite for mobility (Ham, Brandom et al. 2009, Ham, Li et al. 2014, Duan, Zhang et al. 2016, Yang, Perrera et al. 2019, Devers, Brosnan et al. 2020, Fan, Zhang et al. 2022).

Interestingly, among the predicted targets of the mobile sRNAs identified in the grapevine and bean datasets they commonly included genes involved in protein phosphorylation. Protein phosphorylation plays a key role in both the activation and inhibition of other proteins. For example, the BRAHMA (BRM), an ATPase subunit of the Switch/Sucrose Non-Fermentable (SWI/SNF) complex, controls the histone modification levels of target genes, thus influencing their expression (Gao, Lv et al. 2024). The transcription factor, MYB41, is targeted by BRM and under normal conditions it is inactive. However, its expression is activated under osmotic stress when BRM undergoes phosphorylation. This triggers physiological changes including enhanced

suberin deposition (Gao, Lv et al. 2024). Therefore, alterations to the regulation of protein phosphorylation could drive notable physiological changes, such as stress-responses.

Our findings support an overarching concern in the field. Researchers have tried to establish a database of mobile RNAs across species (Paajanen, Tomkins et al. 2024). This database could then be used to derive further understanding of the transport mechanisms, such as specific structural features, and develop predictive models. However, although promising, it's becoming increasingly clear that previous datasets contain an exuberant level of noise which makes it nearly impossible to mine meaningful information (Paajanen, Tomkins et al. 2024). Ultimately, until the challenges associated with detecting mobile RNAs with high confidence and reductions in bias against repetitive sequences are resolved, it is challenging to elucidate conserved structural features that might act as determinants of mobility.

Final points

This work, in line with Chapter 2, illustrates the complexities associated with detecting mobile RNAs using genomic analyses. The results beg the question how much we truly understand of mobile RNA signalling, RNA transport and RNA function, and highlights the need for further research in this area.

4. Supplementary figures and tables

Supplementary Table 3.1. Summary statistics of replicates from the grapevine sRNAseq dataset (Rubio, Stammitti et al. 2022) when processed using the mobileRNA method. The mapped reads refer to unique mappers. Both unmapped and suppressed multimapped reads were discard from analysis.

Data set	Status	Scion/Rootstock	Replicate	Raw reads	Clean reads	Mapped to Vitis vinifera	Mapped to Vitis riparia	Unmapped	Suppresed multimappers
Grapevine	Selfgraft	*Vitis vinifera - Vitis vinifera*	CSCSS_1	22,551,964	17,592,001	407,923	140,972	1,929,043	15,114,063
		Vitis vinifera - Vitis vinifera	CSCSS_2	23,629,375	18,341,152	408,420	161,736	2,193,225	15,577,771
		Vitis vinifera - Vitis vinifera	CSCSS_3	22,010,791	17,560,990	454,809	166,709	2,119,322	14,820,150
		Vitis vinifera - Vitis vinifera	CSCSR_1	21,708,099	18,379,337	420,436	232,356	5,458,966	12,267,579
		Vitis vinifera - Vitis vinifera	CSCSR_2	25,590,164	21,493,210	469,900	290,146	4,462,478	16,270,686
		Vitis vinifera - Vitis vinifera	CSCSR_3	19,027,410	16,055,772	366,346	234,888	4,021,194	11,433,344
	Heterograft	*Vitis vinifera - Vitis riparia*	CSRGMS_1	21,338,797	17,275,868	481,412	155,031	2,167,006	14,472,419
		Vitis vinifera - Vitis riparia	CSRGMS_2	30,912,831	25,851,073	657,247	200,130	2,832,954	22,160,742
		Vitis vinifera - Vitis riparia	CSRGMS_3	24,519,380	20,047,547	471,263	150,880	2,200,252	17,225,152
		Vitis vinifera - Vitis riparia	CSRGMR_1	20,457,486	17,320,751	69,177	708,431	4,471,886	12,071,257
		Vitis vinifera - Vitis riparia	CSRGMR_2	20,056,340	16,938,647	68,972	722,052	4,223,891	11,923,732
		Vitis vinifera - Vitis riparia	CSRGMR_3	23,711,257	19,587,119	74,999	799,063	4,563,675	14,149,382

Supplementary Table 3.2. Summary statistics of replicates from the bean sRNAseq dataset (Li, Wang et al. 2021) when processed using the mobileRNA method. The mapped reads refer to unique mappers. Both unmapped and suppressed multimapped reads were discard from analysis.

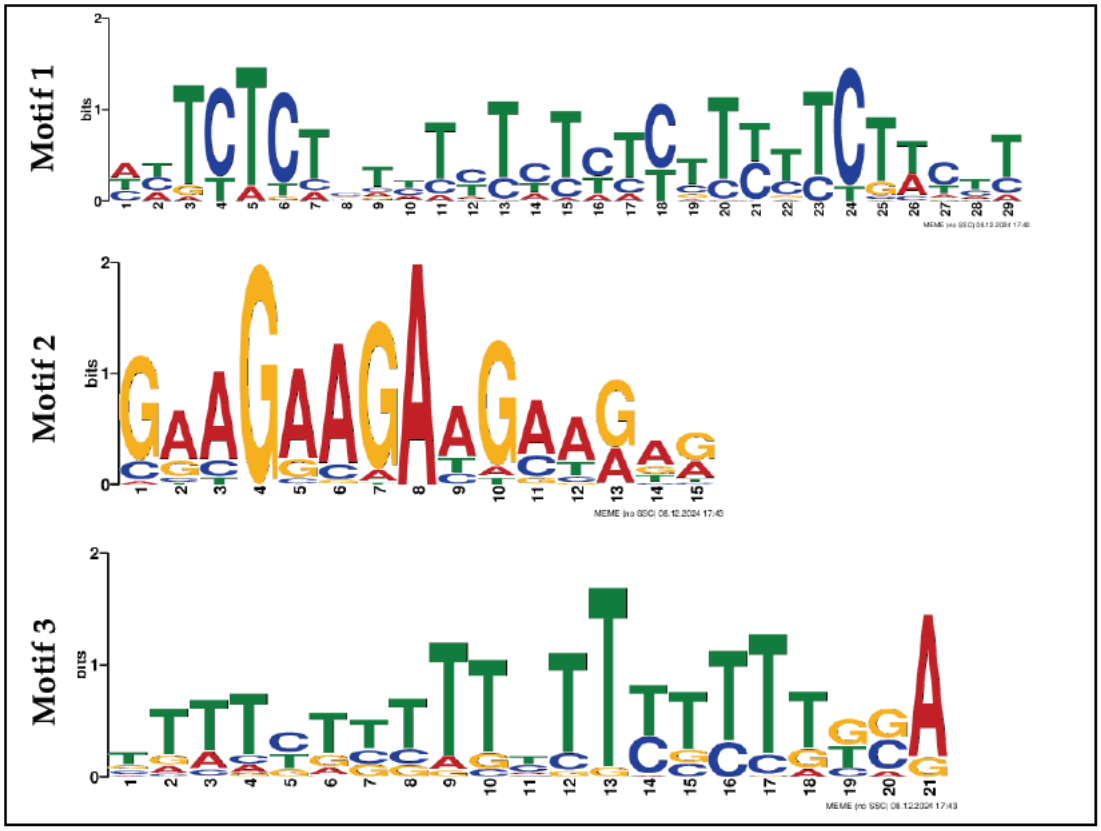
Data set	Status	Scion/Rootstock	Replicate	Raw reads	Clean reads	Mapped to Glycine max	Mapped to Phaseolus vulgaris	Unmapped	Suppresed multimappers
Bean	Selfgraft	*Glycine max* *Glycine max*	SbSb S	11 806 772	11 806 772	1 494 872	38 330	2 174 314	8 099 256
		Phaseolus vulgaris *Phaseolus vulgaris*	CbCb S	13 793 471	13 793 471	281 131	1 026 887	4 436 461	8 048 992
		Glycine max *Glycine max*	SbSb R	12 873 430	12 873 430	968 731	28 170	2 824 870	9 051 659
		Phaseolus vulgaris *Phaseolus vulgaris*	CbCb R	15 013 260	15 013 260	132 124	896 695	8 135 500	5 848 941
	Heterograft	*Phaseolus vulgaris* *Glycine max*	CbSb S	14 718 894	14 718 894	153 248	1 857 861	4 929 159	7 778 626
		Glycine max *Phaseolus vulgaris*	SbCb S	11 255 754	11 255 754	1 077 592	40 587	1 902 707	8 234 868
		Phaseolus vulgaris *Glycine max*	CbSb R	14 390 376	14 390 376	197 167	711 670	908 837	12 572 702
		Glycine max *Phaseolus vulgaris*	SbCb R	12 286 800	12 286 800	793 912	56 142	3 742 496	7 694 250

Supplementary Table 3.3. Distribution of uniquely aligned reads to each genome within the merged reference from the brassica mRNAseq dataset (Notaguchi, Higashiyama et al. 2015) when processed using the mobileRNA method.

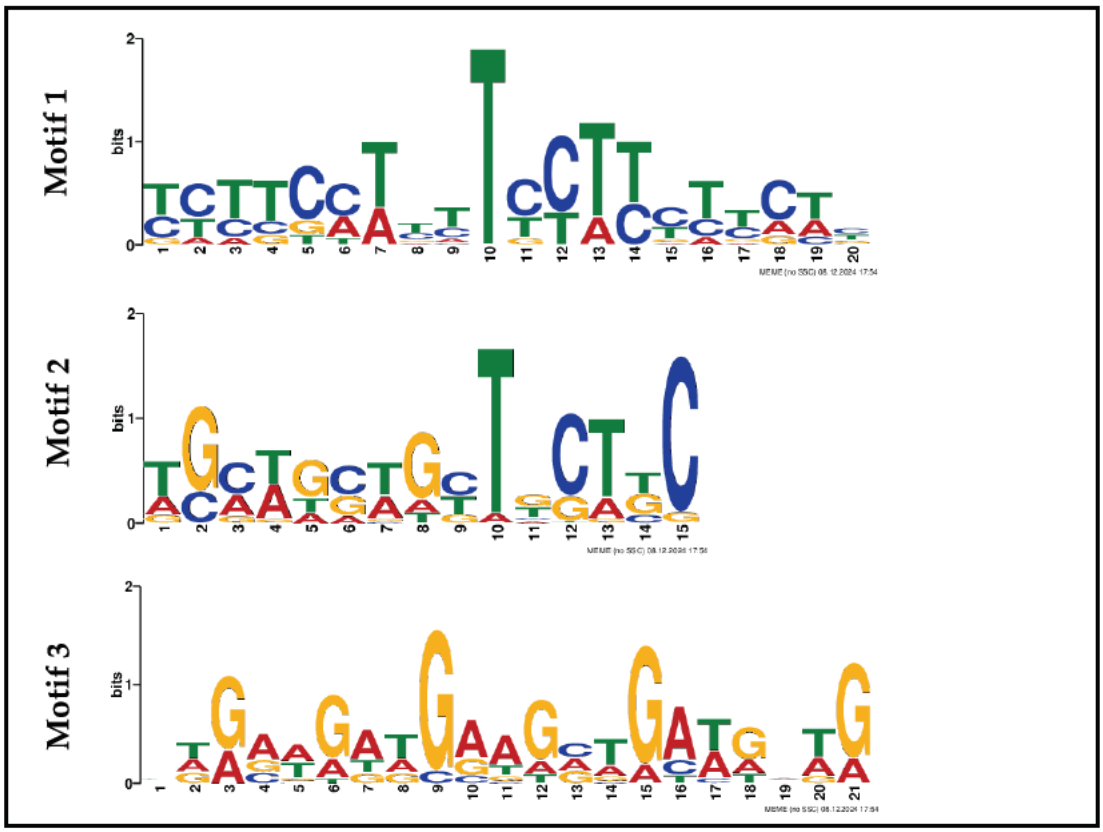
Sample	Uniquely mapped to Solanum lycopersicum	Uniquely mapped to Arabidopsis thaliana
NbAt_heterograft_1	41,134,541	41,134,127
NbAt_heterograft_2	38,687,542	38,686,539
NbNb_control_1	6,298,019	6,297,803
NbNb_control_2	7,994,078	7,993,863

Supplementary Table 3.4. Distribution of uniquely aligned reads to each genome within the merged reference from the solanaceous mRNAseq dataset (Xia, Zheng et al. 2018) when processed using the mobileRNA method.

Sample	Uniquely mapped to Solanum lycopersicum	Uniquely mapped to Nicotiana benthamiana
TobaccoTomato_root_rep1	37,435,051	28,205
TobaccoTomato_root_rep2	42,074,766	10,188
TobaccoTomato_root_rep3	23,257,973	10,670



Supplementary Figure 3.1. De novo motif analysis with MEME suite across mobile transcripts identified in brassica mRNAseq dataset (Notaguchi, Higashiyama et al. 2015). Motif 1 had an E-value of 1.7e-040 and found across 42 sites, Motif 2 had an E-value of 7.5e-028 and found across 54 sites, and Motif 3 had an E-value of 1.2e-014 and found across 56 sites.



Supplementary Figure 3.2. De novo motif analysis with MEME suite across mobile transcripts identified in Solanaceous mRNAseq dataset. Motif 1 had an E-value of 6.1e-013 and found across 2159 sites, Motif 2 had an E-value of 4.2e-005and found across 2270 sites, and Motif 3 had an E-value of 8.7e-009and found across 2131 sites.

CHAPTER 4: INVESTIGATING THE RNA MOBILOME AND ASSOCIATIONS TO GRAFTING VIGOUR IN COMMERCIAL TOMATO LINES

4.1 Introduction

For hundreds of years, horticulturists have used grafting to combine favourable traits from different plants into one. These records go back almost 4,000 years with text references from ancient Chinese and Greek literature, as well as in the Bible. The development of grafting across different civilisations is thought to be driven by inspiration from nature, since grafting occurs naturally (Melnyk and Meyerowitz 2015). Although traditionally used for fruit tree cultivation, herbaceous crops has become hugely popular to introduce desirable traits and improve marketable crop yields (Jeynes-Cupper and Catoni 2023). *Solanaceous* crops are hugely important economic crops. Alone, tomato consumption has increased by around 165% in the last 20 years (Wyngaard and Kissinger 2022), and to meet these demands, around 40% of the global production utilises grafting (Phani, Gowda et al. 2023). Across the USA and the Netherlands all tomatoes grown in soilless conditions are grafted (Phani, Gowda et al. 2023) using tomato hybrid or wild species as rootstocks (Gaion, Braz et al. 2018).

Grafting has been shown to introduce a wide range of traits including resistance to abiotic stress, resistance to soil-borne pathogens, dwarfism and enhanced

crop vigour under non-stress conditions (Foster, McAtee et al. 2017, Gaion, Braz et al. 2018, Maurya, Pandey et al. 2019, Cerruti, Gisbert et al. 2021). Different combinations have been shown to introduce diverse traits to productive scions, and many grafting-induced traits have been associated to the intrinsic properties of the rootstock. For instance, pre-existing drought tolerance in tomato rootstocks (Zhang, Cao et al. 2019) or cold-tolerance in wild-cultivars used as rootstocks (Suchoff, Perkins-Veazie et al. 2018). Hence, commercial companies have invested heavily into breeding programs to develop rootstocks that can induce specific traits to support market demands. To complicate matters, other traits cannot simply be explained by the rootstock's intrinsic properties. The molecular mechanisms driving changes to complex traits such as plant architecture, physiology and vigour (under non-stress conditions) remain largely unclear.

Several studies have demonstrated that a molecular mechanism involved in grafting could be systemic long-distance signalling of RNAs between the roots and shoots (Lewsey, Hardcastle et al. 2016, Heeney and Frank 2023). There has been a particular focus on the role of mobile sRNAs and mRNAs, whereby RNAs have been associated to grafting-induced physiological changes in the scion (Bai, Kasai et al. 2011, Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016, Heeney and Frank 2023). Using grafting as a research tool, they have demonstrated that sRNAs can induced epigenetic variation in the recipient tissues through RNA interference and via RdDM pathway (Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016, Zhang, Lang et al. 2018). These studies demonstrated changes to cytosine methylation, and since, other studies have revealed the association between DNA methylation changes and grafting-

induce phenotypes. For example, genome-wide hypomethylation in the CHH context was associated with increased vigour in the scion in eggplant grafted on commercial tomato hybrid rootstocks (Cerruti, Gisbert et al. 2021). Whereas gray leaf spot resistance is introduced to tomato with a pepper rootstock was associated with hypermethylation in the CHG and CHH contexts in the scion (Liu, Jia et al. 2024).

Despite such progress, genome-wide identification of mobile sRNA and mRNA molecules and their possible association with grafting-induced traits has not been fully characterised. Here, we analysed the transcriptional changes and the RNA mobilomes of tomato scions from intra-specific grafting combinations using two commercial hybrid rootstock lines provided by ENZA ZADEN, referred to as RS-1 and RS-2. Grafted tomato scions onto RS-1 illustrated improved fruit quality while maintaining yields but diminished fruit weight was also observed. By integrated RNA-seq and sRNA-seq from scion leaf tissues from heterografted and self-grafted tomatoes we have illustrated the complex interactions that occur at the molecular levels between the shoots and roots.

4.2 Materials and methods

Plant materials and grafting procedure

The study utilised commercial indeterminate tomato (*Solanum lycopersicum)* lines including one scion line and two tomato hybrid rootstock lines supplied by ENZA ZADEN. The rootstock lines are referred to as Rootstock 1 (RS-1) and Rootstock-2 (RS-2). As a positive control, a self-graft of the scion was used while

each rootstock was additionally self-grafted as negative controls. The RS-1 line was known to introduce improved crop vigour showed as a greater fruit production and fruits with a greater average weight. The RS-2 line is not associated to any improvements in vigour, and instead presents a strong resistance against the fungal infection caused by *pyrenocheata lycopersici* compared to the other rootstock lines. Consequently, the RS-2 line contributes more generative growth to the scion resulting in reduced fruit yields and smaller fruits.

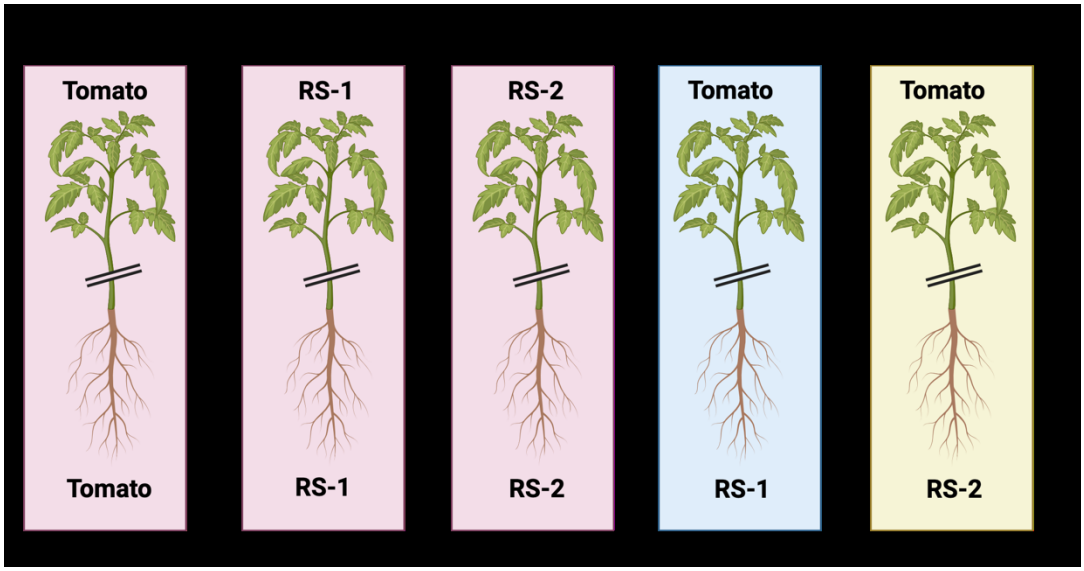


Figure 4.1. Schematic of grafting combinations. Three self-graft and two heterograft combinations were utilised in the analysis. The three self-grafts represent self-grafts between each of the three lines. In the heterograft combinations, tomato was utilised as a scion and the two rootstock lines (RS-1, RS-2) were used as rootstocks. Created using BioRender.com.

Grafting was performed two weeks after germination of seedlings with the use of the horizontal cut method (Pardo-Alonso, Carreño-Ortega et al. 2018). For each grafting combination, there were four bio-replicates. Grafted individuals were placed into a shaded polytunnel for approximately seven days. After a further three days in high-humidity greenhouse conditions, grafted plants were

transferred onto starter blocks and moved into a new greenhouse (19-28° C, 53-87 $g.m^{-3}$, natural light). Plants were watered daily with 200-330 ml fertiliser water.

Phenotypic evaluation

Phenotypical monitoring was performed upon movement to the new greenhouse and occurred twice per week over ten weeks. Agronomical variables including plant height (cm), scion and rootstock diameter (mm), scion architecture including leaf length (cm) and stem diameter (mm), fruit production (average fruit weight (AFW) and total biomass production) were measured during this period.

Tissue sampling, RNA extraction and library preparation

Tissues samples were taken one week after acclimatisation to the new environment. 100mg of flash-frozen leaf tissue was taken from each biological replicate sample for each condition, from which, RNA was extracted. Total RNA was extracted using Nucleospin 96 Plant Core kit (Macherey-Nagel GmbH & Co., Düren, Germany) according to the respective manufacturer's instructions. Novogene Co., LTD (Beijing, China) undertook mRNA library preparation and transcriptome sequencing using poly-A enrichment method and Illumina NovaSeq 6000 (Illumina, California, USA). This used a paired end read length of 150 bp, generating 6 Gb of raw data per sample.

Genome assemblies

The experiment lacked detailed information on the genetic background of the scion and rootstock lines, which included the absence of assembled genome references or SNP information. Based on our understanding of each line, the scions were bred using parents from cultivated tomato lines. Whereas the rootstocks were generated through the hybridisation using cultivated tomato lines and *Solanum habrochaites*, a wild plant species closely related to tomato.

The *Solanum lycopersium* cv. Heinz (version 4.0 genome) genome reference is well-described and commonly used to represent cultivated tomato lines. Here, it was employed to represent the scion genotype (Hosmani, Flores-Gonzalez et al. 2019). The *Solanum lycopersium* genome was downloaded from Sol Genomics Network (Fernandez-Pozo, Menda et al. 2015).

The *S. habrochaites* genome assembly was utilised to represent the rootstock lines (supplied from: http://caastomato.biocloud.net/home) as it was predicted to best represent around 50% of the rootstock genome. However, unlike the *Solanum lycopersium* reference, the *S. habrochaites* is not as well assembled (Li, He et al. 2023) and consists of approximately 2,500 scaffolds with no assembled chromosomes.

mRNA sequencing: transcriptomic analysis & mobile mRNA analysis

Transcriptomic analysis was undertaken to identify differences in gene expression between self-grafts and heterografts. Raw mRNA sequencing reads were trimmed using *Trimmomatic* (Version 0.39) to remove low quality sequences and adaptor sequences (Bolger, Lohse et al. 2014). Cleaned reads

were aligned to using HISAT2 (Version 2.2.1) (Kim, Paggi et al. 2019) to the *Solanum lycopersicum* genome version 4.1 (Hosmani, Flores-Gonzalez et al. 2019). The raw gene count was calculated using HTSeq (Version 0.12.4) (Putri, Anders et al. 2022). Differential expression analysis was undertaken in *R* using the R package *DESeq2 (Love, Huber et al. 2014)*. DEGs were characterised with an adjusted $p\text{-}value < 0.05$.

To detect putative graft-mobile mRNA molecules moving from root-to-shoot in the heterograft combinations, the R package, *mobileRNA*, was utilised. The cleaned mRNA sequencing reads were aligned using HISAT2 (Version 2.2.1) (Kim, Paggi et al. 2019) to the merged genome, excluding multi-mapped reads. The raw mRNA count was undertaken using HTSeq (0.12.4) (Putri, Anders et al. 2022). The output was imported and analysed in R using *mobileRNA* with *DESeq2* (Love, Huber et al. 2014, Jeynes-Cupper and Catoni 2023, Jeynes-Cupper and Catoni 2024). Functional analysis used achieved data from NCBI, Sol Genomics Network resources (Medicine 1988, Fernandez-Pozo, Menda et al. 2015) and GO enrichment analysis with ShinyGO (Ge, Jung et al. 2020).

sRNA sequencing: mobile sRNA analysis & scion-produced sRNA changes

Raw sRNAseq sequencing reads were cleaned using Trim galore (Version 0.6.5) (Krueger F 2021) to remove adaptors, low quality sequences and trim sequences with less than 18 nucleotides or more than 30 nucleotides. Using the *mobileRNA* methodology, cleaned reads were uniquely aligned to the merged genome using Bowtie (1.2.3) (Langmead, Trapnell et al. 2009). ShortStack (Version 3.8.5) was used to undertake *de novo* sRNA cluster detection for each sample (Axtell 2013, Shahid and Axtell 2014). Then, the lists of detected *de novo* sRNAs from all

replicated were merged to generate a sRNA annotation file for the experimental design. The sRNA clustering analysis with ShortStack was performed a second time with the sRNA annotation file supplied as a loci file (--locifile) and a minimum coverage of 5 RPM. The generated TXT files were utilised for downstream analysis with *mobileRNA* (Jeynes-Cupper and Catoni 2023, Jeynes-Cupper and Catoni 2024).

To analyse changes in the sRNA populations derived from the scion genome, sRNAs produced by the tomato genotype were selected for from the dataset. Differentially analysis using *DESeq2* (Love, Huber et al. 2014) and differentially expressed sRNAs had an adjusted *p-value* < 0.05. sRNA clusters with a positive log2FoldChange (> 0) represented an increase in abundance in the heterografts, while a negative log2FoldChange (< 0) value represents a decrease in abundance between the conditions. To identify root-to-shoot mobile sRNAs, *mobileRNA* selected the sRNAs which aligned to *S. habroachaites*. This step also removed additional false positives, which were assumed to be sRNAs that were aligned to the *S. habroachaites* but maintained read coverage in the tomato self-graft controls.

To investigate the sRNAs, the genomic location of sRNA clusters was overlapped with genomic features to access the proportion of genomic features that synthesised the sRNAs, such as promoter regions, repeats and coding regions. A buffer region of 1 kb upstream and downstream to each gene was added based on assumption regarding promoter regions. The RNA sequences were extracted based on the consensus sequence across replicates, only valid sequences were utilised for further functional analysis. Target prediction

analysis was undertaken with psRNATarget (Dai, Zhuang et al. 2018) to select the top three possible targets for supplied – using the standard schema V2 (2017 release) parameters. Target genes were summarised using GO Enrichment analysis using ShinyGO (Ge, Jung et al. 2020) inclusive of parameters: Fisher's exact test, false discovery rate correction and a *p* value cut-off of 0.05.

4.3 Results

Confirming the grafting-induced traits

To study the effects of grafting-induced vigour, we combined a productive tomato scion with either one of two different commercial rootstocks (referred to as RS-1 and RS-2). These rootstocks supplied by ENZA ZADEN are known to produce two different traits. The RS-1 line can introduce improved crop vigour while the RS-2 line is not associated to any improvements in vigour, but instead provides resistance to *p.lycopersici* fungus. A self-graft of the tomato was utilised as a positive control (referred to as SELF).

Over the course of 10 weeks, we measured several plant traits associated with vigour including plant height, fruit production, fruit quality and fruit weight. The results demonstrate that although the heterografts appear to produce more fruits, the large variability in the data prohibits a statically significant finding (Figure 4.2A). Indeed, the trend is what we expected, whereby, the RS-1 rootstock increased fruit production the most and the RS-2 rootstock was able to increase production more than the self-grafts. Interestingly, the fruit produced by the heterografts demonstrated, on average, a significantly lower weight than the self-graft controls (ANOVA, $F(2,9) = 10.82$, $P < 0.05$, $n_g^2 = 0.71$).

The RS-1 combination produced the lightest fruits (Figure 4.2B). As we expected, RS-1 line produced fruit with a statistically significant higher Brix score, a measure of fruit quality, compared to both the self-graft and the RS-2 heterografts (Figure 4.2C). These results demonstrate that fruits produced by heterografting with RS-1 demonstrated distinct qualities, whereas fruits from the RS-2 heterografts and self-grafts were comparable.

Plant height is commonly uses as a proxy for crop vigour, and in these combinations, we expected that at the beginning of the experiments the self-grafts and the heterografts would show similar growth rate. At the close of the season, we expected the heterografts to divert more energy to generative growth rather than vegetive growth. Indeed, this was observed, however, due to the variability within the self-grafted plants there was no statistical significance (Figure 4.2D-E).

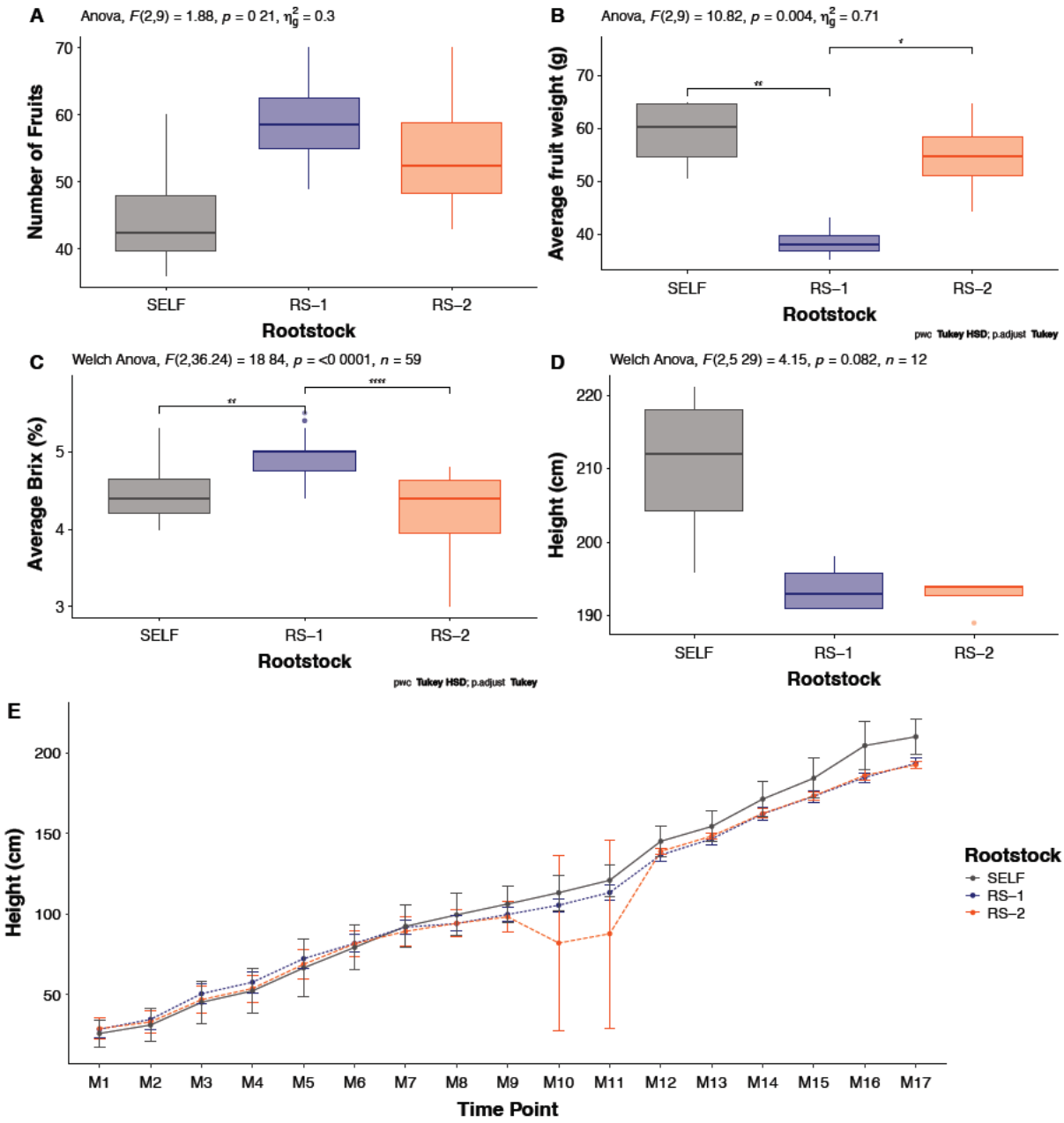


Figure 4.2. Phenotypic analysis of scion traits. Over 10 weeks, measurements including fruit number, fruit weight, fruit Brix score and plant height were taken. There combination included tomato self-grafts (SELF) shown in grey, tomato heterografting with RS-1 rootstock line (RS-1) shown in blue and tomato heterografting with RS-2 rootstock line (RS-2) shown in orange. A) Total number of tomato fruits produced by each grafting combination by the end of the experiment. Text annotations represent summary statistics from ANOVA. B) Average fruit weight produced by each combination. Text annotations represent summary statistics from ANOVA, where asterisks mark a statistically significant difference (ANOVA one-way, $P<0.05$). C) Average Brix (%) score of fruits. Text annotations represent summary statistics from Welsh ANOVA, where asterisks mark a statistically significant difference (Welsh ANOVA one-way, $P<0.05$). D) Height in centimetres (cm) of plants at the end of the experiment. Text annotations represent summary statistics from Welsh ANOVA, where asterisks mark a statistically significant difference (Welsh ANOVA one-way, $P<0.05$). E) Change in height in centimetres (cm) of plants over time points. Error bars represent standard error between replicates in a condition.

Transcriptome indicates changes to photosynthesis & resource allocation

To investigate whether differences in the scion phenotypes were associated to changes in transcription, we profiled the gene expression in the scion tissues using RNAseq. This compared the two tomato heterografts to the tomato self-graft controls. Unsurprisingly, we observed that the transcription profiles for the tomato scions grafted onto RS-1 and RS-2 cluster together whereas the self-grafted controls cluster separately (Figure 4.3). This suggests that the transcriptional profiles are linked to the phenotypical difference in the heterografts. The differential analysis showed that there were marginally more downregulated genes in the tomato scions grafted onto RS-1 (57.6%) (Figure 4.4.A) and RS-2 (50.9%) (Figure 4.4.B). In total, we observed 503 upregulated and 683 downregulated genes in the tomato scions grafted onto RS-1, and 647 upregulated and 672 downregulated genes in the tomato scions grafted onto RS-2 (Figure 4.4).

The DEGs in the tomato scions grafted onto RS-1 and RS-2 were compared to investigate whether there was any overlap (Figure 4.4.C). There were 142 DEGs which were upregulated, and 133 which were downregulated in both conditions. However, there were also nine DEGs which were upregulated in the scion grafted onto RS-1 but downregulated in scions grafted onto RS-2. Similarly, there were four DEGs which were downregulated in the scion grafted onto RS-1 but upregulated in scions grafted onto RS-2 (Figure 4.4.C).

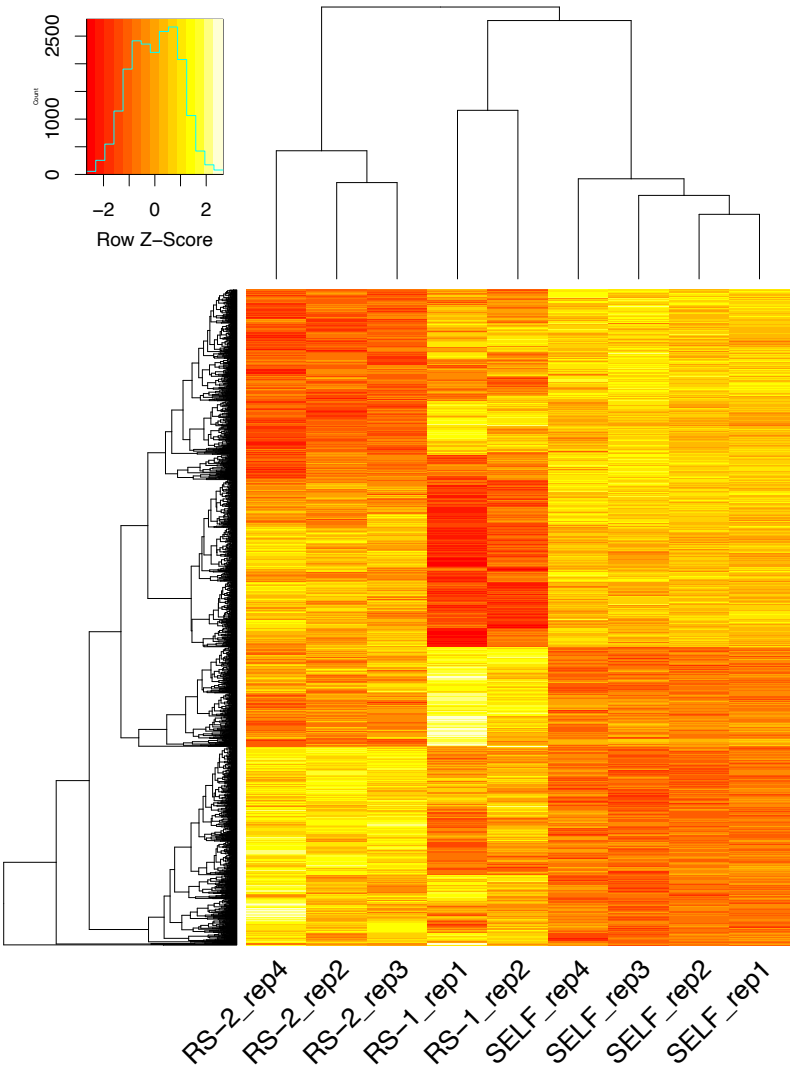


Figure 4.3. Heatmap showing the scaled expression (rlog) of differentially expressed genes using hierarchical clustering. Genes are from tomato scions grafted onto RS-1, tomato scions grafted onto RS-2 and tomato self-grafted scions. The dendrogram along the top and side demonstrate the hierarchical clustering between samples and genes, respectively. The colour scale reflects the relative expression where orange illustrates downregulation and yellow illustrates upregulation.

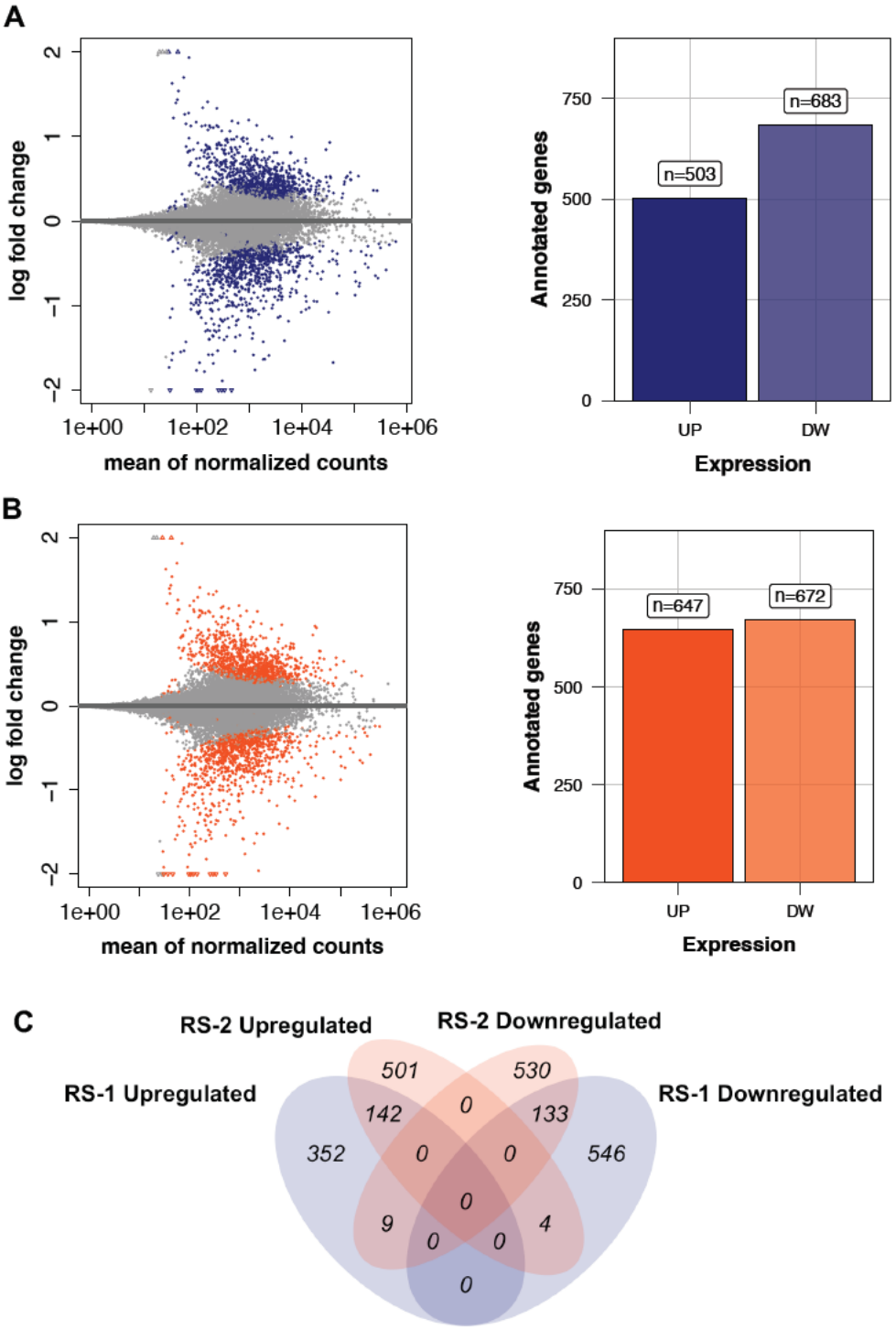


Figure 4.4. Differentially expressed genes (DEGs) isolated in the tomato scions grafted onto either RS-1 or RS-2 lines. A) Scatterplot of annotated genes with non-zero expression levels (n=23,435) in the SELF and RS-1 conditions. Each point represents a gene, blue dots represent DEGs between the conditions (*p* value < 0.05). To the right, a bar plot showing the number of upregulated (UP) and downregulated (DW) genes. B) Scatterplot of annotated genes with non-zero expression levels (n=23,435) in the SELF and RS-2 conditions. Each point represents a gene, orange dots represent DEGs between the conditions (*p* value < 0.05). To the right, a bar plot showing the number of upregulated (UP) and downregulated (DW) genes. C) Venn diagram to show the overlap of DEGs (upregulated and downregulated, individually) identified in the tomato scions grafted onto RS-1 and onto RS-2.

To further access the biological relevance of the DEGs in each condition, we accessed whether key genes related to DNA methylation were differentially expressed. Interestingly, in the scions grafted onto RS-1 rootstock there were three genes that encoded DNA methyltransferase enzymes that were downregulated (SlMET1, slMET1L, SlMET3L) in addition to an Ethylene responsive TF (SlERF53) involved in stress responses (Figure 4.5). In comparison, we isolated the downregulation of SlELF4 and SlPRR5, both involved in the regulation of the circadian rhythm, in the tomato scions grafted onto to RS-2. Unlike the other condition, we observed an upregulated gene, the SlF3H gene that is involved in flavonoid biosynthesis (Figure 4.5). These results imply that epigenetic regulation could be different in the heterografted combination in comparison to the control. In a similar way, we also tested to see whether key genes relating to photosynthesis were differentially expressed. This analysis revealed that in both conditions there was a prevalence of downregulated genes related to photosynthesis (Supplementary Table 4.3). This was predominant in the tomato scions grafted onto the RS-2 line. These results imply that photosynthesis is impacted and modulated differently in the heterografts.

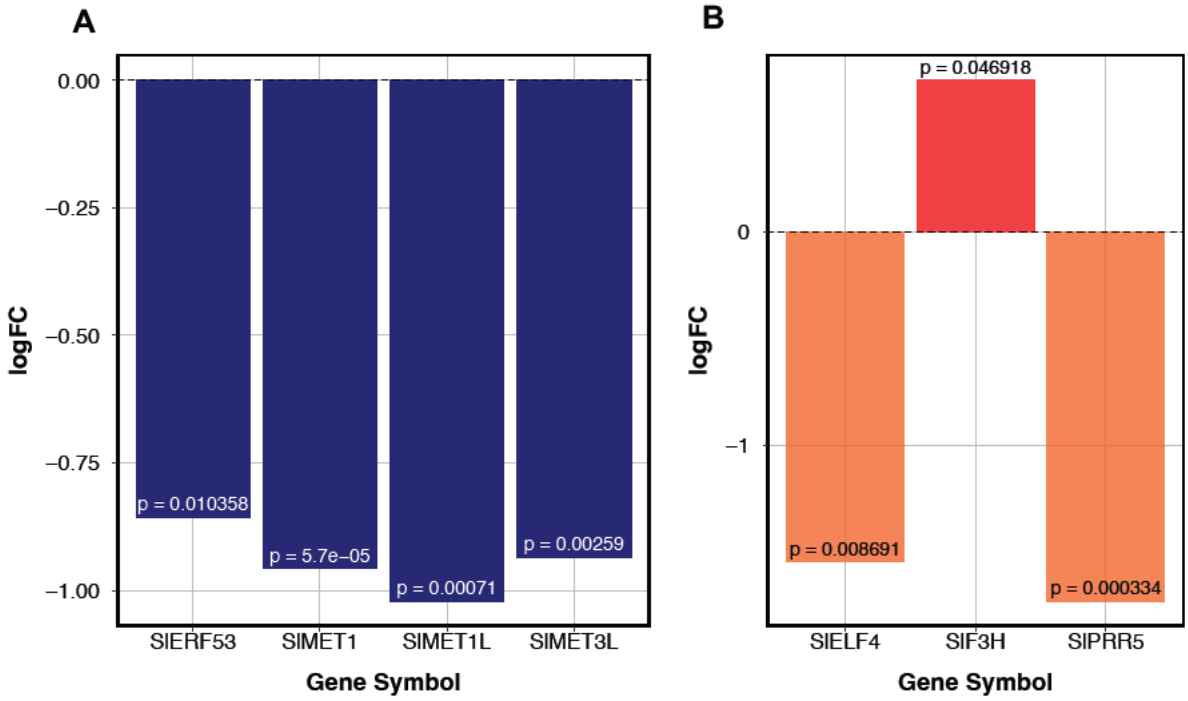


Figure 4.5. The expression of differentially expressed genes (DEGs) of interest involved in epigenetic regulation. Genes related to epigenetic regulated were selected based on homologs in *Arabidopsis thaliana* (see Chapter 3 methods section). Bar charts show expression as the log2 fold change (logFC) scale, and bars are annotated with their respective *p* value. Dash-line represents expression threshold at 0. A) The expression of differentially expressed genes involves in epigenetic regulation in the scion of tomato grafted onto RS-1. A) The expression of differentially expressed genes involves in epigenetic regulation in the scion of tomato grafted onto RS-2.

To investigate whether DEGs were involved in specific biological processes and developmental pathways that could explain the phenotypical changes in the heterografted scions, we undertook GO term enrichment analysis using ShinyGO (Ge, Jung et al. 2020). This analysis was performed separately for the up- and downregulated genes identified in the scions of heterografts using either the RS-1 or RS-2 lines.

In the RS-1 conditions, we observed an enrichment (p value < 0.05) in upregulated genes with a biological function related to xyloglucan metabolic processes and hemicellulose metabolic processes (Supplementary Figure 4.1).

These two categories contained the same gene sets, all of which were genes encoding Xyloglucan endotransglucosylase/hydrolase proteins (XTHs) including SlXTH1, SlXTH2, SlXTH4, SlXTH8, SlXTH13. Xyloglucan is an abundant form of hemicellulose that is essential in the cell wall and is involved in cellulose formation and linkage between polysaccharides and lipid polymers in the primary cell wall. The XTH family cleave and reconnect xyloglucan molecules to both synthesis and reconstruct cell walls enabling flexibility through development. Since, XTHs have been associated with the healing process of plant grafts (Cheng, Zhang et al. 2021, Yang, Chen et al. 2023) and play a role in developmental processes including cell wall extensibility, hypocotyl growth, root elongation, fruit development and opening, and fruit softening (Thompson and Fry 2001, Miedes and Lorences 2009, Harada, Torii et al. 2011, Wang, Lu et al. 2023). The expression of XTHs in the leaves of Arabidopsis have been linked with canopy adjustments under shading conditions including stem elongation (Hussain, Iqbal et al. 2019). Interestingly the overexpression of XTH4 in herbaceous peony (*Paeonia lactiflora*) resulted in thicker secondary cell walls and improved stem strength. In addition, there was also an upregulation of lipid metabolic processes, this gene set included multiple fatty acyl-CoA reductases (FARs) genes which are involved in depositing suberin and other wax deposits (Zhang, Liu et al. 2022) and the upregulation of the SlMYB32 TF (Solyc10g055410) (Zhao, Li et al. 2014, Wang, Wu et al. 2020).

The most significant KEGG pathway in tomato scions grafted onto RS-1 was plant hormone signal transduction (Path:sly04075). Within this category there were six genes including:

- SOLYC06G053290.1: Auxin responsive SAUR protein
- SOLYC07G042170.3: Jasmonate ZIM-domain protein 3 (TIFY)
- SOLYC06G053840.3: Auxin-regulated IAA4 (SlIAA4)
- SOLYC08G076960.1: Abscisic acid receptor (PYR1)
- SOLYC11G011030.2: Pto-responsive gene 1 (TIFY)
- SOLYC05G051200.1: Ethylene-responsive factor 1 (ERF1)

Based on network analysis, we observe that the SAUR and IAA4 enzymes play an essential role in the final step tryptophan metabolism, triggered by auxin, for cell enlargement and plant growth, as well as ubiquitin mediated proteolysis - which is also mediated by Jasmonate ZIM-domain protein 3. The PYR1 enzyme is triggered by abscisic acid (ABA) to negatively control stomatal closure in the carotenoid biosynthesis pathway. Whereas the ERF1 TF is induced by ethylene and jasmonate pathways which in turns regulations the expression of defence related genes (McKendry 2002).

Delving into the gene expression data further of the upregulated genes in the tomato scions grafted onto RS-1, we also observed that one of the most highly upregulated genes was DWARF (Solyc02g089160) whose overexpression has been characterised to cause a reduction in brassinosteroid production (Montoya, Nomura et al. 2005, Li, Chen et al. 2016). As a result, it has been associated with changes to plant architecture including reduced heights, improved germination and CO^2 assimilation yet no changes to fruit yields (Li, Chen et al. 2016).

Similarly, we investigated downregulated genes in tomato scions grafted onto RS-1 and observed an enrichment in biological processes including plastid and chloroplast organisation, and non-coding RNA metabolic processes (Supplementary Figure 4.2). At a molecular level, these genes were related to purine binding, ATP binding and carbohydrate derivative binding. Moreover, when the gene set was subjected to KEGG analysis, we identified an enrichment in downregulated genes that were associated with Aminoacyl-tRNA biosynthesis and Circadian rhythm pathways. One of the downregulated genes involved in the circadian rhythm was GIGANTEA (SOLYC04G071990, Solyc12g056650) which is involved in circadian rhythm, light signalling, cold tolerance, hormone signalling but mainly in photoperiodic flowering. In terms of photoperiodic flowering, it acts as the master switch controlling the expression of *FLOWERING LOCUS T* (*FT)* (Imaizumi, Tran et al. 2003, Sawa, Nusinow et al. 2007, Brandoli, Petri et al. 2020).

In comparison, we undertook functional enrichment of the upregulated genes identified in the tomato scions grafted onto RS-2 in comparison to self-grafted samples. We observed an enrichment in biological processes including cell wall biogenesis, glucan metabolic processes, and lipid biosynthesis processes. Further investigation revealed that these groups included multiple genes involved in cellulose biosynthesis and cell wall waxes including sterols and squalene. The gene set was also subjected to KEGG analysis we identified an enrichment in Fatty acid elongation pathways for cutin, suberin and wax biogenesis, plus, fatty acid degradation. The second enriched pathway was Stilbenoid diarylheptanoid and gingerol biosynthesis that leads into both flavonoid and phenylpropanoid biosynthesis pathways. It appears that the gene

sets involved in these pathways produce intermediates for the synthesis of flavonoids and all three lignin contexts.

In comparison, the downregulated genes identified in the tomato scions grafted onto the RS-2 rootstock were enriched in biological processes relating to photosynthesis and chlorophyll metabolic and catabolic processes (Supplementary Figure 4.2). There was the string enrichment in molecular functions related to carbohydrate derivative transmembrane transporter activity and chlorophyll a-b binding proteins (Solyc01g105030, Solyc09g014520, Solyc10g006230, Solyc12g006140, Solyc12g011280) which suggests that the tomato scions could have impaired photosynthetic abilities (Liu, Xu et al. 2013).

Mobile sRNAs may re-program responses to light

In the past, grafting has been utilised to demonstrate the systemic long-distance movement of sRNAs and their ability to manipulate the regulation of gene expression in recipient tissues through the RdDM pathway (Lewsey, Hardcastle et al. 2016). sRNAs can impact gene regulation through numerous other methods including inhibition of translation through blocking or cleaving target mRNAs (Zhan and Meyers 2023). The *mobileRNA* method simultaneously aligned the sequencing reads to the tomato and *S. habrochaites* genome references. Roughly the same proportion of sequencing reads in the tomato scions aligned to the S. *habrochaites* genome reference. There were up to 18% of sequencing reads in the tomato scions grafted onto RS-1 that were aligned to the *S. habrochaites* genome reference, whereas there were up to 14% which were aligned in the tomato scions grafted onto RS-2 (Figure 4.6A). As expected, a proportion of the sequencing reads in the tomato self-grafted scions were aligned to the *S. habrochaites* genome reference, likely due to introgression

during hybridisation (Figure 4.6A). Following this, we identified candidate mobile sRNAs in the heterografted plants (Figure 4.6.B). There were only two heterografted replicates using the RS-1 rootstock, and across the two replicates they both shared 68% of all the sRNA candidates. In comparison, there were four heterografted replicates with the RS-2 rootstock (Figure 4.6.B). Across the four replicates, they shared only 3.57% of all the sRNA candidates in the experimental design. However, in at least half of the replicates, they shared 23.81% of all the sRNA candidates (Figure 4.6.B)

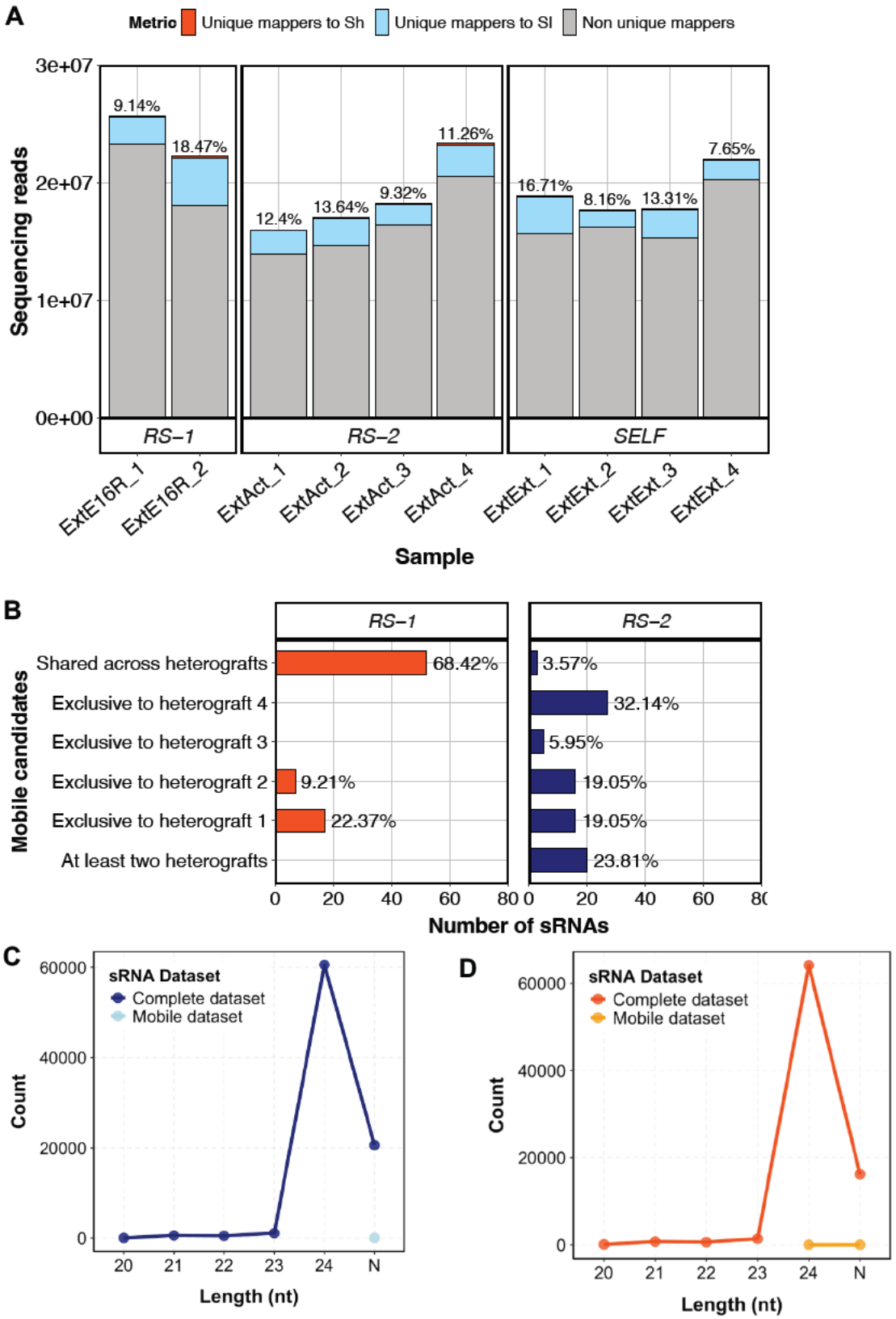


Figure 4.6. Identification of candidate root-to-shoot mobile small RNAs (sRNAs) produced by the rootstock. Small RNA sequencing reads (sRNAseq) were aligned to a merged genome that contained the *Solanum lycopersium* and *Solanum habrochaites* genome references. A) For each biological replicate in the experimental design, the bar plot shows the proportion of the sequencing reads that were non-unique mappers (i.e. mapped to more than

one location), the reads that uniquely aligned to the *S. habrochaites* (Sh) genome reference (orange) and the reads which aligned uniquely to the *S. lycopersium* (Sl) genome (light blue). B) The distribution of candidate mobile sRNAs across tomato scions heterografted onto either the RS-1 line or the RS-2 line. Shared across heterografts refers to sRNA that were in all replicates within the condition. C) The dark blue represents all detected sRNAs in the tomato scions grafted onto RS-1 and in self-grafted scions. The light blue represents the detected mobile sRNA produced by the RS-1 line. D) The dark orange represents all detected sRNAs in the tomato scions grafted onto RS-2 and in self-grafted scions. The light orange represents the detected mobile sRNA produced by the RS-2 line.

In this analysis, we identified 52 mobile sRNA produced by the RS-1 line located in the tomato scion tissue based on a consensus across two replicates (here, this is all replicates). Of which, all had an unclassified dicercall (Figure 4.6.C). We investigated the loci that synthesised the mobile sRNAs and revealed that 12 sRNAs (23%) were produced from genomic regions that overlapped with genes (+/- 1 kb, n =14), however, the overlap with repeat regions or TEs could not be accesses due to a lack of annotation. To investigate the functional role of the putative mobile sRNAs, we undertook target prediction analysis using psRNATarget (Dai, Zhuang et al. 2018) followed by GO term enrichment analysis of the target genes (Figure 4.7.A). From the 52 mobile sRNAs, there were 21 sRNAs that had predicted targets, accounted for 92 targets genes. These target genes had varying molecular functions, but there was an enrichment in ribosomal small subunit binding, functions related to ribonucleotides and DNA polymerase activity (Figure 4.7.A). Furthermore, we identified target genes which were identified as DEGs in the tomato scions grafted onto RS-1 in comparison to self-grafted plants (Figure 4.7.B). The analysis revealed that four gene targets were differentially expressed whereby the target gene Solyc07g063610.4 was upregulated while the other three gene targets (Solyc08g074370.4, Solyc06g076850.3, Solyc07g054220.1) were downregulated (Figure 4.7.B). Commonly across the downregulated gene targets, they were all

related to DNA and/or protein binding functions. Within this group, the Solyc07g054220.1 gene is an ethylene responsive TF which could suggest a reduced sensitivity to ethylene which could alter processes such as fruit ripening, leaf abscission or stress responses, in particular drought or salt. In comparison the upregulated gene target, Solyc07g063610.4, encodes the Dynein light chain 2 protein in the cytoplasm which is involved in microtubule-based processes, and at a molecular level assist cytoskeletal motor activity. This could suggest that the plant cells in the leaf are actively transporting materials to support metabolic processes.

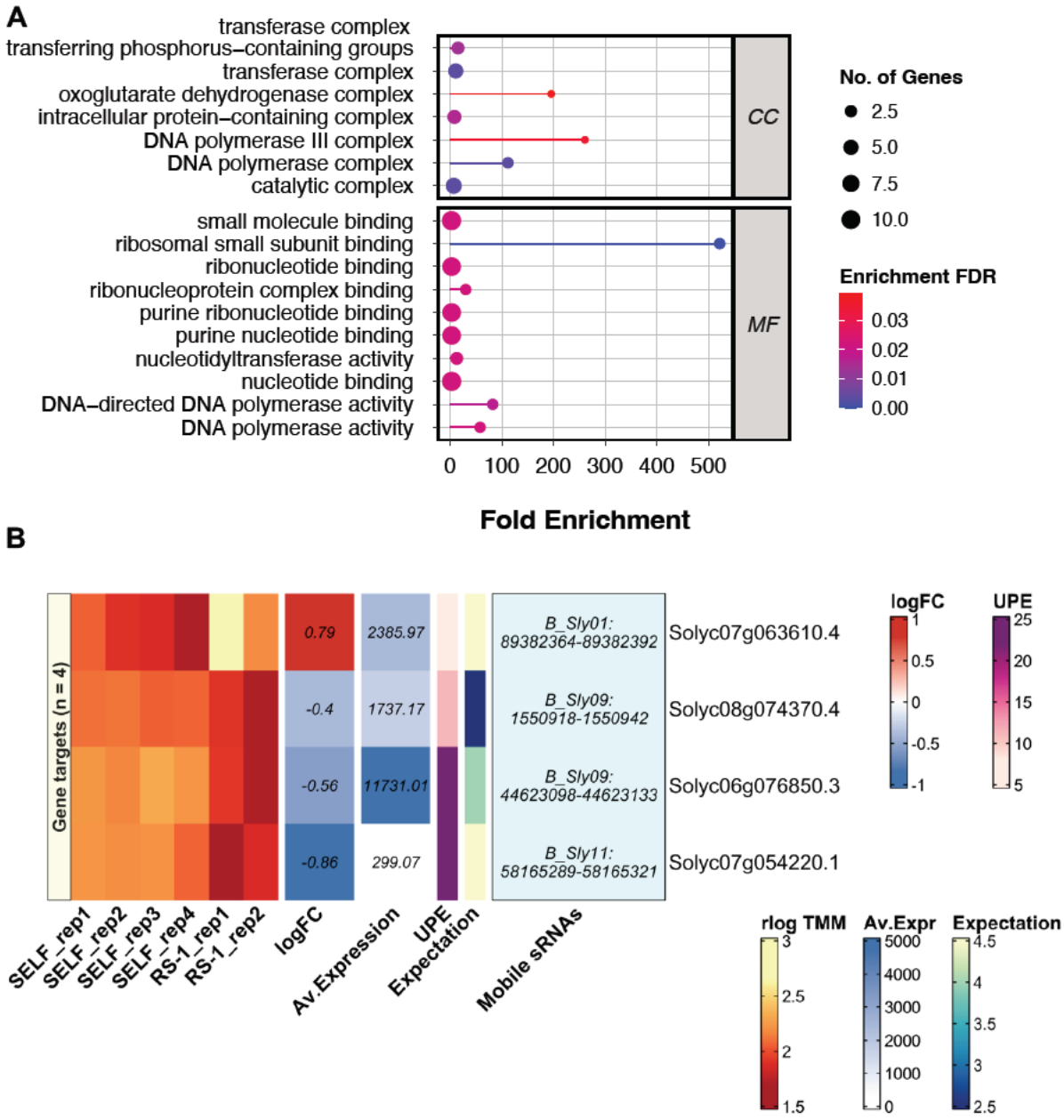


Figure 4.7. Functional analysis of the predicted gene targets of mobile sRNAs produced by the RS-1 line. Gene targets were predicted using psRNA`Target and GO term enrichment analysis of gene targets was undertaken using ShinyGO. A) GO term enrichment analysis of gene targets in the *Solanum lycopersium* genome (Version 3). The panels are split based on type, whereby "CC" represents cellular compartment and "MF" represents molecular function. B) Heatmap showing the relative rlog-transformed TMM values of differentially expressed target genes ($p < 0.05$) ordered by the log2 fold change (logFC). Each column represents a replicate, and each row represents a tomato sRNA ($n = 6$). The gradient bars on the below show the expression level for rlog TMM values. The column for logFC represents the log2 fold change, and the Av. Expression column represents the average expression value (rlog) across the experimental design. The UPE represents the maximum accessibility energy to unpair the sRNA from the target site and where the Expectation represents the penalty for mismatches between the sRNA and target site.

In this analysis, we identified 20 mobile sRNA produced by the RS-2 line located in the tomato scion tissue based on a consensus across two replicates (here, this is all replicates). Of which, 7 had a dicercall size of 24 nucleotides (nt) while the other 13 had an unclassified dicercall (Figure 4.6.D). We investigated the loci that synthesised the mobile sRNAs and revealed that 8 sRNAs (40%) were produced from genomic regions that overlapped with genes (+/- 1 kb, n =8). To investigate the functional role of the putative mobile sRNAs, we undertook target prediction analysis using psRNATarget followed by GO term enrichment analysis of the target genes. From the 20 mobile sRNAs, there were 7 sRNAs that had predicted targets, accounted for 19 targets genes. None of these target genes were differentially expressed. The GO term enrichment analysis revealed that the target genes were enriched in biological functions to responses to light, responses to radiation, positive regulation of macromolecule biosynthetic processes, copper ion homeostasis, mitochondrial translation and gene expression, and peptidyl-lysine monomethylation (Figure 4.8). These appear to be localised in the plastid and have a molecule function related to translation activator activity, sigma factor activity and mitochondrial ribosome binding (Figure 4.8)

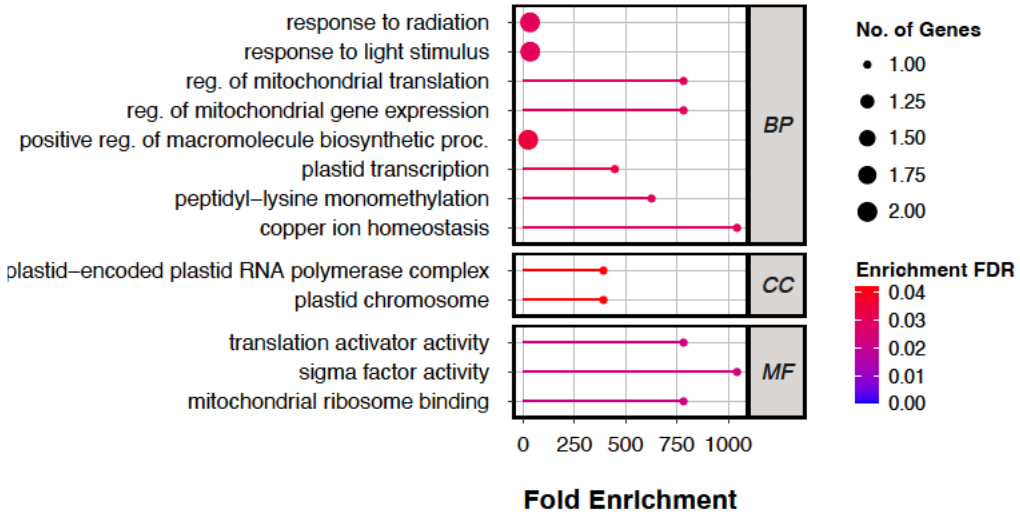


Figure 4.8. Functional analysis of the predicted gene targets of mobile sRNAs produced by the RS-2 line. Gene targets were predicted using psRNATarget (Dai, Zhuang et al. 2018) and GO term enrichment analysis of gene targets was undertaken using ShinyGO (Ge, Jung et al. 2020). A) GO term enrichment analysis of gene targets in the *Solanum lycopersium* genome (Version 3). The panels are split based on type, whereby "CC" represents cellular compartment and "MF" represents molecular function.

Mobile mRNAs might be involved in metabolic processes to allocate energy stores

The movement of mRNAs between cells and tissues has been supported by numerous studies, however, out of the thousands of mobile mRNAs only a fraction have been associated with physiological roles (Heeney and Frank 2023). The molecular mechanism determining the mobility of mobile RNAs are poorly understood, however, recent studies have indicated an enrichment in TLSs within transcripts described as mobile and similarly the proximity of tRNA genes. In this analysis, we utilise the *mobileRNA* approach to detect putative mobile mRNAs produced by the either the RS-1 or RS-2 rootstocks in the tomato scions. Followed by putative functional analysis, and motif analysis to detect the presence of TLSs.

The analysis revealed 666 putative mobile mRNAs produced by the RS-1 line, and a consensus of 49 mRNAs were found across all heterograft replicates (n =2). Functional enrichment analysis determined that the 49 transcripts were related to 33 GO terms. The mobile transcripts produced by the RS-1 rootstock were enriched in biological processes including lipid droplet organisation and DNA recombination which suggests these mobile transcripts are involved in lipid storage and DNA repair mechanisms. The enrichment of gene expression related to DNA recombination is normally indicative of responses to oxidative stress or environmental stress. Moreover, there is an enrichment in transcripts related to response to brassinosteroid processes which could imply that the mobile transcripts are produced in response to plant hormone signalling between the roots-and-shoots and may influence cell expansion and photosynthesis. Moreover, the transcripts showed a molecular functional enrichment in transporter-related processes including glucose-6-phosphate transmembrane transporter activity and phosphoglycerate transmembrane transport. These results point to potential roles in sugar transport, which is essential to photosynthesis. Moreover, the results illustrate a prominent enrichment in metabolic processes including acyl-CoA dehydrogenase activity and 3-oxo-5-alpha-steroid 4-dehydrogenase activity which is suggestive of a role in lipid metabolism for energy allocation.

Furthermore, the analysis explored whether our candidates contained TLSs in the coding regions or were in close proximity to tRNA genes in the *S. habrochaites* genome. The results revealed that only two mobile transcripts (Shab03g003210, Shab08g021360) contain TSLs, while none of the mobile transcripts were in 1kb (upstream/downstream) of tRNA genes.

Lastly, we were interested in identifying the tomato homologs of the mobile mRNAs to explore whether the mobile transcripts could be contributing to the regulation of the homologous genes (Figure 4.11.A). The homologous genes were identified through reciprocal protein sequences analysis, and the normalised expression levels from RNAseq data were plotted as a heatmap that was ordered based on the mobile mRNA abundance (Figure 4.11.A). The results did not reveal a consistent pattern, however, for the most abundant mobile mRNA the homologous gene was downregulated in the heterografted tomato scion in comparison to the self-grafted scion. These results could suggest the highly abundant mobile transcripts could contribute to a feedback loop.

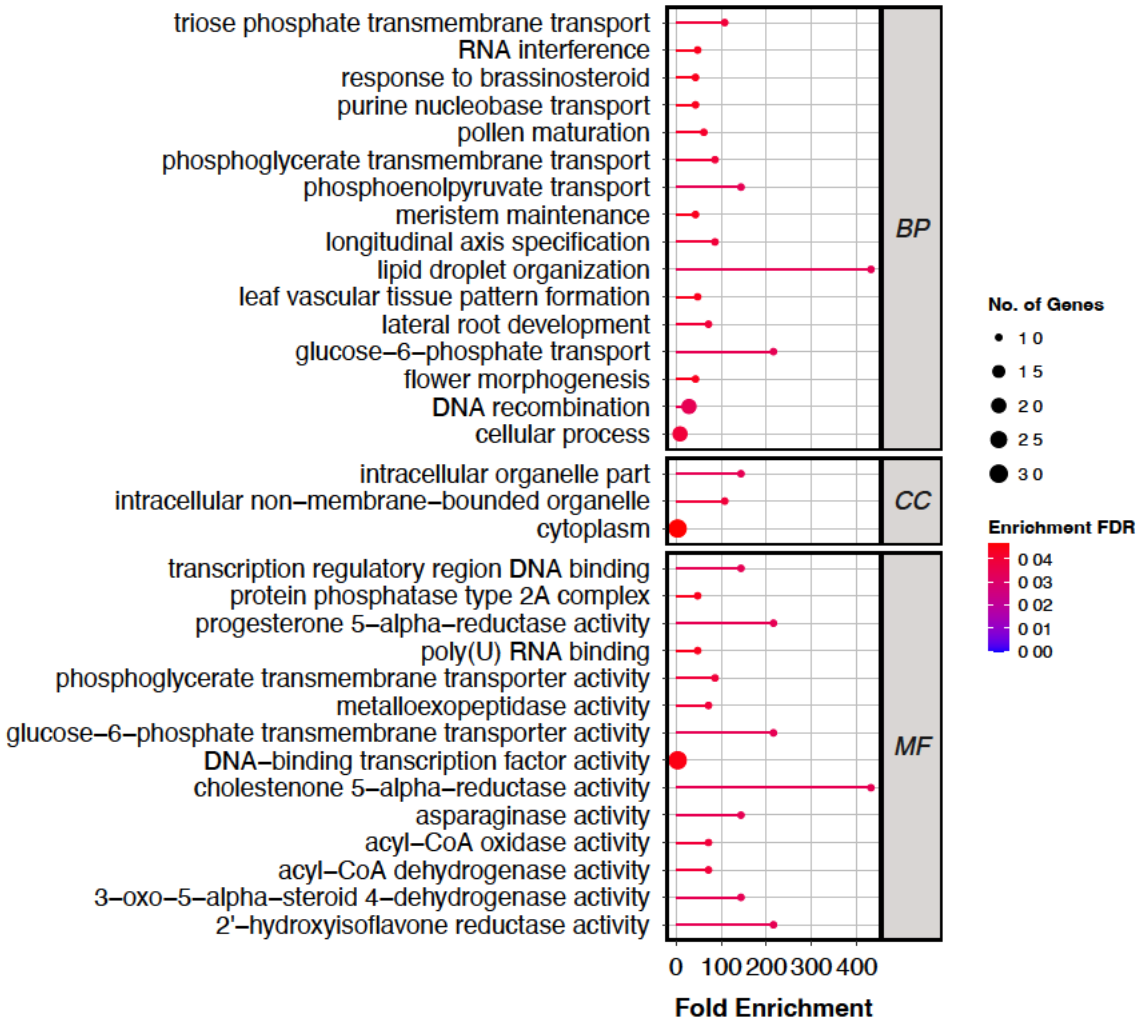


Figure 4.9. Functional analysis of the mobile messenger RNAs (mRNAs) produced by the RS-1 line. Gene Ontology (GO) term enrichment analysis was undertaken in R using a custom script using the *Solanum habrochaites* functional annotations from http://caastomato.biocloud.net/home.

From the RS-2 line, we detected 1,454 putative mobile mRNAs with a consensus of 16 (n = 4). The consensus mobile mRNAs were utilised for downstream analysis. To access the possible role of mobile transcripts in the tomato scions, we utilised GO term enrichment analysis. The results revealed that mobile transcripts were enriched in biological functions related to metabolism, specifically in UDP-L-arabinose metabolic process which points towards cell wall biosynthesis and polysaccharide metabolism. Similarly, there was an

enrichment in the biological process of gluconeogenesis which suggests that transcripts are involved in sugar biosynthesis. Moreover, in terms of enrichments in molecular functions we observe an enrichment of enzymatic activities including 3-oxo-5-alpha-steroid 4-dehydrogenase activity, progesterone 5-alpha-reductase activity and glycogenin glucosyltransferase activity. These results reveal that the mobile transcripts could be involved in changes to hormone regulation and glucose metabolism, either to store or mobilizing energy reserves.

Furthermore, the analysis explored whether our candidates contained TLSs in the coding regions or were in close proximity to tRNA genes in the *S. habrochaites* genome. The results revealed that only one mobile transcripts (Shab08g005180) contain TSLs, while none of the mobile transcripts were in 1kb (upstream/downstream) of tRNA genes. Finally, we explore whether mobile transcripts could contribute to the regulation of homologous genes in the tomato scion (Figure 4.11.B). The homologous genes were identified through reciprocal protein sequences analysis, and the normalised expression levels from RNAseq data were plotted as a heatmap that was ordered based on the mobile mRNA abundance (Figure 4.11.B). The results did not reveal any clear pattern.

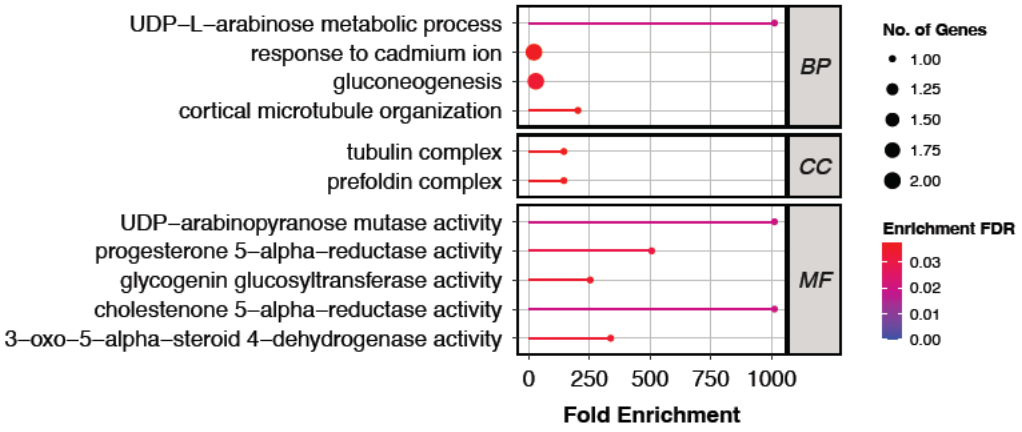


Figure 4.10. Functional analysis of the mobile messenger RNAs (mRNAs) produced by the RS-2 line. Gene Ontology (GO) term enrichment analysis was undertaken in R using a custom script using the *Solanum habrochaites* functional annotations from http://caastomato.biocloud.net/home.

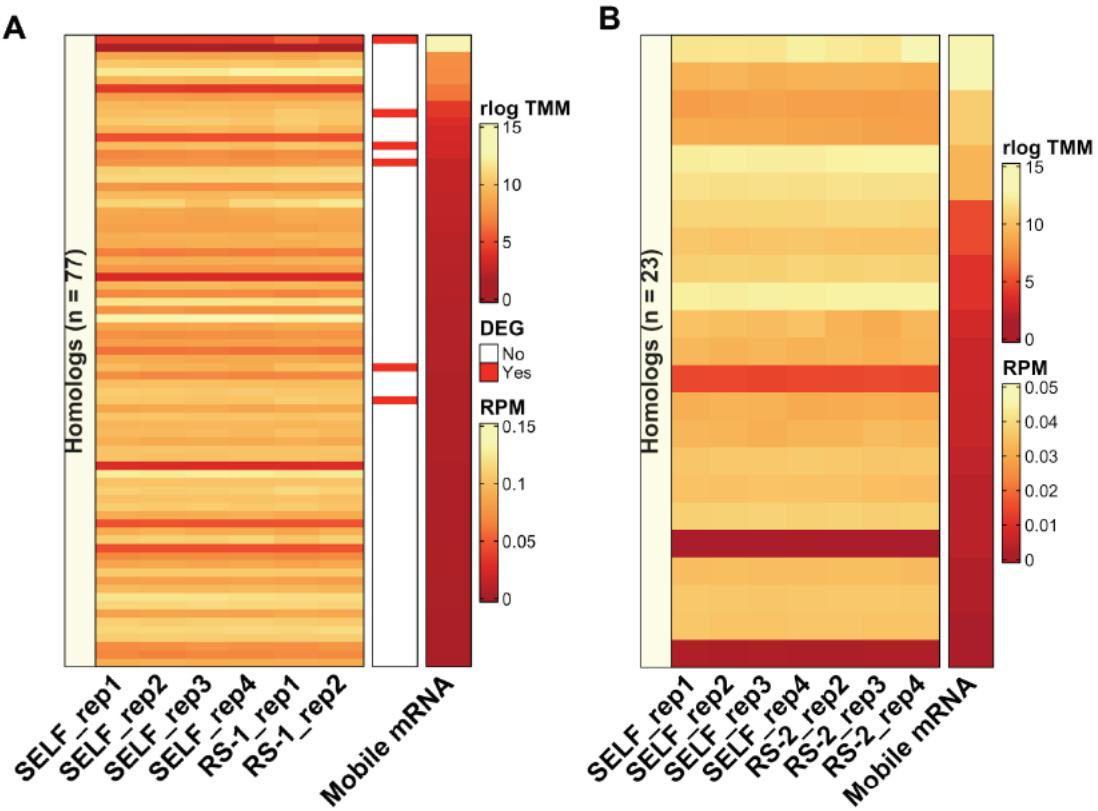


Figure 4.11. Heatmap illustrating the normalised expression of homologous genes to mobile messenger RNA (mRNAs) transcripts from RNAseq data. The homologous genes are ordered based on the abundance of the mobile mRNA transcripts. The identify homologous genes reciprocal protein sequence analysis was undertaken. The expression of the putative homologs were scaled and plotted with ComplexHeatmaps (Gu, Eils et al. 2016). Differentially expressed homologous genes (p value < 0.05) were identified, and labelled is present. Genes were ordered based on the abundance (Reads Per Million, RPM) of mobile transcripts. A) Homologs of mobile mRNA transcripts produced by the RS-1 line. B) Homologs of mobile mRNA transcripts produced by the RS-2 line.

Comparing the effects of RS-1 and RS-2 lines as rootstocks

To cultivate tomatoes, rootstocks have been developed to introduce specific traits. In this study, we investigated two heterograft conditions in comparison to a self-grafted condition. The two rootstocks had been previously described to introduced varying degrees of vigour, whereby RS-1 introduces more vigour than RS-2. In fact, RS-2 had been previously characterised to introduced fungal pathogen resistance, however, we did not access this quality in this work. Hence, we expect that between RS-1 and RS-2 lines there might be some overlap in their abilities. To assess this, we compared the changes in the transcriptome and RNA mobilomes.

To access the common molecular changes, we first identified the DEGs in the tomato scions that were common between heterografts with either the RS-1 or RS-2 rootstock (Figure 4.12). Approximately 22-24% of DEGs in the tomato scions between the heterografted conditions were common which accounts for 142 shared upregulated genes, 133 and shared downregulated genes (Figure 4.12.A). Plus, 9 upregulated genes in tomato scions grafted onto RS-1 but downregulated in scions grafted onto RS-2, and conversely, 4 downregulated genes in scions grafted onto RS-1 were also upregulated in scions grafted onto RS-2 (Figure 4.12.A). Functional enrichment was undertaken to identify KEGG pathways in the sets of common DEGs. The common upregulated genes in the scions were enriched in functions relating to stilbenoid diarylheptanoid and gingerol biosynthesis, metabolic pathways, flavonoid biosynthesis, carbon metabolism and biosynthesis of secondary metabolites (Figure 4.12.B). Although these genes only represent a small fraction of all upregulated genes in the heterografted scions, these results mirror the enrichment analyses

undertaken on the total datasets for each condition (Supplementary Figures 4.1 and 4.2). In comparison, the shared downregulated genes were enriched in several pathways, however, the most significant were Circadian rhythm, Thiamine metabolism and alpha-Linolenic acid metabolism. There were three genes associated in Circadian rhythm including Solyc03g081240 whose ortholog in *Arabidopsis* is PSEUDO-RESPONSE REGULATOR 5 (PRR5) which acts as a transcriptional repressor. Interestingly the triple mutant *prr5/7/9* shows enhance salt and drought tolerance (Nakamichi, Kusano et al. 2009). Moreover, the other two were isoforms of GIGANTEA which has been described previously in this analysis. Intriguingly the main role of alpha-Linolenic acid is to synthesis components in the cell membrane and supports defence against abiotic stress (Mata-Pérez, Sánchez-Calvo et al. 2015). The two genes which were associated with thiamine metabolism encoded thiamine biosynthesis enzymes.

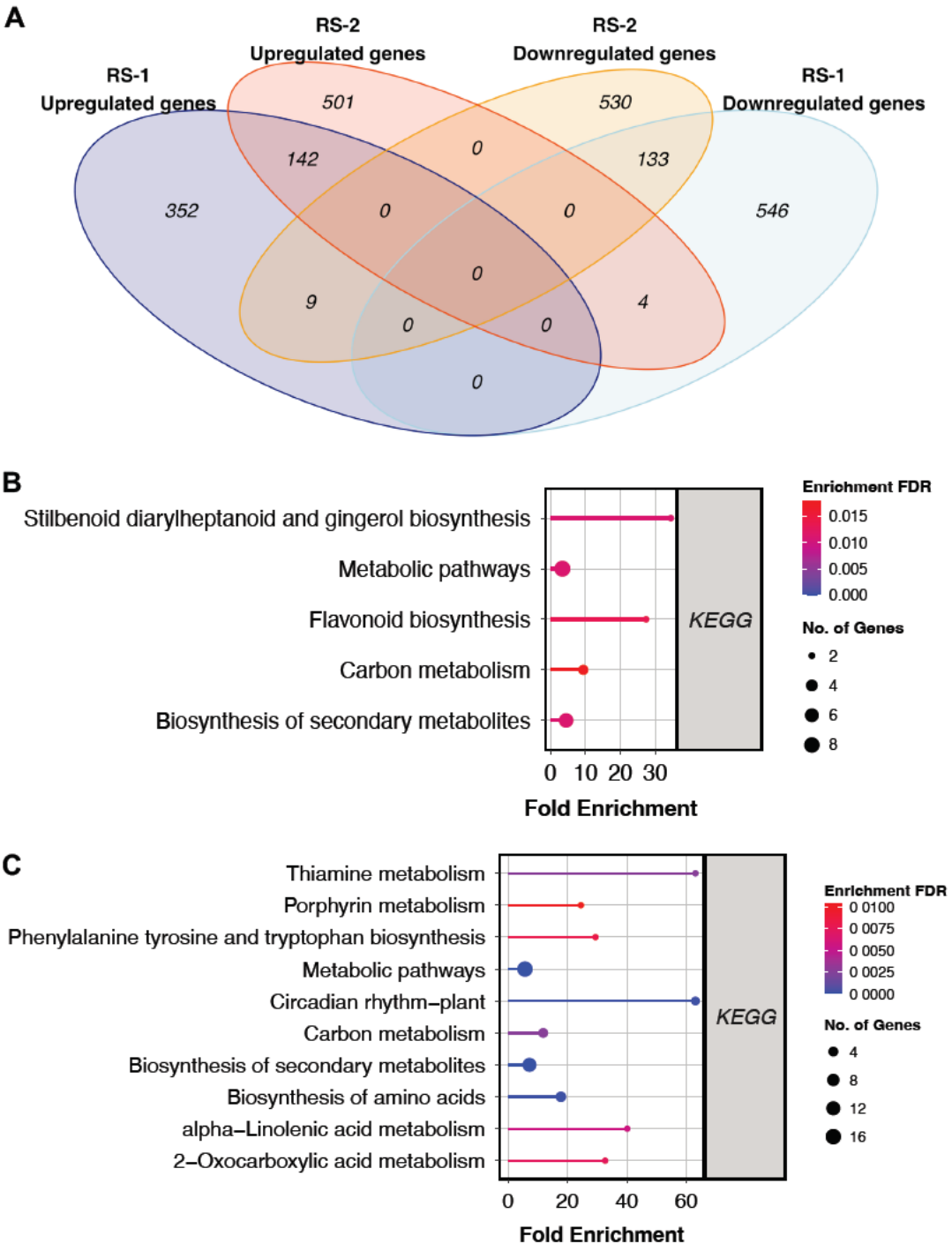


Figure 4.12. Overlapping comparison between differentially expressed genes in scions grafted onto RS-1 and RS-2 lines. A) Venn diagram showing overlap in differentially expressed genes in scions. B) Significant KEGG pathways associated with the upregulated genes commonly found in scions grafted onto RS-1 and RS-2. C) Significant KEGG pathways associated with the downregulated genes commonly found in scions grafted onto RS-1 and RS-2.

To investigate whether the rootstock lines produced similar mobile RNAs we compared the mobile sRNA and mRNA populations. We discovered that between RS-1 and RS-2 they simultaneously produced 12 mobile sRNAs located in the tomato scions, and of these 12, five had predicted gene targets (n = 90). Using functional analysis, we observed that the gene targets were enriched in biological processes involved in cell wall glycoprotein biosynthetic processes and mannoprotein metabolic and biosynthetic process. In comparison, we identified common mobile mRNA transcripts produced by the rootstocks. The analysis revealed three common mobile mRNAs (Shab02g014830, Shab10g017190, Shab10g023440). The first transcript, Shab02g014830, shows homology to the MUCILAGE-RELATED 70 (MUCI70) which is a hemicellulose biosynthetic enzyme involved in seed coat in *Arabidopsis thaliana* (Voiniciuc, Engle et al. 2018). The second transcript, Shab10g017190, is likely a stress-associated protein similar to Solyc10g079080 which is specifically the Zinc finger A20 and AN1 domain-containing stress-associated protein 6 (SlSAP6). Genes from this family are responsive to more than one environmental stress, whereby SlSAP6 is the most upregulated of the gene family under salt stress or high heat stress (Solanke, Sharma et al. 2009). Lastly, the Shab10g023440 shows high similarity to a Steroid 5-alpha-reductase (DET2) transcript in tomato which is involved in brassinosteroid biosynthesis. The overexpression of the *DET2* gene in poplar (*Poplus alba* × *Poplus glandulosa*) has been demonstrated to enhance both apical and radial growth resulting in enhanced stem height and diameter (Wang, Hao et al. 2022).

4.4 Discussion

In this chapter, we investigated the molecular mechanisms associated with grafting-induced alterations in tomato with the use of commercial rootstocks from ENZA ZADEN. This investigation compared self-grafted controls to tomato scions grafted onto commercial rootstocks, including RS-1 and RS-2. The RS-1 line has been previously characterised by ENZA ZADEN to introduced enhance vigour by elongating the growing season while maintaining fruit quality. The RS-2 was used as a negative control since it had been previously described to introduce fungal pathogen resistance instead of enhanced crop vigour. Due to unforeseeable problems, the growing season was cut short which made it challenging to observe the full extent of the grafting vigour.

The phenotypical analysis determined that the RS-1 rootstock impacted the scion differently to the RS-2 rootstock which demonstrated similar results to the self-grafted control. There was no difference in the total fruit production between the conditions. The scions grafted onto RS-1 produced fruits with enhanced quality, demonstrated by a higher sugar content, and a reduced weight in comparison to the positive and negative controls. Moreover, as expected the tomato scions grafted onto either RS-1 or RS-2 grow shorter than the self-grafted controls. These results suggested that the heterografts could be regulating their resource partitioning differently to the self-grafted controls.

The molecular mechanisms driving grafting-induced vigour are poorly described, however, recent studies have demonstrated that interactions between the rootstock and scion and induce epigenetic modifications in the

scion (Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016, Cerruti, Gisbert et al. 2021). Using transcriptomic analysis, we observed the downregulation of SlMET1 and SlMET3 genes in the tomato scions grafted onto RS-1. The corresponding *Arabidopsis* homologous gene MET1 is a main methyltransferase enzyme responsible for maintaining CG methylation, and the downregulation of MET1 expression has been linked to genome-wide hypomethylation in the CG context (Cao, Ju et al. 2014, Liu, Wu et al. 2022). Whereas little is known about the *Arabidopsis* MET3 homologous gene, its expression has been shown to specifically occur in the endosperm (Tirot, Bonnet et al. 2022) and recent findings have shown its expression is inducible under brassinosteroid treatment (Goda, Sawa et al. 2004). In previous *solanaceous* grafting studies, differential DNA methylation changes have been observed in the scion in response to interaction with a given rootstock. For instance, grafting vigour was associated with hypomethylation in the CHH context in eggplant scions grafted onto tomato hybrid rootstocks (Cerruti, Gisbert et al. 2021) and similarly genome-wide hypermethylation in the CHH and CHG contexts have been associated with increased resistance to gray leaf spot in tomato scions grafted onto pepper (Liu, Jia et al. 2024). In tomatoes and other fruits, it has been readily shown that DNA methylation affects fruit ripening and fruit quality (based on the sugar-acid ratio) (Li, Wang et al. 2022, Liu, Wu et al. 2022). However, these findings based on fruit quality were based on DNA methylation changes in the fruit tissue.

Plant growth is directly linked to the availability of accessible carbon and energy to the plant apparatus (Calderan-Rodrigues and Caldana 2024). In plants, a significant amount of energy produced though photosynthesis is

stored within dense cell wall polymers, primarily cellulose, hemicellulose and lignin (Pirrello, Jaimes-Miranda et al. 2006, Slavov, Allison et al. 2013). Hence, the molecular mechanisms have been fine-tuned to ensure the optimal investments of energy into the cell wall. In both the heterograft conditions, the rootstocks-scion interactions have initiated transcriptomic changes that suggest they are undergoing cell wall remodelling. In the scions grafted onto RS-1, there is the upregulation of XTHs genes which are involved in cell wall remodelling by cleaving and rebuilding connection between cellulose and hemicellulose. This adjustment can alter cell properties including thickness and size and promote adaptive responses such as drought or salt tolerance as well as the proper control of fruit ripening (Calderan-Rodrigues and Caldana 2024). In sugar beet (*Beta vulgaris)*, both XTH1 and XTH2 homologous genes were identified to be wound inducible and to facilitate secondary cell walls loosen and expansion (Dimmer, Roden et al. 2004). In the transcriptomic data, we also observed the upregulation of secondary metabolite biosynthesis, many of which catalyse fundamental steps in lignin, steroid, and anthocyanin biosynthesis - some of which are upregulated in response to abiotic stress conditions (Liu, Huang et al. 2016). Based on these transcriptomic results, we surmised that the interactions between XTHs and secondary metabolites could result in cell wall remodelling, potentially leading to enhanced secondary cell wall thickening and increased lignin deposits (Kushwah, Banasiak et al. 2020). Alterations to the balance of the deposited cell wall polymers has been demonstrated to affect plant traits (Elkind, Edwards et al. 1990, Sederoff, MacKay et al. 1999, Boerjan, Ralph et al. 2003, Dixon, Srinivasa Reddy et al. 2014). This includes improved tolerance to abiotic stressors, and although stress tolerance was not accessed,

based on these results the heterografted plants could have improved environmental tolerance (Choi, Lee et al. 2023).

Plant hormones play an essential role in coordinating developmental responses for vegetative and reproduction tissues (Aloni, Cohen et al. 2010). Using grafting, their signal transduction has been extensively studied and can initiate new traits (Nanda and Melnyk 2018, Liu, Jia et al. 2024). The transcriptomic results suggest the possible involvement of auxin, jasmonic acid and brassinosteriod signalling in the scions grafted onto RS-1 lines. Jasmonic acid plays an integral role in plant responses to wounding and resistance, and responds to such cue by triggering the activation of TFs (Zhang, Zhao et al. 2019). ERF1 is directly activated by jasmoic acid signalling and activates plant defence-related genes, including those in the phenylpropanoid pathway for the biosynthesis of lignin and flavonoids (Yadav, Wang et al. 2020). Consequently, the expression of ERF1 homologous genes has been associated with improved tolerance to abiotic stress, including drought (Yadav, Wang et al. 2020, Wang, Guo et al. 2024). The signal transduction of jasmonic acid can trigger downstream auxin production. (Zhang, Zhao et al. 2019). Auxin has been demonstrated to have a direct up-regulatory effect on several XTH genes and SlIAA4 – which were both upregulated in our dataset (Nakamura, Yokoyama et al. 2003). In *Citrus* tree grafts, the leaf expression of IAA4 has been negatively linked to plant height (Liu, Li et al. 2017). The existing literature demonstrates that hormone signalling occurs in heterografted plants which contribute to phenotypical traits and demonstrate how hormone responses could be involved within this study.

A growing body of evidence has illustrated the importance of plant mobile RNA signalling molecules in the communication between the shoots and roots (Liu and Chen 2018). These studies have notably demonstrated sRNAs as signalling molecules capable of induce systemic gene silencing through the RdDM pathway (Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016, Cerruti, Gisbert et al. 2021). Yet very few studies have detected multiple graft-mobile RNA signals, at a genome-wide level, and associated their signal transduction with grafting-induced traits (Li, Wang et al. 2021). In previous studies, they have isolated the ability of sRNAs, specifically miRNAs, to induce the production of siRNAs from endogenous genes. Hence, although dis-entangling the regulatory mechanisms that could be in play is extremely challenging (Boualem, Laporte et al. 2008, Zhai, Jeong et al. 2011, Zhao, Meyers et al. 2015). In this study, we detected populations of mobile sRNAs produced by either the RS-1 or RS-2 rootstock in the tomato scions. Between the populations, the RS-1 rootstock produced more mobile molecules in comparison to RS-2, which could be indicative of the interactions between the rootstocks and scion. Using target prediction, we identified putative gene targets of the mobile sRNAs produced by the RS-1 line. The results revealed that gene targets were related to ribosomal small subunit binding and DNA-directed DNA polymerase activity. These processes are essential for transcription and translation, and hence, mediated changes to the expression of these target genes could introduce mRNA-protein imbalances resulting in mRNA degradation or stability issues. The gene targets were overlapped with the transcriptomic results to capture gene targets which were differentially expressed in the leaves of the tomato scions. In total there were four differentially expressed gene targets, with 3 downregulated and one

upregulated. Of keen interest, is the downregulation of SlERF2A (Solyc07g054220). There is little characterisation of SlERF2A, only that it has been associated as a transcription factor induced to confer pathogen resistance (Singh, Foley et al. 2002, Ru, Osorio et al. 2017). Another downregulated gene target was Solyc06g076850, associated with protein binding; although this gene has not been characterised it has been previously determined to be a gene target of a miRNA to initiate a stress response to potassium deficiency (Liu, Tan et al. 2020). Based on ortholog analysis, this gene is likely homologous to Tetratricopeptide repeat (TPR)-like superfamily protein (AT1G07280) which are widely involved in the regulation of cell cycle and protein degradation (Zhou, Zheng et al. 2021).

The traits supporting *Pyrenochaeta lycopersici* resistance are not well described. The fungus is thought to colonise through the roots by degrading cell wall polymers including pectin and lignin (Kaniyassery, Thorat et al. 2023). The RS-2 line did not induced changes to tomato fruit production in non-stress conditions; however, the RS-2 line had been previously described to introduce tolerance to *P. lycopersici*. Hence, it was expected that the molecular interactions between the RS-2 rootstock and scion would be comparable to the self-grafted plants. This was not the case, and the tomato scions grafted on to the RS-2 lines illustrated negative effects to photosynthesis, including the downregulation of chlorophyll a-b binding proteins, and in collaboration with an upregulated expression of cellulose biosynthesis and cell wall waxes including sterols and squalene. In addition, we observe an enrichment on mobile mRNAs with role related to the synthesis of cell wall and glycoproteins. The increased deposition of cell wall waxes is indictive of stress tolerance adaptions, as previously cell

wall wax deposits have been linked to fungal pathogen resistance (Batovska, Todorova et al. 2008, Spanova, Zweytick et al. 2012). However, although these results suggest hampered carbon assimilation and increased carbon allocation to cell wall polysaccharides and lipids, the fruit production were indifferent to the self-grafted controls. That being said, we also observe mobile mRNAs produced by the RS-2 rootstocks that are involved in gluconeogenesis – a metabolic pathway that syntheses glucose from non-carbohydrate sources which could be the driving force behind the carbon re-allocation (Walker, Chen et al. 2021).

To complicate matters further, in *Arabidopsis* cellulose synthesis and deposition was found to be highly regulated by photosynthesis. The complex nature of cellulose synthesis and photosynthesis has been excessively discussed (Boex-Fontvieille, Davanture et al. 2014) and recent suggests have come to pass based on finding from drought tolerant plants varieties. For example, drought tolerance in common bean is thought to derive from sustained photosystem II efficiency (Gregorio Jorge, Villalobos-López et al. 2020). In recent grafted studies in higher plants, the signalling of sugar and cellulose has been identified as an important process for healing in heterografts. This was first recognised by when β-1,4-glucanases was identified as an essential regulatory enzyme to facilitate cell-cell adhesion between grafting partners (Xiao, Zhang et al. 2004, Zhang, Kang et al. 2016, Notaguchi, Kurotani et al. 2020, Xiong, Liu et al. 2021). In plant cells, β-1,4-glucanases catalyses the breakdown of cellulose to glucose and promotes the connections between vascular bundles resulting in healing. Moreover, the transcriptome of grapevine tissue from the graft junction showed an upregulation of cell wall biosynthesis accompanied with downregulation of photosynthesis, and with further analysis of the callus formation at the function

there was indeed an increased accumulation of callose, lignin and cellulose (Cookson, Clemente Moreno et al. 2013). This illustrates the importance of the sugar signalling balance in graft healing.

Due to the vast quantity of graft-inducible traits in tomatoes, seed production companies have invested considerable resources into developing rootstocks lines (King, Davis et al. 2010, Huang, Kong et al. 2014, Singh, Kumar et al. 2020). In tomato grafting, it has been challenging to simultaneously improve both fruit yield and fruit quality (Singh, Kumar et al. 2017, Singh, Kumar et al. 2020). To complicate matters further, grafting combination appears to be stimulated by abiotic stress, whereby abiotic stress hampers tomato yields but enhances the fruit quality (Singh, Kumar et al. 2017). For example, using wild tomato varieties as rootstocks can improve the soluble compounds and vitamin C content in tomato fruits but only when exposed to stress condition such as salinity (Flores, Sanchez-Bel et al. 2010, Singh, Kumar et al. 2017). One proposal has been that the rootstock interactions promote enhanced cell membrane stability, possibly through enhanced calcium uptake from the soil, which prevented excessive ion leakage (Kumar, Rouphael et al. 2015). In this study we utilised, hybrid rootstock lines from ENZA ZADEN that are in part produced through the hybridisation with *S. habrochaites*, the wild and unproductive variety. Based on the results, it appears that the rootstocks could be initiating physiological changes to replicate stress responses which in term have contributed to the improved fruit quality.

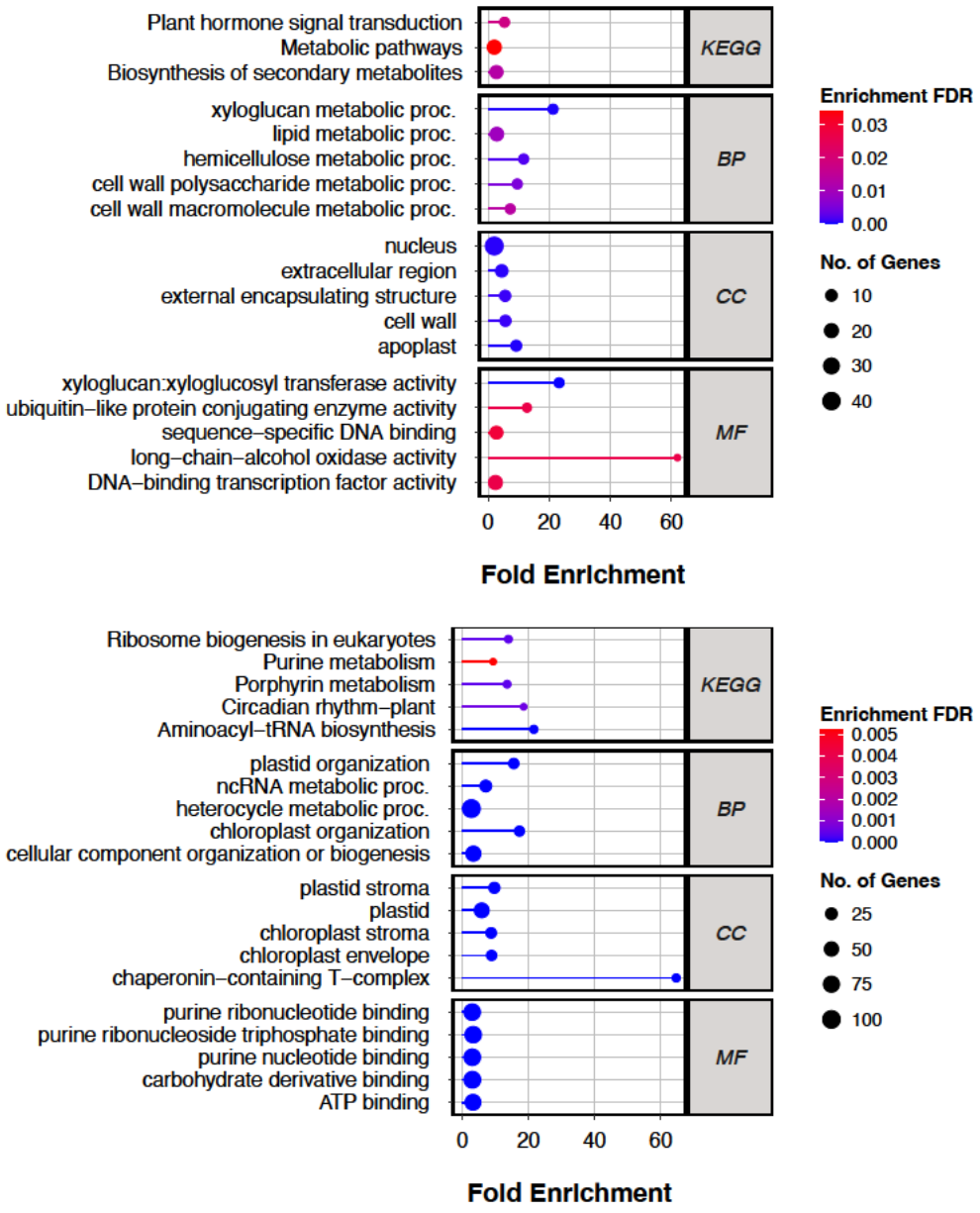
Overall, this study demonstrates that grafting tomato scions on to the commercial RS-1 line can improve fruit quality. In comparison, grafting tomato

scions onto the commercial RS-2 line resulted in no change in fruit production in comparison to the self-grafted controls. In this analysis, we aimed to utilised computational approaches to gain further insight into the underpinning molecular mechanisms associated with grafting traits in tomato. Our results illustrate the complex nature and association between genome-wide transcriptomic profiles and possible regulation through mobile RNA, including sRNAs and mRNAs.

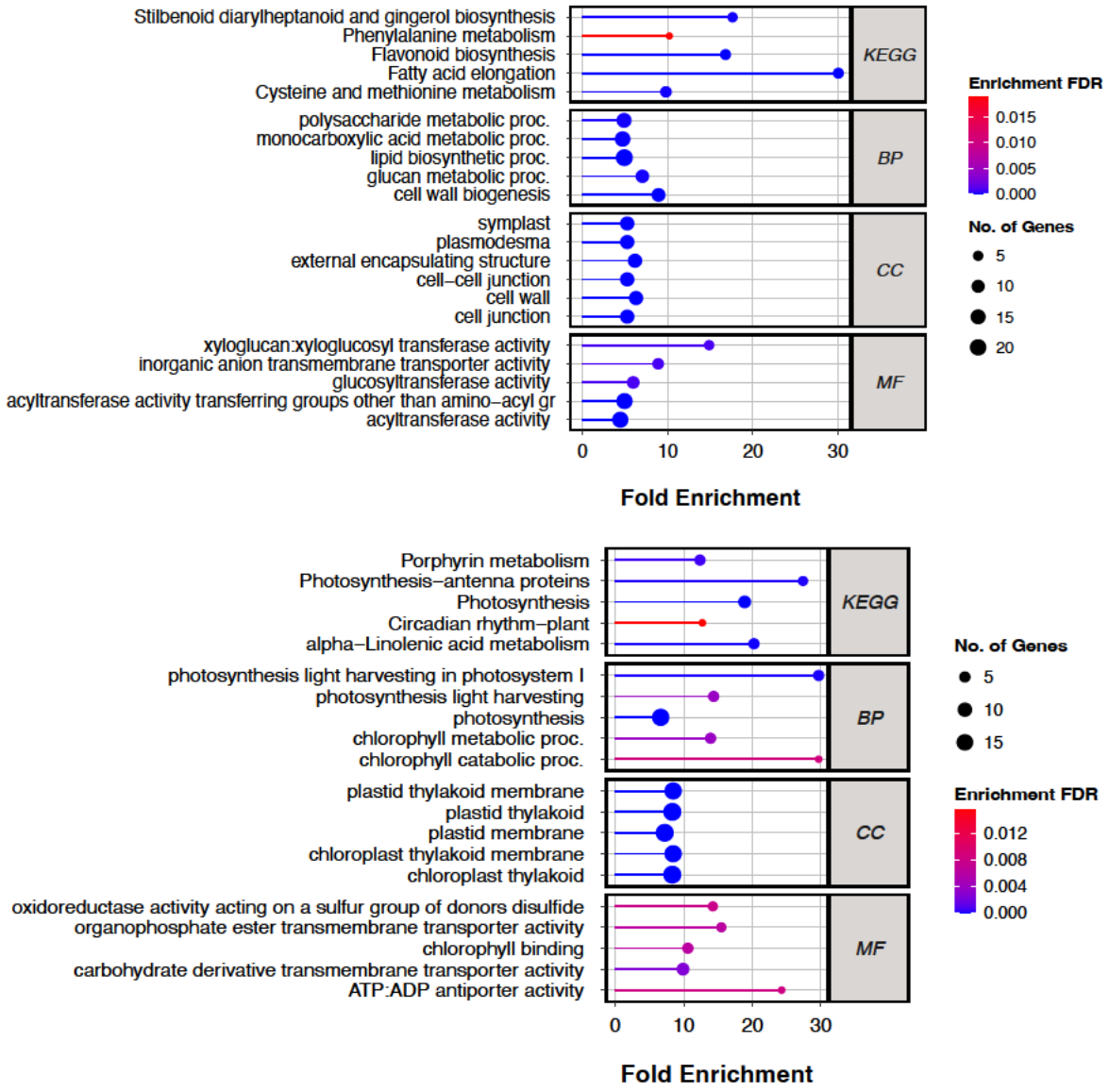
4.5 Supplementary figures and tables

Supplementary Table 4.1. Differentially expressed genes related to photosynthesis.

Analysis	Gene	Homolog	Homolog, other name	logFC	padj
RS-1 vs SELF	Solyc01g066910.3	AT5G48490	DEG15	1.49	0.033
	Solyc01g081490.3	AT1G08540	ABC1	-0.57	0.040
	Solyc03g081240.3	AT5G24470	APRR5	-1.66	0.006
	Solyc04g082010.1	AT1G76100	PETE1	-0.99	0.009
	Solyc07g054210.3	AT4G27440	PORB	-0.43	0.036
	Solyc08g076220.3	AT1G32060	PRK	-0.41	0.015
	Solyc11g012850.2	AT1G44446	ATCAO	-0.46	0.020
	Solyc12g094630.2	AT1G42960	CTI1	0.35	0.040
RS-2 vs SELF	Solyc01g105030.3	AT1G15820	CP24	-0.32	0.043
	Solyc03g081240.3	AT5G24470	APRR5	-1.73	0.000
	Solyc04g082010.1	AT1G76100	PETE1	-0.81	0.014
	Solyc04g082910.1	AT1G76560	CP12-3	-0.90	0.002
	Solyc06g008030.3	AT2G20180	PIF1	-1.16	0.002
	Solyc06g009630.1	AT2G47400	CP12-1	-0.62	0.000
	Solyc06g009630.1	AT3G62410	CP12-2	-0.62	0.000
	Solyc06g051680.1	AT2G40080	ELF4	-1.55	0.009
	Solyc07g063350.3	AT4G27430	CIP7	0.63	0.050
	Solyc09g014520.3	AT3G08940	LHCB4.2	-0.36	0.009
	Solyc10g005080.3	AT1G01060	CCA1	0.85	0.000
	Solyc10g005080.3	AT2G46830	LHY1	0.85	0.000
	Solyc10g006900.3	AT4G27440	PORB	-0.55	0.005
	Solyc11g017470.2	AT1G01720	ANAC2	-0.55	0.023
	Solyc12g006140.2	AT3G27690	DEG13	-0.62	0.003
	Solyc12g006140.2	AT2G05070	LHCB2	-0.62	0.003
	Solyc12g013710.2	AT4G27440	PORB	-0.59	0.005
	Solyc12g094630.2	AT1G42960	CTI1	-0.35	0.012



Supplementary Table 4.2. Gene Ontology (GO) term enrichment analysis in the comparison of tomato scions grafted onto RS-1 and tomato self-grafted scions. A) Upregulated KEGG and GO terms. B) Downregulated KEGG and GO terms.



Supplementary Table 4.3. Gene Ontology (GO) term enrichment analysis in the comparison of tomato scions grafted onto RS-2 and tomato self-grafted scions. A) Upregulated KEGG and GO terms. B) Downregulated KEGG and GO terms.

CHAPTER 5: MOBILE RNAS AND THEIR POTENTIAL ROLE IN GRAFTING-INDUCED TRAITS IN *SOLANACEOUS* HETEROGRAFTS

5.1 Introduction

Plant grafting is a horticultural technique that can combine or introduce novel traits by physically joining multiple plants. For example, it is traditionally utilised to confer biotic/abiotic resistance or increase crop yields (Gaion, Braz et al. 2018, Gautier, Chambaud et al. 2019). Given the benefits of grafting, understanding how traits are introduced would be valuable and advance breeding programs (King, Davis et al. 2010, Thompson, Pico et al. 2017). Some grafting traits can be explained by the intrinsic properties of the rootstock, such as resistance or tolerance to biotic and abiotic stress (Warschefsky, Klein et al. 2016, Colla, Pérez-Alfocea et al. 2017). Whereas other traits, such as improved crop yields under non-stress conditions, are not as easily explainable. Nevertheless, the continued demand for improved yields through grafting in crops like tomato (*Solanum lycopersicum*), cucumber (*Cucumis sativus*) and melon (*Citrullus lanatus*) has prompted seed production companies to place a significant investment in developing rootstocks (Jeynes-Cupper and Catoni 2023).

Researchers have exploited plant grafting as a tool to study the long-distance transport of RNAs (mobile RNAs) between distant tissues and their role in

regulating physiological responses (Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016, Melnyk 2017). The transport of RNAs has been associated to physiological processes such as flowering, potato tuberization (Banerjee, Chatterjee et al. 2006, Bhogale, Mahajan et al. 2014, Ghate, Sharma et al. 2017), changes to leaf morphology (Kim, Canio et al. 2001), root development (Omid, Keilin et al. 2007, Notaguchi, Wolf et al. 2012) and environmental stress tolerance (Haywood, Yu et al. 2005, Wang, Liu et al. 2012, Davoudi, Song et al. 2022). These traits have also been associated with epigenetic changes in the recipient tissues, specifically DNA methylation (Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Lewsey, Hardcastle et al. 2016). For example, eggplant (*Solanum melongena*) grafted to tomato hybrid rootstocks is associated with greater vigour and genome-wide hypomethylation (Cerruti, Gisbert et al. 2021). Conversely, grafting of tomato onto a pepper (*Capsicum*) rootstock, linked to an enhanced resistance to gray leaf spot, revealed hypermethylation in the CHG and CHH contexts in the scions (Liu, Jia et al. 2024). The alterations in DNA methylation have been shown to be trans-generationally inherited in a way which suggests that mobile RNAs could be signalling the immediate and long-term molecular alteration (Cao, Yu et al. 2016, Kundariya, Yang et al. 2020). Down the line, the ability to introduce stable and transmissible epigenetic traits through grafting could offer a platform to develop new crop varieties (Jeynes-Cupper and Catoni 2023).

As mentioned, grafting can induce favourable traits such as improved vigour and these alterations have been linked alterations in the transcriptome and epigenome. To evaluate whether the rootstock signals can change the scion's photosynthetic ability, researchers have utilised advanced field tools to measure

the photosynthetic assimilation as a function of carbon dioxide. In tomato the use of wild-relative rootstocks has been shown to increase water-use efficiency (WUE_i) by diminishing the leaf biomass (Cantero-Navarro, Romero-Aranda et al. 2016). Similarly, tomato heterografts demonstrated changes at a cellular level whereby the leaf mesophyll layer and spongy parenchyma were thicker in comparison to the controls (Nawaz, Wang et al. 2017, Žanić, Vuletin Selak et al. 2018). That being said, although *Solanaceous* heterografting can improve WUE_i in some case it has not resulted in improved crop yields (Fullana-Pericàs, Conesa et al. 2020). Other cases of *Solanaceous* heterografting have exhibited drought tolerance that was associated to improved net carbon assimilation rate, stomatal conductance and sub-stomatal carbon dioxide concentration (López-Marín, Gálvez et al. 2017). In comparison, in cucumber heterografts that exhibited saline stress tolerance demonstrated enhanced Rubisco activity and upregulation of genes in the photosynthesis pathway, ultimately contributing to the plant ability to convert nitrates to amino acids under these conditions (Liu, Bie et al. 2013). These works demonstrate that use heterografting can manipulate carbon fixation in the scion.

The association between genomic and physiological changes associated with grafting induced traits has been weakly studied. In this study, we investigate the interspecific heterografting of tomato onto eggplant rootstocks at the phenotypic, physiological and genomic level in the scion. Both tomato and eggplant are members of the *Solanaceous* family and are graft compatible (Gaion, Braz et al. 2018). Traditionally, tomatoes are grafted onto hybrid tomato rootstock that are a combination of wild and modern cultivars. For example, these rootstocks can introduce drought tolerance in sensitive scions by

regulating abscisic acid (ABA) biosynthesis and signalling pathways (Zhang, Cao et al. 2019). That being said, the regulatory mechanisms driving changes to the scion through the rootstock resulting in new traits requires further research, specifically in *solanaceous* crops (Gaion, Braz et al. 2018). Eggplant cultivars have been previously used as rootstocks to tomato, and such combinations have been associated to gray leaf spit resistance, increased production of reactive oxygen species (ROS), increased fruit quality (increased soluble solid content, increased vitamin C), and inhibited growth resulting in smaller fruit size and reduced yields (Miskovic, Ilic et al. 2016, Zhang, Cao et al. 2019). In our analysis, we observed reduced fruit weight in the tomatoes collected from the heterografts in comparison to the self-grafts. This could be explained by the difference in triose phosphate usage (TPU) which denotes to the allocation and utilisation of carbon. The genomic results suggest that mobile mRNAs could be a source of mobile sRNAs in the destination tissue. Such sRNAs might go onto influence the gene expression, potentially through mechanisms such as target mimicry. Our results reveal a possible molecular mechanism associated to carbon allocation which is potentially diverting more carbon to cell wall modifications which is in line with the observed changes in fruit quality.

5.2 Materials and Method

Plant material and sampling

The grafting experiments utilised tomato (*Solanum lycopersicum*, cv. 'Heinz') as a scion and eggplant (*Solanum melongona,* cv. 'BlackBeauty') as a rootstock (Figure 5.1.A). For additional controls for downstream validation, the opposite graft combination was also undertaken whereby the scion was eggplant and the

rootstock was tomato. This experiment considered six biological replicates for each condition.

Seeds were germinated in soil comprised of compost and perilight, 4:1 respectively, along with slow-release feed pellets (Vitax Q4, Vitax Ltd, Skelmersdale, Lancashire, England). Plants were grown under long day conditions (22°C, 42.6%Rh, 16-h light, 8-h dark, 200umol) in the Wolfson Experimental Glasshouse Facility at the University of Birmingham. Grafting was performed 17 days after germination of seedlings (Figure 5.1.B) and employed the cleft method (Gisbert, Prohens et al. 2011). Grafted individuals were covered with transparent bags for approximately 6 days before cutting the corner of the bag to allow acclimation to the external humidity. Plant feed (solufeed, 18:18:18+3MgO+TE) was applied around fruiting.

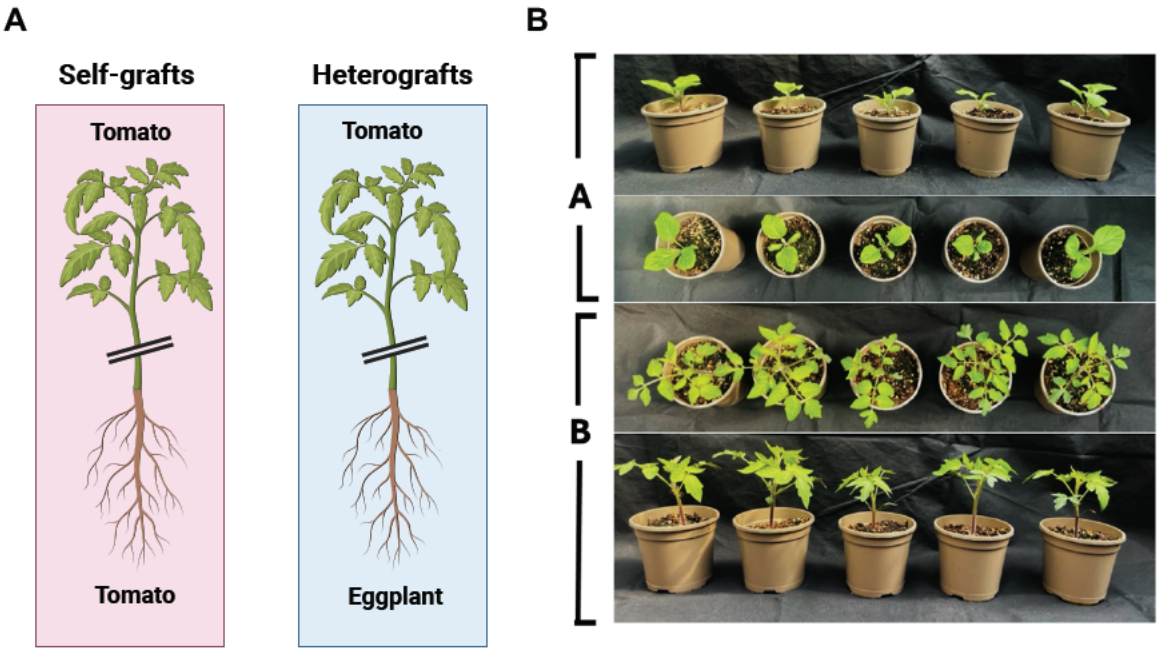


Figure 5.1. Experimental design of plant grafting combinations. Eggplant (*Solanum melongena* cv. BlackBeauty) and tomato (*Solanum lycopersicum* cv. Heinz) were grown and grafted at 2.5 weeks after sowing, where germination occurred around 2 weeks after propagating. A) Illustrates the self-graft control combination (tomato/tomato) and the heterograft combination (tomato/eggplant). B) Picture of plant replicated on the day of grafting where rows A are eggplant replicates and rows B are tomato replicated. Created using BioRender.com.

Plant phenotyping and physiology

Agronomical fruit production variables including fruit yield and fruit weight were measure approximately 4-months after grafting when fruit production had cessed. Plant physiological measurements were taken using a Li-Cor 6800 Portable Photosynthesis System (Li-Cor, Lincoln, Nebraska, USA), specifically to measure leaf gas exchange and the assimilation rate (A). All physiological measurements were taken between 8:00-15:00 on the youngest fully expanded leaf. Differences in leaf area within the chamber were accounted for by determining the coverage of the chamber by photographing the leaf position in the chamber and analysed using open-source image analysis software ImageJ version 1.52a (Schneider, Rasband and Eliceiri, 2012). To measure the leaf gas

exchange, a constant flow rate of 500 μmol s-1 was used, along with the constant cuvette conditions: 400 μmol mol-1 CO_2, vapour pressure deficit of 1 .2 (±0.2) kPa and a 23°C leaf temperature. In contrast, *A* was measured as a function of intercellular Carbon dioxide (CO_2) (Ci) levels commonly known as the A/Ci curves. The A/Ci curves were measured at 1500 μmol m-2 s-1 Photosynthetic Photon Flux Density (PPFD). Before measuring the A/Ci curves, leaves were stabilised in the chamber at the ambient CO_2 level of 400 μmol mol-1. After the first measurements, the CO_2 level in the chamber were dropped at increments and measurements were taken at each. These levels included 300, 200, 100, 80, and 50 μmol m-2 s-1 before returning to ambient CO_2. After which, the CO_2 level in the chamber were increased to 550, 700, 900, 1100, 1300, and 1500 μmol -1. At each new CO_2 level, A was stabilised, and measurements were taken. The data was fitted to the modified Farquhar, von Caemmerer and Berry photosynthesis model that includes the carbon and electron requirements for nitrogen assimilation via photorespiration (Busch, Sage et al. 2018).

Nucleic acid extraction

Leaf samples were taken at 5.7 weeks post grafting during normal growth. 100mg of flash frozen leaf tissue was taken from each biological replicate sample for each condition. Total RNA was extracted using the Trizol reagent (ThermoFisher Scientific, Massachusetts, USA) according to the manufacturer user guide. RNA integrity and purity was assessed using NanoDrop ND-1000 UV-Vis spectrophotometer and the NanoDrop V3.1 software (Labtech International Limited, UK).

Library preparation and sequencing

The RNA library was prepared, and the transcriptome sequenced by Novogene Co., LTD (Beijing, China). mRNA library preparation with conducted with the poly-A enrichment method, and sequencing was undertaken with the on Illumina NovaSeq 6000 (Illumina, California, USA), employing a paired end read length of 150 bp and generated 6 Gb of raw data per sample.

Determining orthologs of photosynthetic genes

A curated list of photosynthesis genes of interest from *Arabidopsis thaliana* were used (Emmerson 2023). The gene orthologs in tomato (Version SL3.0) were determined using EnsemblPlant BioMart-martview. The gene orthologs in eggplant were determined using the tomato orthologs with reciprocal best hit analysis using DNA and protein sequences.

Merged Genome

To facilitate the simultaneous alignment of sequencing reads to both the scion and rootstock genotypes with the *mobileRNA* approach, a merged genome reference was generated. Before combining the individual genome references into a single file (FASTA), a unique prefix is added to each chromosome in each reference. For the analysis, we utilised the *Solanum melongena* version 4.1 genome which has a size of 1,180 Mb (Barchi, Rabanus-Wallace et al. 2021) and the *Solanum lycopersium* cv. Heinz version 4.0 genome with a size of 795.6 Mb (Hosmani, Flores-Gonzalez et al. 2019). Both genomes were downloaded from Sol Genomics Network (Fernandez-Pozo, Menda et al. 2015).

Genome mappability and index calculation

The genome mappability estimates the degree of repetitiveness of a genome (Derrien et al. 2012), and allows users to evaluate how unique or repetitive a DNA regions is in a given genome. Mappability is expressed, at every genomic location, with a score from 0 to 1, where 1 is represents a unique region and 0 represents a hypothetical infinitely repeated region. We used GenMap (1.3.0) (Pockrandt, Alzamel et al. 2020) to compute the mappability at single nucleotide resolution (-K 30) for each of the genome used, taken alone or in combination in pairs (merged genomes). The mean mappability value across each exonic region was determined using BEDtools (bedtools map -c 4 -o mean) (Quinlan and Hall 2010). For each gene, a single mean was obtained by averaging the value of each exon weighted on they nucleotide length. These averaged values have been used to estimate gene repetitiveness in single or merged genomes. The genome mappability index represents the proportion of the merged genome that is above a mappability threshold of 0.5.

Transcriptomic analysis

Transcriptomic analysis was undertaken to identify differences in gene expression between self-grafts and heterografts using RNAseq data. Cleaned mRNA sequencing reads were aligned to the tomato genome (Version 4.1) using HISAT2 (Version 2.2.1) (Kim, Paggi et al. 2019). The raw gene count was calculated using HTSeq (Version 0.12.4) (Putri, Anders et al. 2022). Data was imported into R for downstream analysis. FPKM was calculated for each sample, and transcripts with zero raw read counts were excluded from analysis. Outliers were removed based on principal component analysis. Differential analysis was undertaken with *DESeq2* (Love, Huber et al. 2014), and DEGs were selected based on a p-adjusted value < 0.05. Functional analysis comprised of

the use of NCBI, Sol Genomics Network resources (https://solgenomics.net/) and GO enrichment analysis with ShinyGO (Ge, Jung et al. 2020).

Detection of mobile mRNA molecules

To detect mobile mRNA molecules travelling from root-to-shoot in heterograft combinations, the Bioconductor/R package, *mobileRNA*, was utilised. Cleaned reads were aligned to the merged genome (*S. melongena* genome version 4.1 assembly (Barchi, Rabanus-Wallace et al. 2021) and *S. lycopersicum* genome version 4.0 assembly (Hosmani, Flores-Gonzalez et al. 2019)) using HISAT2 (Kim, Paggi et al. 2019) with default settings. Aligned reads were filtered to select only those which aligned to a single location, discarding reads which aligned to multiple locations. This was accomplished by utilising the "NH:i:1" flag. Filtered reads were sorted using SAMtools (Danecek 2021). Raw counts for mRNA transcripts were surmised by HTSeq (Putri, Anders et al. 2022) (--order=pos -a=0 --stranded=no --mode=union --nonunique=none --type=mRNA --idattr=ID). Downstream analysis of raw count files was undertaken using the Bioconductor/R package, *mobileRNA* (Jeynes-Cupper and Catoni 2023). The analysis calculated the FPKM, transcripts with a raw count value of zero were discarded. This was followed with GO term enrichment analysis with a custom script and protein-interaction analysis with STRINGdb (Szklarczyk, Kirsch et al. 2023). Analysis of tRNA-like structures was undertaken using RNAmotif (Macke, Ecker et al. 2001). In the eggplant genome, tRNA genes were detected using ARAGORN (Laslett and Canback 2004). *De novo* motif identification was undertaken with MEME suite (Bailey, Johnson et al. 2015). Read coverage was calculated using BEDtools (Version 2.29.2) (Quinlan and Hall 2010).

sRNA analysis & detection of mobile sRNA molecules

Raw sRNA sequencing reads were cleaned and trimmed using Trim Galore (version 0.6.5) to remove adaptor sequences, low quality reads and eliminate reads shorter than 16 nucleotides or longer than 30 nucleotides (Krueger F 2021). Reads were aligned to the merged genome using Bowtie (-p 6 -v 0 -a -m 1) (Version 1.3.1) and sorted using SAMtools (Version 1.17) (Langmead, Trapnell et al. 2009, Danecek 2021). ShortStack (Version 4.02) was utilised to undertake *de novo* sRNA clustering (Axtell 2013, Shahid and Axtell 2014). ShortStack identifies sRNA clusters (sometimes referred to as sRNA-producing loci) by building "islands" which are genomic locations defined by the minimum alignment depth/coverage and the required distance between "islands". sRNA clusters were selected between nucleotides of 21-24 and clusters were defined by a minimum coverage of 0.5 RPM and with a 200-nucleotide distance between "islands" (--dicermin 20 --dicermax 24 --pad 200 --mincov 0.5). For each dataset, a sRNA loci file was generated which contained all *de novo* sRNA clusters identified across the sample replicates. Analysis with ShortStack was repeated utilising the sRNA loci file to define the sRNA clusters in each sample. Results were imported into R and downstream analysis was undertaken using the Bioconductor/R package, *mobileRNA* (Jeynes-Cupper and Catoni 2023). Differential analysis was performed with the DESeq2 method (Love, Huber et al. 2014).

To identify genomic features associated with the sRNA-producing loci, otherwise called a sRNA cluster, *mobileRNA* overlapped the genomic regions with a genome annotation file(s). Target prediction analysis with psRNAtarget (Dai, Zhuang et al. 2018) was undertaken using the consensus sequence for each mobile sRNA identified by *mobileRNA*. This was followed with GO enrichment analysis using ShinyGO (Ge, Jung et al. 2020)or custom scripts.

5.3 Results

Homology of coding regions between tomato and eggplant genomes

Eggplant and tomato are economically important plant species a part of the *Solanaceous* family, which also includes peppers and potatoes. These two diploid species diverged around 15.5 million years ago, yet despite that the two genomes have maintained some similar characteristics (Wu and Tanksley 2010). This includes chromosome features, such as the number of chromosomes (2n=24), and chromosome architecture (Wu, Mueller et al. 2006). Comparative mapping studies have demonstrated that the genomes of *Solanaceous* species differ largely due to inversions during genome rearrangement, in which there are 24 inversions and 5 translocations between tomato and eggplant (Wu, Eannetta et al. 2009). In comparison, potato and tomato diverged more recently (~7.3 million years ago) and 6 inversions have been isolated between the two genomes (Tanksley, Ganal et al. 1992).

In this study, we utilized the tomato genome reference for Heinz 1706 (SL4.0, ITAG4.0) which was assembly *de novo* using PacBio long reads which were scaffolded with Hi-C contact maps (Hosmani, Flores-Gonzalez et al. 2019). The

assembly has a size of 782,520,133 bp with only 0.006% N bases and the analysis implied a 99.24% completeness of the genome assembly with 71.77% of the assembly being repetitive (Hosmani, Flores-Gonzalez et al. 2019). The annotation contains 34,075 protein coding genes with 87% containing a predicted function (Hosmani, Flores-Gonzalez et al. 2019). In contrast, our work used the eggplant pan-genome reference assembly that was generated from 23 eggplant accession and one accession each from the closest wild relatives of *S. insanum* and *S. incanum*. The assembly is 1.16 Gb in size and only 9.10% of the base pairs are Ns, along with 34,916 protein coding genes in the annotation (Barchi, Rabanus-Wallace et al. 2021).

To detect mobile RNAs moving from the eggplant rootstock into the tomato scion, we utilised the *mobileRNA* approach. This approach leverages the sequence polymorphisms and structural variations between the scion and rootstock genomes to distinguish the genomic origins of sequencing reads. This is accomplished by supplying a merged genome as the reference to the alignment tools, minimising the need for complex downstream selection processes. The algorithms employed by mapping tools have been purposely built to place reads to the best location in the provided genome reference by considering sequence variations and sequencing errors. However, this method accepts a reduced mapping efficiency subject to the level of homology between the two genomes. The homology can be estimated using a genome mappability score that measures the uniqueness of the coding regions of each genome when combines into a merged reference. The genome mappability was calculated for the tomato and eggplant genomes, and illustrated that 77.1% and 69.7% of the genomes, respectively, were highly unique (mappability >0.5) (Figure 5.2).

Similarly, the mappability of the merged genome was compared to the individual genomes and illustrated a similar proportion of highly unique regions. These results infer that the merging of the two genomes did not significantly impact the mappability, and sequencing reads will likely be placed to their correct genomic origin with high confidence.

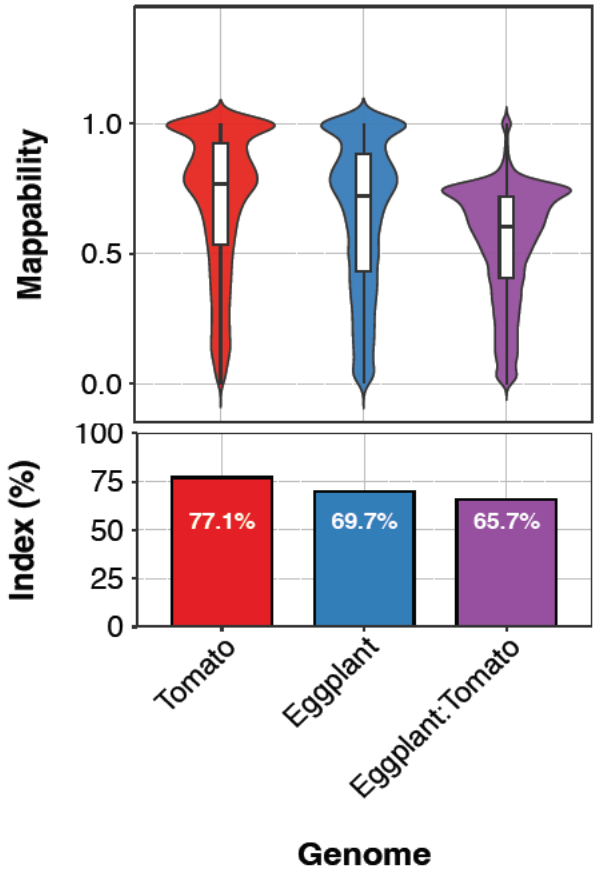


Figure 5.2. Comparison of eggplant and tomato genomes. Genome mappability for individual eggplant and tomato genome references against the merged genome references. The genome mappability value is represented as in a scale of the schema where 0-1 where 0 represents a highly repetitive region and 1 signifies a highly unique region. The genome mappability is calculated across the genome, and the plot illustrates the distribution across coding regions of the genome. The Index (%) is the proportion of the genome with a mappability above 0.5

Generating orthologs of photosynthetic genes from *Arabidopsis thaliana*

Here, we characterise the orthologs of photosynthetic genes of interest from *A. thaliana* in tomato and eggplant. Photosynthetic genes have been well characterised in *A. thaliana*, and based on current literature a list of genes of interests were previously curated by Dr R Emmerson (Emmerson 2023). The tomato orthologs of *Arabidopsis thaliana* are publicly available through BioMart in Version 3 of the tomato genome. Annotated gene names in Version 3 are easily converted to the gene names in Version 4. The eggplant orthologs are not publicly available, henceforth, the eggplant orthologs were computed using reciprocal BLAST DNA and protein sequence analysis to the tomato orthologs. Figures 5.3A-C show the results from reciprocal analysis of DNA sequence analysis and D-E show the protein sequence analysis. The two analyses show similar results, as expected the protein analysis displayed improved results. The bit score is a value which represents how good the alignment between sequences were, here, a higher score indicated a better alignment. Figures 5.3.A and 5.3.D show a histogram of the best reciprocal matches and from a value upwards of 4 log-bit score orthologs have a high sequence similarity. Without the reciprocal analysis additional noise is generated, and small peaks around 1-3 log-bit score are observed. These smaller peaks are representative of matches with either a short sequence with high similarity or long sequences with low similarity. The 3-dimensions of the comparison between the bit score and the percentage identical residues where the darkness/intensity of the colour refers to the frequency were accessed (Figures 5.3.B-E). The best matches lie in the upper half of the plot. Figures 5.3.C and 5.3F show the proportion of the query sequence that covers the total region of the subject sequence. The most probably

best matches are in the top righthand corner. In comparison, values in the bottom lefthand corner may represent times where a larger proportion of the query is covered by the target, therefore, represents poor candidates for functional homology.

Based on the exploratory results (Figure 5.3), filtering considered the output from the analysis. From the DNA sequence analysis, the dataset was filtered to select homologs with a percentage identify greater than the anti-logarithm (exponentiation) of 4.3, a bit score greater than the anti-logarithm (exponentiation) of 5 and a percentage differential coverage above 10. Similar filtering was utilised for protein orthologs, including thresholds of a percentage identify greater than the anti-logarithm (exponentiation) of 4.3, a bit score greater than the anti-logarithm (exponentiation) of 4.5 and a percentage differential coverage above 10. The results were joined to produce the final list of eggplant homologs. There were 26 genes of interest that did not have an identified ortholog in tomato and 43 genes of interest that did not have an identified ortholog in eggplant. Of the gene of interests from *Arabidopsis thaliana* we located 121 orthologs in tomato and 102 orthologs in eggplant.

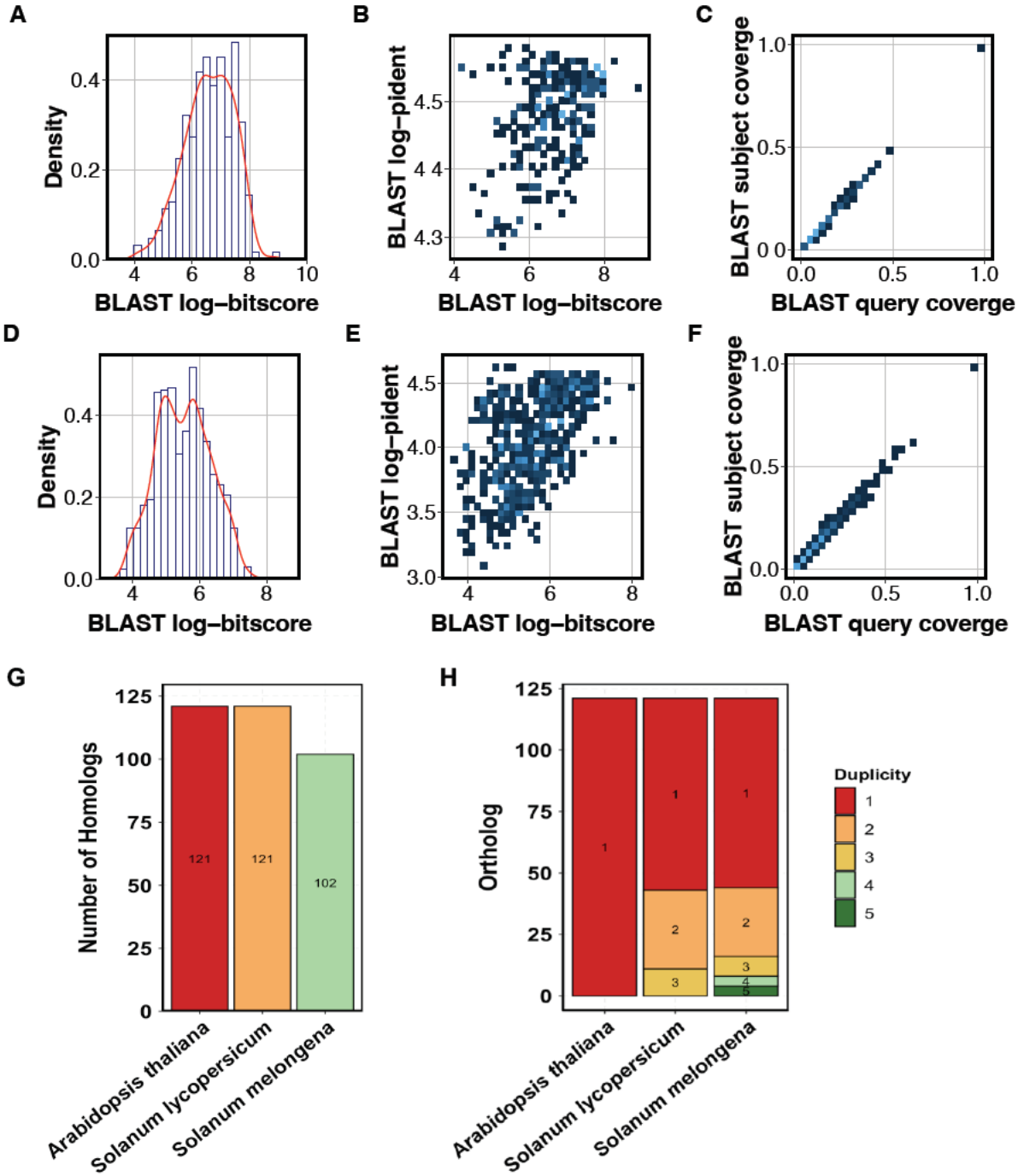


Figure 5.3. Exploratory analysis of results from reciprocal BLAST analysis of DNA and protein sequences. The plots A-C show results from DNA sequence analysis and plots D-F show results from protein sequence analysis. Candidate homologs were selected based on the reciprocal identification of matches between the two genomes, this refers to undertaking two BLAST analyses where each genome is either the query or the subject. Plot axes refer to values generated from BLAST including the log transformation of the bit-score and percentage identity and scaled coverage. G) Illustrates the distribution in the number of photosynthesis gene orthologs within the three genomes (*Arabidopsis thaliana*, tomato; *Solanum lycopersicum*, eggplant; *Solanum melongena*). H.) Illustrated the distribution of the duplicity of a photosynthesis gene ortholog in the three genomes (*Arabidopsis thaliana*, tomato; *Solanum lycopersicum*, eggplant; *Solanum melongena*).

Eggplant rootstocks alter fruit yields & carbon allocation from photosynthesis

The weight of individual fruits and the total number of fruits were recorded for each replicate. In the self-graft condition, of a total of 201 fruits from six replicates had a mean weight of 22.86 g (sd=12.3). In the heterografts, the average fruit weight was 19 g (sd = 9.12) across 244 fruits from seven replicates. As expected, the eggplant rootstock impacted fruit production, specifically resulted in lighter fruits. This phenotypes has been previously observed (Liu, Jia et al. 2024) (Figure 5.4.A). There was no difference in the total fruit production or the total biomass production (Figure 5.4.B-C). This suggests that the overall productive output of the heterografted plants is not severely affected, yet grafting does affect fruit quality based on the changes in weight.

To access whether heterografting impacted photosynthesis in the scion, we measured the leaf gas exchange and the assimilation rate. No changes were observed in photosynthetic capacity (Supplementary Figure 5.1) yet there was a statistically significant increase in the triose phosphate utilisation (TPU) compared to the self-graft condition (Figure 5.4.D). TPU is the process by which triose phosphate are utilised from photosynthesis (McClain and Sharkey 2019). The results reveal that although photosynthetic rate is not changed, the heterografted plants can fix carbon more efficiently. The phenotypic results suggest the extra carbon is contributing to changes in fruit quality, possibly through the differential expression of metabolic processes. Furthermore, using the reciprocal grafts (eggplant/eggplant vs. eggplant/tomato), we show that there is a statistical difference ($p = 0.02392$) between the tomato and eggplant

scions implying they are not similar, and the tomato/eggplant TPU is distinct. That being said, the mean TPU in the eggplant/eggplant samples were 6.7 mol $m^{-2}s^{-3}$ and in the tomato self-grafted samples the mean was 3.5 mol $m^{-2}s^{-3}$, while the tomato heterografted samples were averaging at 5.0 mol $m^{-2}s^{-3}$. This observation indicates that the TPU of the tomato heterografted plants lies between the mean values of the self-graft controls (Supplementary Figure 5.2).

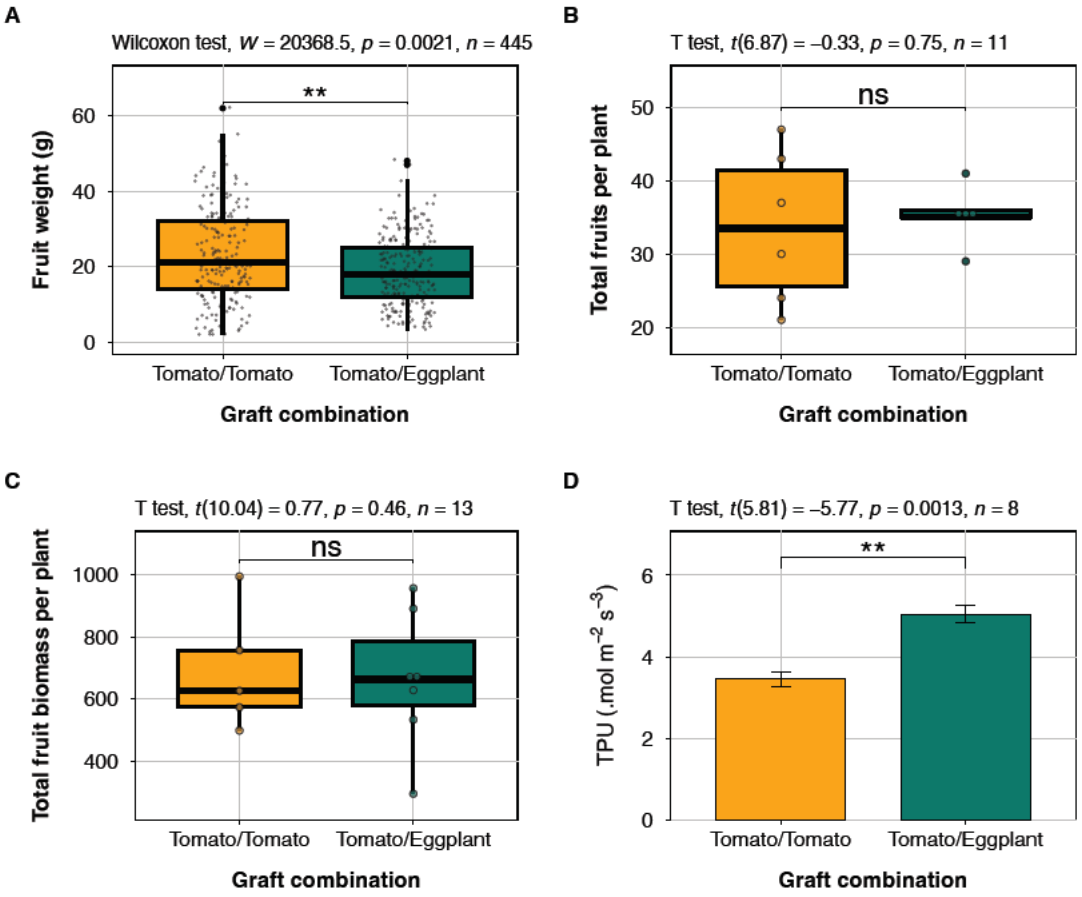


Figure 5.4. Phenotypic traits, including fruit production and physiology. The grafting combinations are referred to Tomato/Tomato self-graft and Tomato/Eggplant heterograft. A) The fruit weight in grams of all fruits in each condition. Statistical analysis was undertaken using a Wilcoxon test; $W = 20368.5$, $p = 0.0021$, n = 445. B). The total number of fruits produced by each replicate within a condition. Statistical analysis was undertaken using a *T*-test; $t = 0.33$, $p = 0.75$, n = 11. C) The total fruit biomass per plant in each condition. Statistical analysis was undertaken using a *T*-test; $t = 0.77$, $p = 0.46$, n = 13. D) The Triose Phosphate Utilisation (TPU) (mol $m^{-2}s^{-3}$) of replicates in each condition. Error bars represent mean standard error. Statistical analysis was undertaken using a *T*-test; $t = -5.77$, $p = 0.0013$, n = 8.

Eggplant rootstocks alter the transcriptomic profile in the tomato scion

We observe that the transcription profiles of tomato scions grafted onto eggplant rootstocks cluster well together and are divergent from the self-graft controls. This suggests that the transcription profiles are associated with grafting-induced phenotype (Figure 5.5). The differential expression analysis identified 1,103 DEGs out of 23,169 genes (4.8%) with a greater number of upregulated genes to downregulated genes in the tomato scions grafted onto the eggplant rootstock. Specifically, we observe 631 (2.8%) upregulated and 462 (2%) downregulated genes – of which, there are six upregulated gene that are classified as essential photosynthetic genes of interest (Figure 5.5 & 5.6).

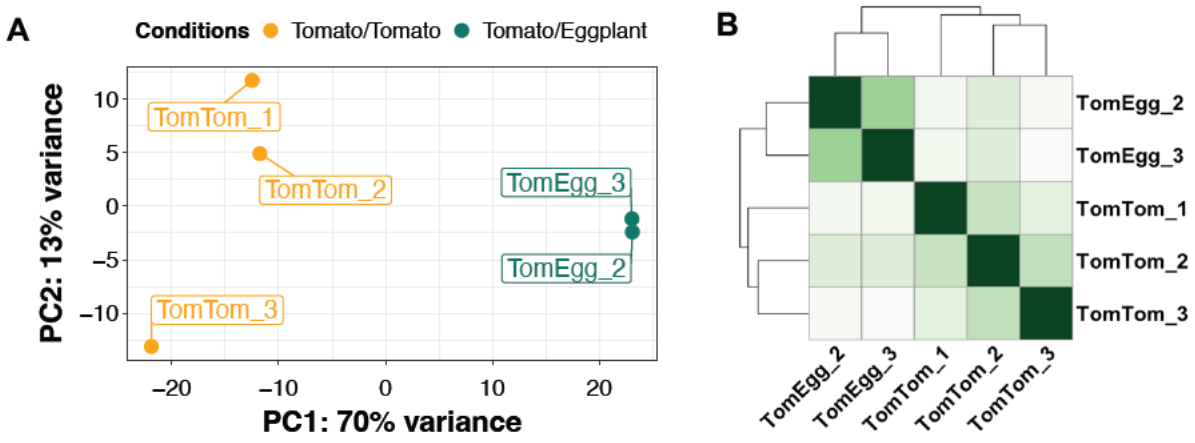


Figure 5.5. Clustering and quality control assessment of RNAseq samples. Raw gene count data was transformed using a variance stabilizing transformation format skipping the re-estimation of the dispersion. The Tomato/Tomato self-graft controls (n=3) are denoted as "TomTom", and the Tomato/Eggplant heterograft samples (n=2) are denoted as "TomEgg". A) Principal component analysis (PCA) of transformed counts shows tomato/tomato self-graft controls (n=3) in orange, and the tomato/eggplant heterograft samples (n=2) in green. B) Distance matrix of tomato/tomato self-graft controls and tomato/eggplant heterograft samples where the colour intensity represents the similarity. A greater colour density represents a closer similarity.

The differential expression analysis suggests that there is a grafting-induced mechanism driving these changes, possibly by epigenetic means, such as changes in DNA methylation and the involvement of sRNAs. To investigate whether there could be changes in DNA methylation patterns we studied the expression of 25 genes related to DNA methylation, including those that encoded DNA methyltransferase and demethylase enzymes, in the scion (Figure 5.6.D). While there were no changes in 23 genes, the expression of genes SlAGO4 and SlDRM1 were upregulated in the heterografts (Figure 5.6.D). Both SlAGO4 and SlDRM1 are associated with the RdDM pathway. This suggests the control of epigenetic regulation in the scion could be different in the heterografts compared to the self-grafts. For example, due to their role in RdDM there could be alterations in *de novo* DNA methylation patterns.

To investigate whether the DEGs were involved in biological processes that could help us explain the alterations in carbon allocation we undertook GO term enrichment analysis. In the heterografts we observed upregulated DEGs to be enriched ($p < 0.05$) in functions relating to transmembrane transport and homeostasis (cellular and cell redox) with a cellular function within the extracellular space and at the cell interface (Figure 5.7.A). The molecular function of the upregulated genes is related to oxidoreductase activity specifically for glutathione and disulfide, protein-disulfide reductase activity, and electron transfer activity (Figure 5.7.A). There functional relations were surmised by KEGG analysis that grouped the upregulated genes into key functions including plant hormone signal transduction, metabolic pathways, MAPK signalling pathways, and cutin suberin and wax biosynthesis (Figure 5.7A). The downregulated DEGs we observed an enrichment in genes relating

to glutamine family catabolic processes and secondary metabolic processes which were concentrated in the cell membrane (Figure 5.7.B). Using KEGG analysis we showed that the downregulated genes were related to flavonoid biosynthesis, biosynthesis of secondary metabolites, and phenylpropanoid biosynthesis (Figure 5.7.B).

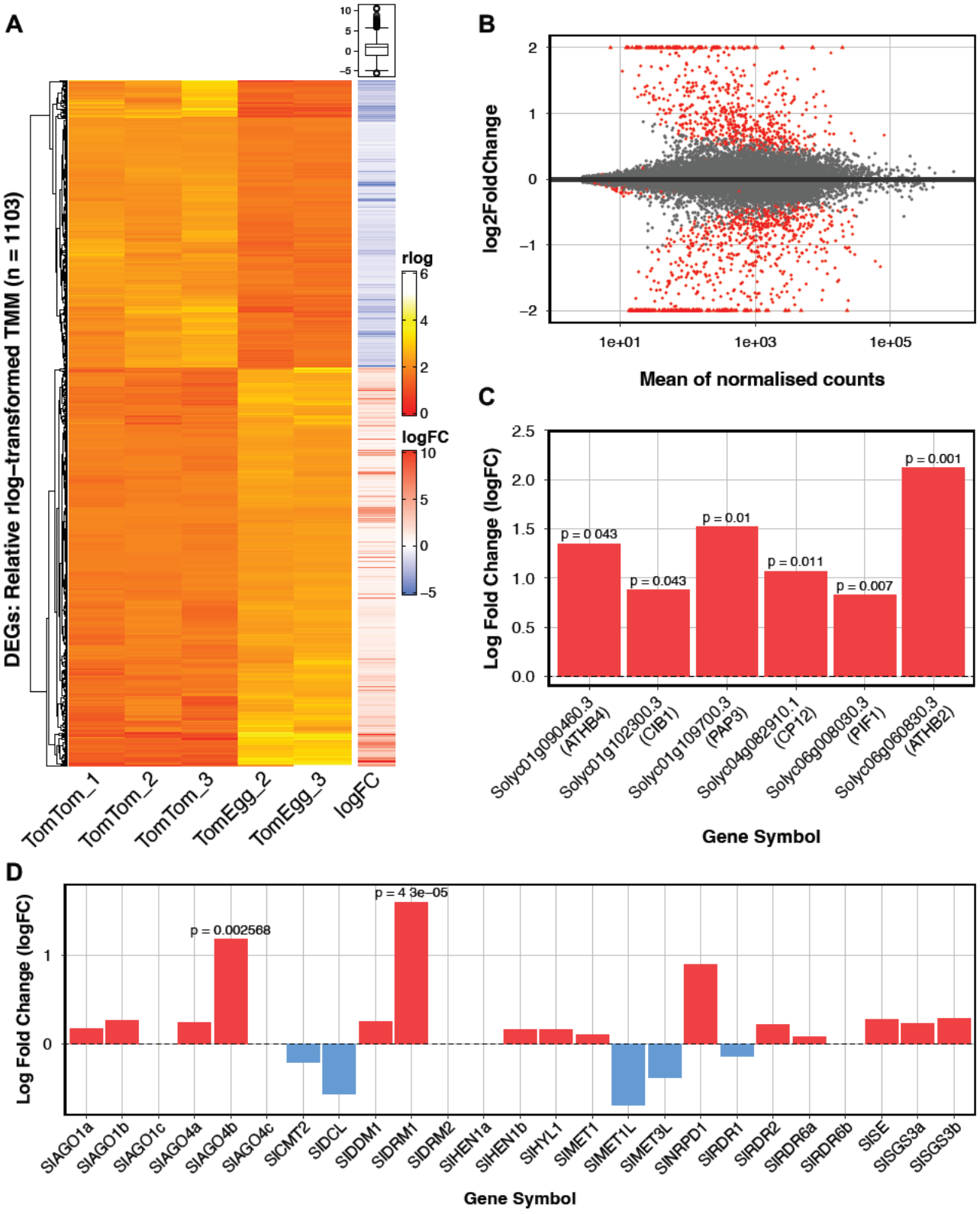


Figure 5.6. Transcriptomic analysis of tomato scions in heterografted plants and self-grafted controls. The Tomato/Tomato self-graft controls (n=3) are denoted as "TomTom", and the Tomato/Eggplant heterograft samples (n=2) are denoted as "TomEgg". A) Heatmap illustrating the relative rlog-transformed TMM values of differentially expressed genes (DEGs, $p < 0.05$) and ordered based on the log2 fold change (logFC) and hierarchical clustering of expression. The resulting Euclidian cluster dendrogram is visible to the left. Each column

represents a sample replicate, and each row represents a gene (n = 1,103). The gradient bars on the right show the expression level for rlog values and log fold change. B). MA-plot of shrunken log2 fold change values. The log2 fold change values were shrunken to remove background noise associated with values from low count genes without the need to utilise arbitrary filtering thresholds. Each point represents a gene, red points represent genes with an FDR < 0.1. C) Bar plot representing photosynthetic genes which were differentially expressed ($p < 0.05$) and are represented as the tomato gene name with the common *Arabidopsis thaliana* ortholog name in brackets. Red bars represent upregulation (logFC > 0), and text annotation above the bars displayed the FDR, *p-value.* D). Bar plot representing genes associated with DNA methylation which were differentially expressed ($p < 0.05$) and are represented as the common name. Red bars represent upregulation (logFC > 0), and blue bars represent downregulation (logFC < 0) and text annotation above the bars displayed the FDR, *p-value*.

Based on these results we can infer that the alteration in the heterograft phenotype could be related to transcriptional changes in metabolic and transport processes, plus redox homeostasis. We observed enhanced TPU in heterografts, no changes in fruit production, but a change in fruit quality – specifically a reduction in fruit weight. These results suggested that carbon allocation is being directed to other physiological processes. The upregulation of oxidoreductase activity could contribute to cell wall mortifications, altering its composition and structure. Similarly increased oxidoreductase in the vacuole and extracellular components may improve the detoxification of harmful reactive oxygen species (ROSs). In the vacuole this can support the storage of sugars whereas in the extracellular components this could contribute to increase efficiency in cellular communication and nutrient transport. Whereas the downregulation of secondary metabolite pathways suggest that the fruit may have reduced levels favourable components that contribute to the fruit development, such as flavonoids.

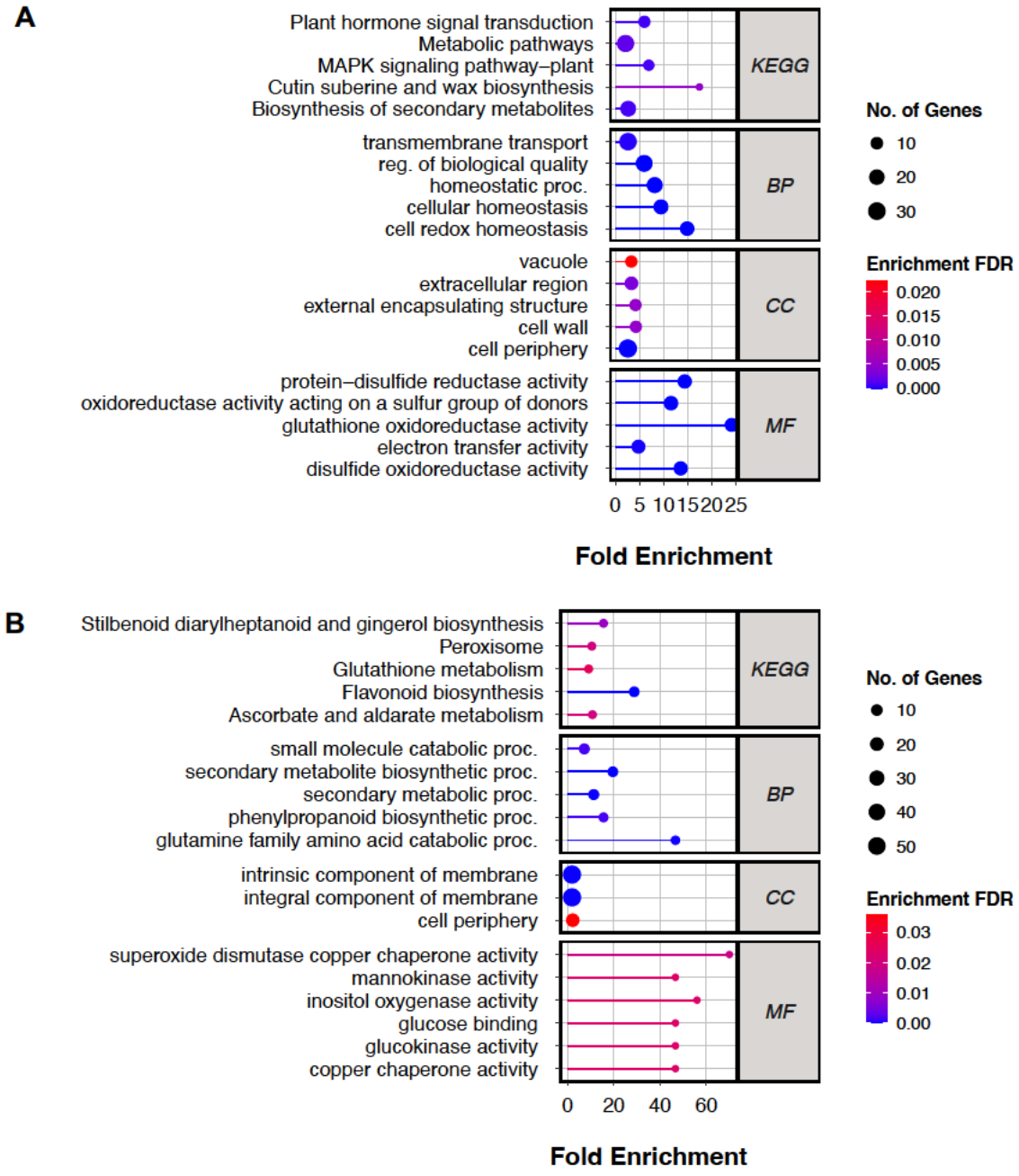


Figure 5.7. KEGG and GO term enrichment analysis of differentially expressed genes. The differentially expressed genes (DEGs, $p < 0.05$) were split into two group, upregulated genes and downregulated genes. Each group underwent enrichment analysis using ShinyGO (Ge, Jung et al. 2020). The panels are split based on type, whereby "KEGG" represents KEGG, "BP" represents biological processes, "CC" represents cellular compartment and "MF" represents molecular function. A) Enrichment terms for upregulated genes ($n = 631$). B) Enrichment terms for downregulated genes ($n = 462$).

Small RNA populations in the scion differ in heterografts

To investigate whether the population of sRNAs produced by the scion changes in response to heterografting with an eggplant rootstock. On average, in tomato self-graft controls 17.5% of reads aligned uniquely to the tomato genome, whereas in the heterograft samples 18.3% of reads aligned uniquely to the tomato genome (Supplementary Table 5.3). Across the self-graft samples, 137,042 tomato sRNA clusters were identified and 136,833 were in the heterograft samples. This demonstrated that heterografts produced 0.15% fewer native tomato sRNAs than self-grafts. The results revealed that the samples in each condition cluster together, however as we may expect any difference are minimal as demonstrated by the PCA analysis (Figure 5.8.A & Figure 5.8.B).

The sRNA length plays an important role in distinguishing different sRNA types. In plants, this typically ranges from 20-nt to 24-nt long whereby miRNAs have a length between 20-22-nt and siRNAs have a length of 24-nt. The abundance of each sRNA class was comparable between samples and conditions, however, the heterograft samples showed greater consistence between samples. Interestingly, we observed a greater number of 23-nt sRNA across all samples in comparison to 21- or 22-nt sRNAs which was not expected since we expect a peak in 21-22-nt over 23-nt sRNAs (Figure 5.8.C).

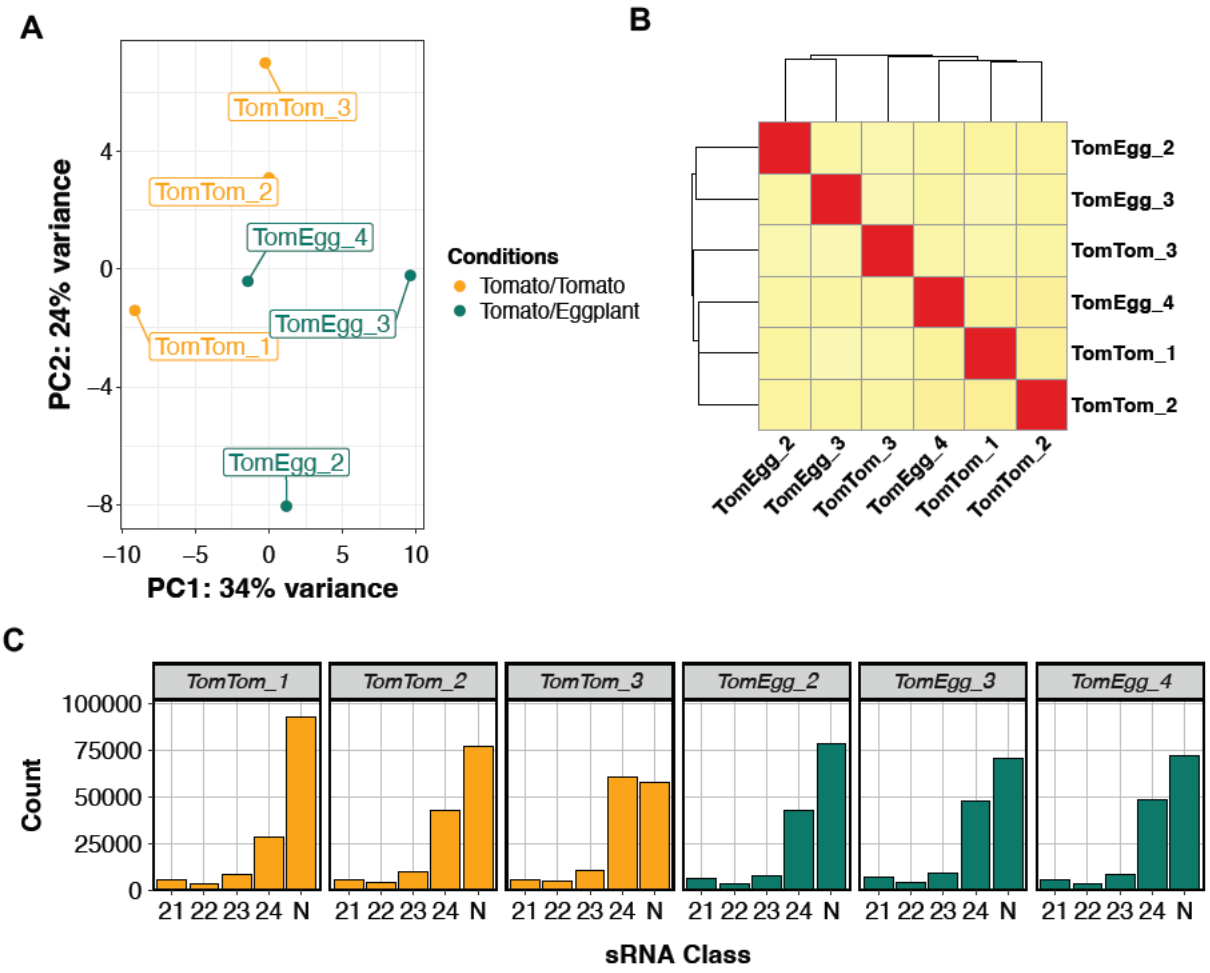


Figure 5.8. Variability in tomato sRNA population in self-graft controls and heterografts samples. Raw tomato sRNA count data was transformed using a variance stabilizing transformation format skipping the re-estimation of the dispersion. The tomato/tomato self-graft controls (n=3) are denoted as "TomTom", and the tomato/eggplant heterograft samples (n=3) are denoted as "TomEgg". A) Principal component analysis (PCA) of transformed counts shows tomato/tomato self-graft controls (n=3) in orange, and the tomato/eggplant heterograft samples (n=3) in green. B) Distance matrix of tomato/tomato self-graft controls and tomato/eggplant heterograft samples where the colour intensity represents the similarity. A greater colour density represents a closer similarity. C) Distribution of sRNA lengths as classes from 21-24 nucleotide (nt). "N" refers to unclassified or unambiguous size classification.

To access the variability in the population of tomato sRNA between the self-graft controls and the heterograft samples, differential quantitative analysis was undertaken to investigate the loss/gain ratio and the differential abundance of sRNAs. We revealed that there were 29,728 statically significant sRNA (FDR, $p < 0.05$), whereby 15,075 were showed an upregulated expression and 14,653

sRNAs illustrated a downregulated expression. These sRNAs are further described as "DE-sRNAs".

Log fold change was utilised as further filtering criterion to assist downstream analysis by prioritising sRNAs that have a larger magnitude of change. Here, we looked to define a meaningful log2 fold change threshold to reduce noise and select sRNAs with a biological relevance. Consequently, the log2 fold change threshold was set at +/- 3 based on the results to mitigate background noise (Supplementary Figure 5.3). As a result, we selected for 696 differential sRNAs; 302 upregulated and 394 downregulated (Figure 5.9.A). Of the 302 upregulated sRNAs, 257 (85%) are solely produced in the heterografts and not located in the self-grafts (denoted as gained sRNAs). In comparison, 344 (0.87%) of the downregulated sRNAs are not synthesised in the heterografts (denoted as lost sRNAs) (Figure 5.9.A).

To investigate the distribution and functional role of the upregulated and downregulate sRNAs we explored the genomic features which their cluster overlap with, specifically, mRNA, exons, gene, promoter, 5' UTR and 3' UTR. There were 104 (34%) upregulated sRNAs which were associated with genomic features, and all overlapped with more than one features (Figure 5.9.B). Similarly, there were 157 (40%) downregulated sRNAs which were associated with genomic features and all overlapped with more than one features (Figure 5.9.B). We expanded the analysis of sRNA-producing genes to investigate the functional role by identifying DE-sRNAs which the overlapped with genes and their +/- 1 kb (upstream, downstream) regions. There were 144 upregulated sRNAs which overlapped with these regions, and the genes were enriched in

functions related to Dephosphorylation of RNA polymerase II C-terminal domain, transcription by RNA polymerase I, post-transcriptional regulation of gene expression and negative regulation of macromolecule metabolic processes. Similarly, 199 downregulated sRNAs which overlapped with 211 gene regions, however, none of these genes had an ontology annotation thus we were unable to draw a functional enrichment.

Many sRNAs produced in plant species are derived from repeat sequences, including TEs, and play a crucial role in the epigenetic silencing of these regions (Simon and Meyers 2011). Major changes in these sRNAs have been associated with alteration in chromatin structure, which ultimately affects the genome architecture (Simon and Meyers 2011), and since around 72% of the tomato genome is repetitive it is expected that the role of sRNAs in epigenetic silencing of TE activity cannot be understated (Hosmani, Flores-Gonzalez et al. 2019). In this study, we investigated the sRNAs derived from repetitive regions and revealed that 196 (65%) of upregulated sRNAs and 246 (62%) of downregulated sRNAs are produced within repeat sequences (Figure 5.9.B). More specifically, we also explored sRNAs produced by TEs and observed that 104 (194 including putative TEs) upregulated sRNAs overlapped with TE superfamilies – the most enriched being Gypsy (Figure 5.9.C). In contrast, 137 (240 including putative TEs) downregulated sRNAs overlapped with a TE superfamily, whereby Gypsy was the most enriched (Figure 5.9.D).

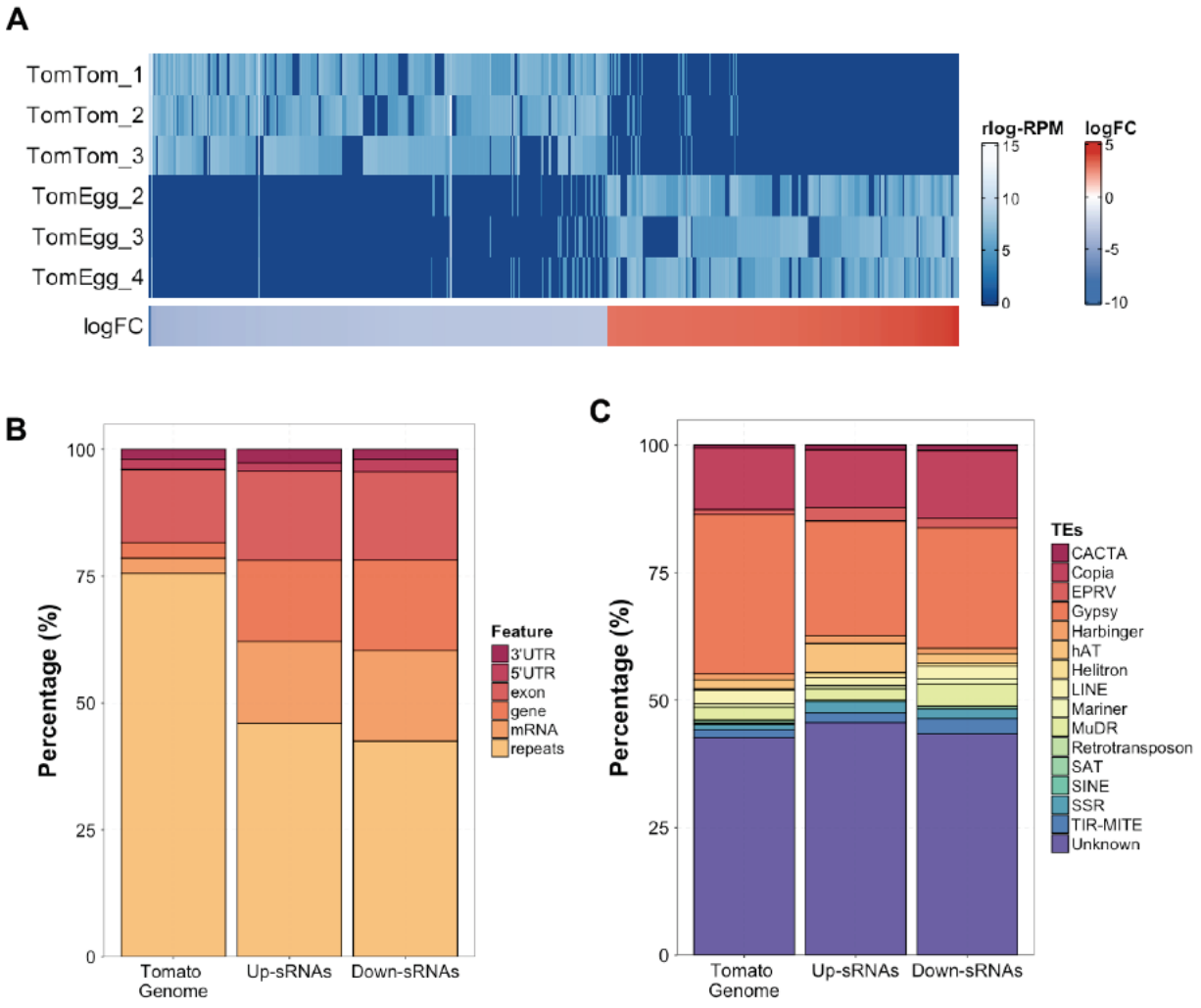


Figure 5.9. Differential analysis of tomato sRNA populations in self-graft controls and heterografts samples. The tomato differential sRNAs were selected based on statistical significance ($p < 0.05$) and a log2 fold change threshold of 3. The arbitrary log2 fold change was selected based on the distribution total significant population. A) Heatmap illustrating the relative rlog-transformed RPM values of differentially expressed tomato sRNAs ($p < 0.05$, log2foldchange = 3) and ordered based on the log2 fold change (logFC) and hierarchical clustering of expression. Each column represents a sample replicate, and each row represents a tomato sRNA ($n = 696$). Gradient bars show the expression level (rlog, log fold change). B) Distribution of differential tomato sRNAs cluster loci across genomic features. "Tomato Genome" represents the distribution of features across genome, "Up-sRNA" represents distribution of upregulated sRNAs across genomic features and "Down-sRNA" represents distribution of downregulated sRNAs across genomic features. Colours represent each feature. C) Pie chart of distribution of upregulated sRNA cluster loci across transposable element superfamilies in the tomato genome. D) Pie chart of distribution of downregulated sRNA cluster loci across transposable element superfamilies in the tomato genome.

Target prediction analysis was used to predict mRNA target sites in the tomato genome across sRNA sizes. The consensus RNA sequence for upregulated and downregulated sRNAs was extracted using *mobileRNA*, and only those with valid sequences were formulated into the output file (FASTA). Valid sequences only contained nucleotides. psRNATarget is an online tool designed for sRNA target prediction which mainly supports the prediction of miRNA cleavage and inhibition sites, however, adjustment to the parameters can also support siRNA functional analysis (Dai, Zhuang et al. 2018). Of the 302 upregulated sRNAs clusters, 48 had valid sequence were extracted from which 23 sRNA had predicted targets across 53 interactions. In this instance, none of the sRNAs targeted their target in multiple locations, similarly, none of the sRNAs targeted the same mRNA. The genes associated to these target sites were involved in clathrin complex and clathrin coat, based on GO term enrichment analysis. Similarly, 47 out of 394 downregulated sRNAs had valid sequences. There were 27 sRNAs with predicted targets that spanned 57 unique sites. There was one sRNA that targeted the same target in more than one location. No GO term enrichment was associated with the sRNA targets, but there were 30 associated GO terms and the most common included ATP binding (n=7), protein kinase activity (n=4), protein phosphorylation (n=4), protein binding (n=2), zinc ion binding (n=2), oxidoreductase activity (n=2) and obsolete oxidation-reduction process (n=2).

To investigate whether the tomato DE-sRNAs overlapped with DEGs, we plotted the results as a Venn diagram (Figure 5.10). The sRNA-producing genes refer to genes which overlapped with the DE-sRNA loci and similarly gene

targets were predicted using psRNAtarget (Dai, Zhuang et al. 2018). We observed that of the sRNA-producing genes related to upregulated sRNAs, 13 were upregulated DEGs and 2 were downregulated DEGs. Similarly, we observed that of the sRNA-producing genes related to downregulated sRNAs, 3 were also upregulated DEGs and 7 were downregulated DEGs. Only 3 or 2 DEGs were predicted as sRNA gene targets for upregulated and downregulated sRNA respectively (Figure 5.10).

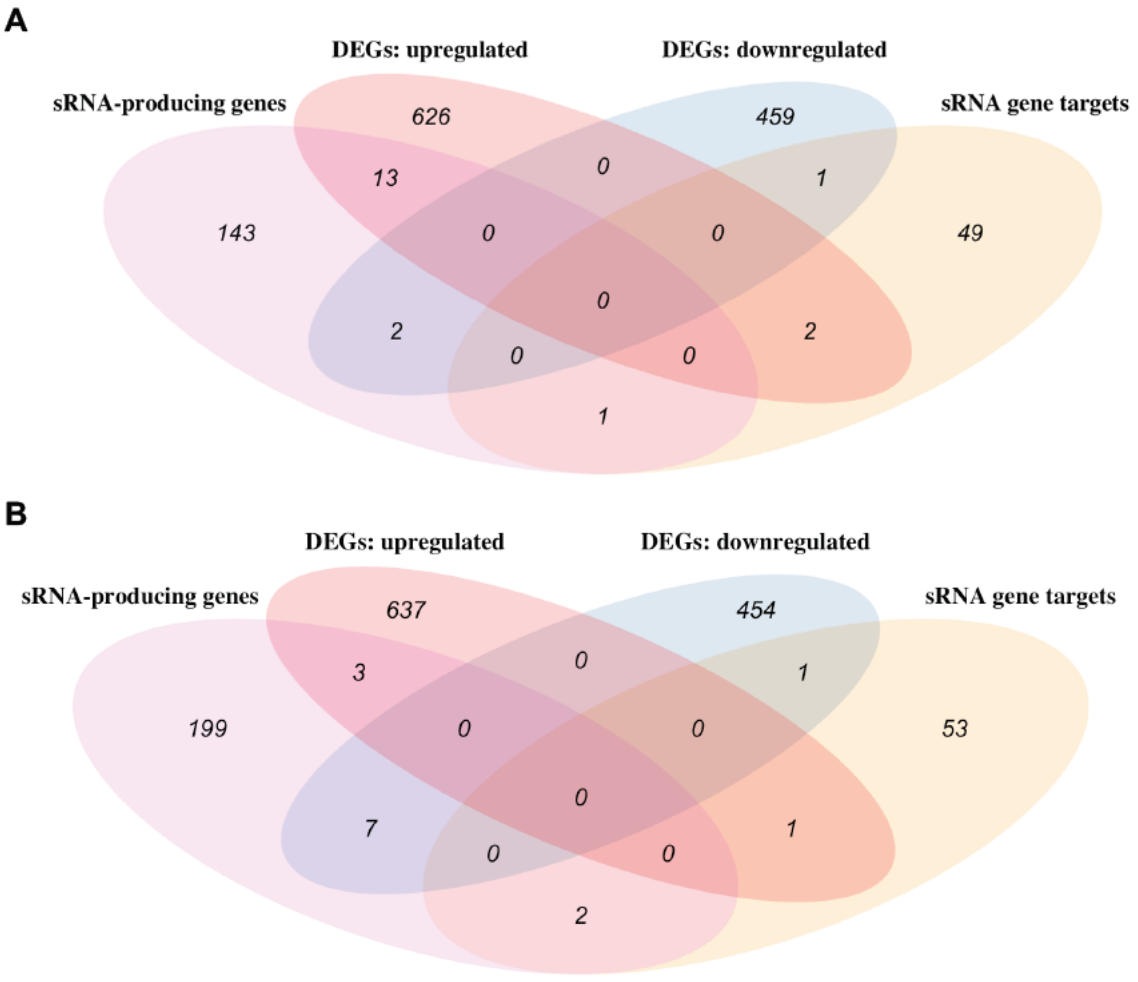


Figure 5.10. Venn diagrams of differentially expressed genes (DEGs), tomato sRNA gene targets and sRNA-producing genes. The DEGs were selected based on statistical significance ($p < 0.05$) and split into upregulated and downregulated based on a log2 fold threshold of 0. The genes which overlapped with sRNA clusters were selected and are referred to as sRNA-producing genes. sRNA gene targets were predicted using psRNATarget (Dai, Zhuang et al. 2018). A) Upregulated tomato DE sRNAs. B) Downregulated tomato DE sRNAs.

Mobile sRNAs might be diverting carbon to lignin biosynthesis

Here, we investigate whether root-to-shoot mobile sRNAs play a role in the grafting- induced changes to the scion. We characterised, on average, ~3.6% of sequencing reads which were uniquely mapped to the eggplant (rootstock) genome in the heterograft replicates (Supplementary Table 5.3). After *de novo* clustering and downstream selection, we determined that 6,994 (48.56%) of the eggplant sRNA clusters were false positives. This resulted in a total of 7,409 (51.44%) putative mobile sRNAs which represented approximately 5% of the total sRNAs in the scions of the heterografted plants. From the 7,409 putative mobile sRNAs, we selected those which were consistent across all heterograft replicates. This resulted in the characterisation of 117 (1.58%) root-to-shoot mobile sRNAs (Figure 5.11).

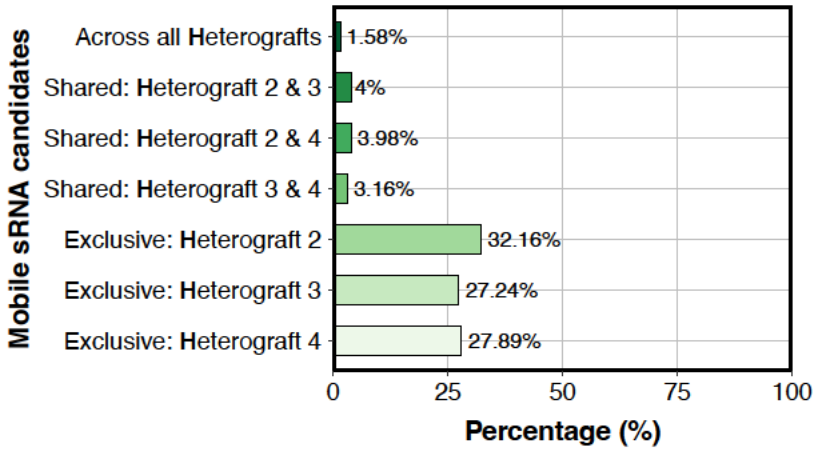


Figure 5.11. Distribution of candidate mobile sRNAs located in the leaf tissue of tomato scions across heterografted samples. The distribution of mobile sRNA candidates between replicates. Note that heterograft replicate 1 was eliminated as an outlier.

The length in nucleotides (nt) of a sRNA plays an important role in their function and, in plants, these typically range between 21-24 nt. This metric can act as a proxy for the sRNA's biological role within an organism. In plants, miRNAs are usually 21-nt in length whereas siRNAs are usually 24-nt and 22-nt sRNAs assist the targeting other siRNAs (Lu, Kulkarni et al. 2006, Kasschau, Fahlgren et al. 2007, Chen, Chen et al. 2010, Cuperus, Carbonell et al. 2010). As expected, we observed peaks in sRNAs with a size of 21-nt and 24-nt, as well as distribution of 22-nt and the least in 23-nt sRNAs (Figure 5.12.B). Additionally, there were a significant enrichment in unclassified sRNAs (N) which specify that the nucleotide size profile was inconsistent with Dicer-catalysed biogenesis. These unclassified sRNAs either represent degraded fragments of other RNAs in the system (i.e. contamination) or represent potentially new sRNA genes (Axtell 2013).

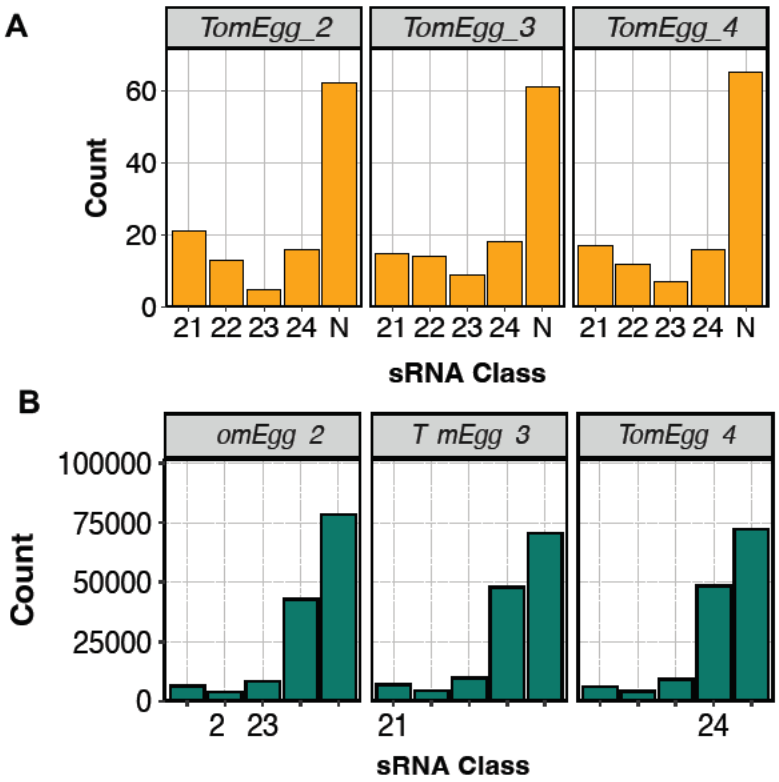


Figure 5.12. Distribution of nucleotide (nt) size of candidate mobile small RNAs (sRNAs) in comparison to the distribution of tomato sRNAs (i.e. produced by the scion). A) Distribution across mobile sRNAs (n = 117). B) Distribution across tomato sRNAs.

Mobile sRNAs were classified as clusters, otherwise referred to as sRNA-producing loci, and we can investigate these loci to gain further insights. Of the 117 mobile sRNA, 30 of these overlapped with at least one genomic feature. Specifically, 33 genes overlapped with a sRNA locus, 45 exons overlapped with a sRNA locus, and 27 promoter regions overlapped with a sRNA locus (Figure 5.13.A). To assess the functional relation of the sRNA-producing loci, we identified mobile sRNAs which overlapped with gene regions and their +/- 1 kb promoter region (upstream/downstream). Here, we identified 54 sRNAs which overlapped with a total of 63 gene loci. GO term enrichment analysis found that the sRNA-producing genes were enriched in processes relating to transcription initiation at RNA polymerase III promoter, threonine metabolic

process and abscisic acid-activated signalling pathway (Figure 5.13.C). Most of the mobile sRNAs (90 sRNAs, 77%) were associated with repeat sequences (n=187), that attributed to 128 key TEs with a string enrichment in gypsy (Figure 5.13.B).

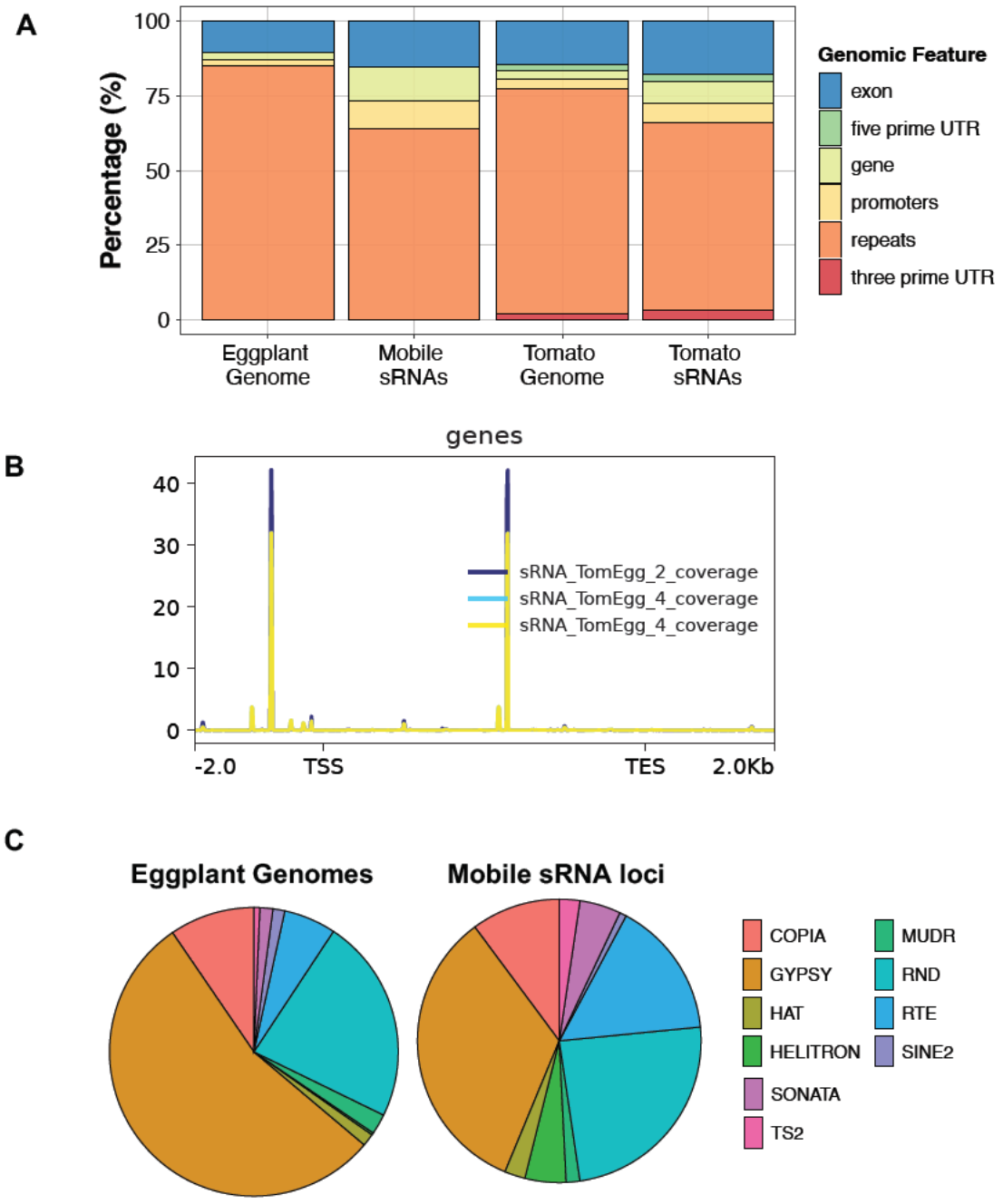


Figure 5.13. Summary statistics of mobile eggplant sRNAs located in the leaf tissue of tomato scions. A) Distribution of mobile sRNAs cluster loci across genomic features. "Eggplant Genome" column represents the distribution of features across genome, and "Mobile sRNAs" column represents the distribution of mobile sRNAs across genomic features. Colours represent each feature including exons, 5' untranslated regions (UTR), gene, promoters, repeats, 3' UTR. B) The average density of mobile sRNA loci across the gene regions (normalized to 5,000 base pairs) with 2,000 base pairs upstream and downstream regions of the transcription start site (TSS) and transcription end site (TES) calculated using deepTools (Ramírez, Ryan et al. 2016). C) Pie chart of distribution of mobile sRNA cluster loci across transposable element superfamilies in the tomato genome.

Across mobile sRNA studies, researchers have additionally aimed to elucidate the transport mechanisms facilitating the RNA mobility. This avenue has been primarily led by research on mRNA mobility, but researcher on sRNA alike has identified specific sequences that assist cell-to-cell and long-distance transport. In sRNAs, there does not appear to be a specific motif that assists movement (Pant, Buhtz et al. 2008, Martin, Adam et al. 2009, Molnar, Melnyk et al. 2010). Here, we attempted to access whether there were any consensus sequences shared across sRNAs by utilising hierarchical clustering and sequence analysis with *bioseq* R package (Keck and Mahon 2020). The analysis determined there was no clustering of sRNAs nor a sequence consensus.

sRNAs are known to play a key role in the regulation of gene expression through a target specific manner that can either promote or inhibit the gene expression. To predict potential target transcripts of mobile sRNAs psRNATarget (Dai, Zhuang et al. 2018) was employed and parameters were adjusted based on the sRNA size, whereby for 24-nt sRNAs the mismatch tolerance was lowered (1 mismatches allowed in seed region) to consider that they require near-perfect complementarity to their target. Of the 117 mobile sRNAs, we extracted 51 with valid RNA sequences and from which we predicted 95 interactions. The interactions comprised of 91 target sites and a total of 25 sRNA with a predicted target. Interestingly, none of the 25 sRNAs targeted the same gene target, however, 4 sRNAs targeted their given gene target in multiple sites or locations. To investigate whether the target transcripts were involved in biological processes that could help us explain the alterations in carbon allocation and the phenotypical alterations we undertook GO enrichment analysis using ShinyGO (Ge, Jung et al. 2020). The results revealed

an enrichment in molecular functions related to GTPase regulator activity, nucleoside-triphosphatase regulator activity and transferase activity (Figure 5.14). The functionality of these gene targets appears to be concentrated jointly across the cytoplast, plasmodesmata, cell-cell junction, and anchoring junction. This result mirrors the central themes highlighted in the transcriptomic changes (Figure 5.14).

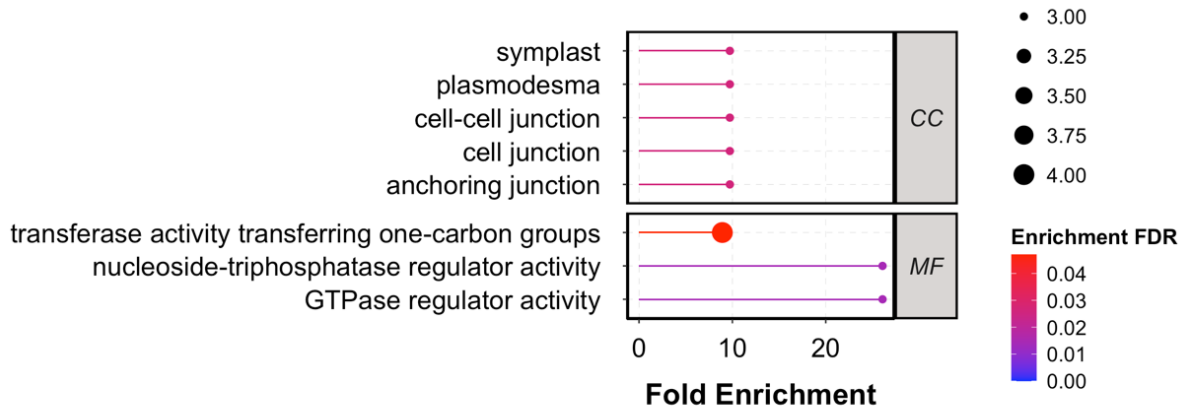


Figure 5.14. Functional analysis of predicted targets of the mobile sRNAs in either the tomato or eggplant genome. Statistically significant terms were deemed only for cellular compartments (CC) and molecular functions (MF). The colour represents the enrichment false discovery rate (FDR), the bar represents the fold enrichment, and the size of the point represents the number of genes in the population of interest.

That being done, the results were further evaluated by identifying gene targets which were differentially expressed in the transcriptomic data (p value < 0.05). There were 6 targets which were differentially expressed in the scion, and all upregulated (Figure 5.15.A). The three gene targets which were the most highly upregulated and of most interest included a laccase enzyme (Solyc05g052360.2), a calcium-dependant protein kinase (Solyc12g099790.3) and a MYB TF (Solyc02g036370.3) (Figure 5.15.B). Other included Solyc01g107430.2 (Zinc finger protein 7), Solyc04g072020.3 (Choline kinase) and Solyc12g006520.2: (Cycloartenol synthase).

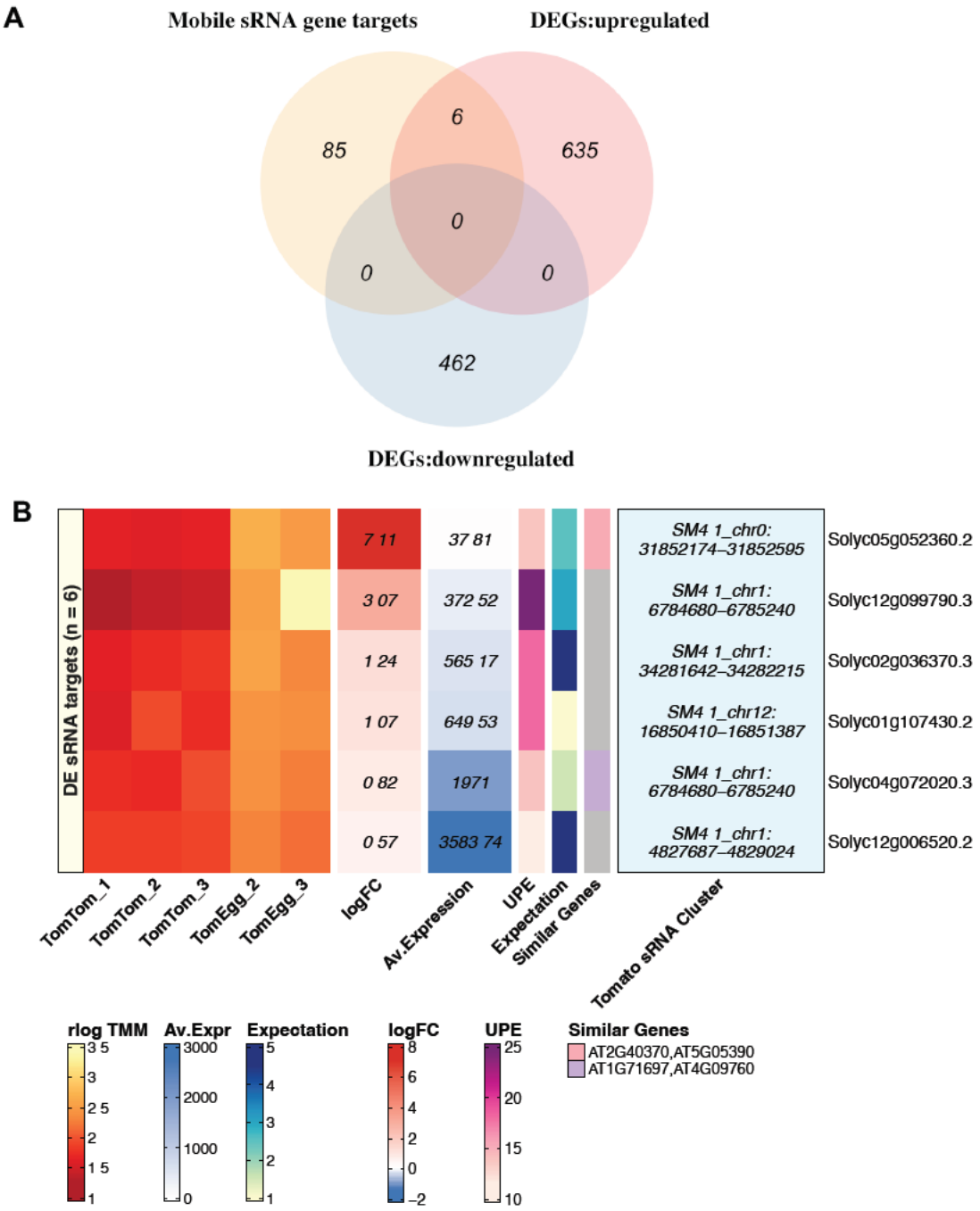


Figure 5.15. Differentially expressed sRNA gene targets in tomato. A) Venn diagram of the overlaps between mobile sRNA gene targets and differentially expressed genes (DEGs) split into upregulated and downregulated (log2 fold change > 0). B) Heatmap showing the relative rlog-transformed TMM values of differentially expressed target genes ($p < 0.05$) ordered by the log2 fold change (logFC). Each column represents a replicate, and each row represents a tomato sRNA ($n = 6$). The gradient bars on the below show the expression level for rlog TMM values. The column for logFC represents the log2 fold change, and the Av. Expression column represents the average expression value (rlog) across the experimental design. The UPE represents the maximum accessibility energy to unpair the sRNA from the target site and where the Expectation represents the penalty for mismatches between the sRNA and target site.

To further explore the relevance of the six mobile sRNAs and their DE targets, we investigate whether the tomato sRNAs in the self-graft controls and heterografts were also predicted to target the six genes. Indeed, this was the case. In the self-grafts, 12 sRNAs were predicted to target only the top 5 DE genes, ranking based on log2 fold change expression (Solyc05g052360.2, Solyc12g099790.3, Solyc02g036370.3, Solyc01g107430.2, Solyc04g072020.3, Solyc12g006520.2). While in the heterografts 18 tomato sRNAs were predicted to target all six. None of these tomato sRNAs were differentially expressed which suggests that their tomato sRNAs are ubiquitous and there could be competing for these target genes in the scion. The results from psRNATarget allow us to observe the predicted strength of the interactions between the sRNA and the target. For which the binding sites have been illustrated in gene tracks in Figure 5.16. For the case of the three most interesting gene targets, the Solyc05g052360.2 target has a stronger interaction with the mobile sRNA, requiring less energy to bond. For the Solyc12g099790.3 target, the tomato sRNA has a stronger interaction that the mobile sRNA. Finally, the Solyc02g036370.3 target appears to have a somewhat equal strengths between interactions of the tomato and mobile sRNAs, however, interestingly the mobile sRNA targets the gene at a more upstream location than the tomato sRNAs which target further downstream.

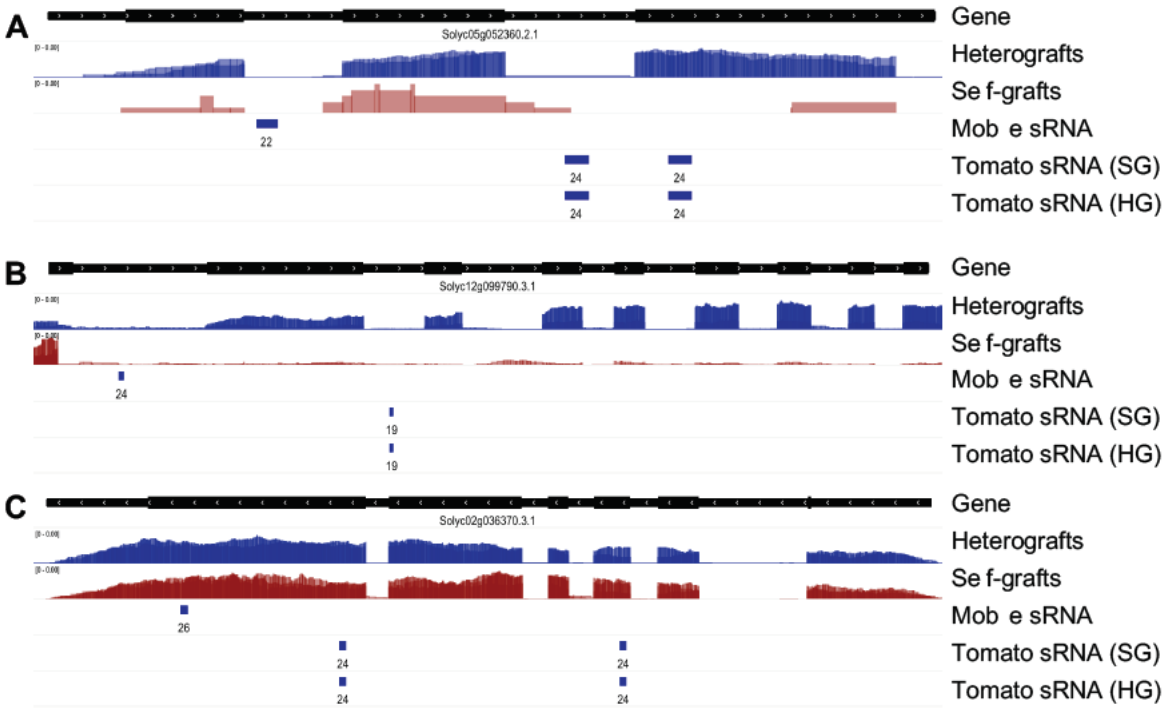


Figure 5.16. Predicted sRNA binding sites to differentially expressed target genes. The RNAseq read coverage for the three most upregulated gene targets was plotted as an alignment track against the predicted sRNA binding sites. The "Heterografts" and "Self-grafts" tracks represent the overlayed normalised gene expression coverage tracks for the heterograft replicates and self-graft replicates, respectively. The "Mobile sRNA" tracks refer to the predicted binding site of the mobile sRNAs on the target gene. The "Tomato sRNA" tracks refer to the binding sites of tomato sRNAs, where "SG" refers to self-grafts and "HG" refers to heterografts. A) Track illustrating the Solyc05g052360 gene transcript and associated binding sites. B) Track illustrating the Solyc12g099790 gene transcript and associated binding sites. C) Track illustrating the Solyc02g036370 gene transcript and associated binding sites.

To access the directionality, expression and function of mobile sRNAs located in tomato scions, we explored their expression in eggplant scions. To identify the mobile eggplant sRNAs in the eggplant scion, we retrieved clusters with an 80% partial overlap match since we expect that the clusters may shift several nucleotide bases in different tissue samples. Using this approach, we identified 93 (79%) of the mobile sRNAs to be present in the eggplant scions and plotted their abundance (Figure 5.17.A). In comparison to the expression of the sRNAs in the tomato scion, their expression in the eggplant scions was highly variable,

yet marginally downregulated in the eggplant scions grafted onto tomato rootstocks (Figure 5.17.A). Furthermore, to access the role of the mobile sRNAs in their genome of origin (i.e. eggplant), we replicated the target prediction and functional enrichment analysis in the eggplant genome. There were 27 mobile sRNAs that had a predicted target gene interaction whereby 25 of these had predicted targets in the tomato genome and 4 of the 27 mobile sRNAs each target a specific gene in more than one location. Next, we wanted to evaluate whether the predicted gene targets in the tomato and eggplant genomes were homologs of one another. Using reciprocal analysis, we determined that 15 target eggplant genes (n = 101) were homologs of predicted target genes in the tomato genome (n = 91). This included two of the DEGs which were predicted as targets in the tomato scions (see Figure 5.15.A). This Solyc05g052360.2, a laccase enzyme, and Solyc12g099790.3, a calcium-dependant protein kinase. There were two homologs of Solyc05g052360.2 (SMEL4.1_05g001290.1, SMEL4.1_05g001300.1) which were predicted targets of the same mobile sRNA. Similarly, there was one homolog of Solyc12g099790.3 which was a predicted target in eggplant (SMEL4.1_00g001250.1) that were both targeted by the same sRNA.

Based on these results, we investigated the expression of the mobile sRNAs and specific gene targets of interest in the tomato and eggplant genomes. Using functional analysis, we characterised the enrichment of biological processes related to the gene targets in the eggplant genome (Figure 5.17.B). Interestingly, these gene targets were enriched in functions related to lignin catabolism and obsolete oxidation-reduction processes. The molecular functions of the gene targets in eggplant appear to be different from targets in the tomato scions (Figure 5.17.B).

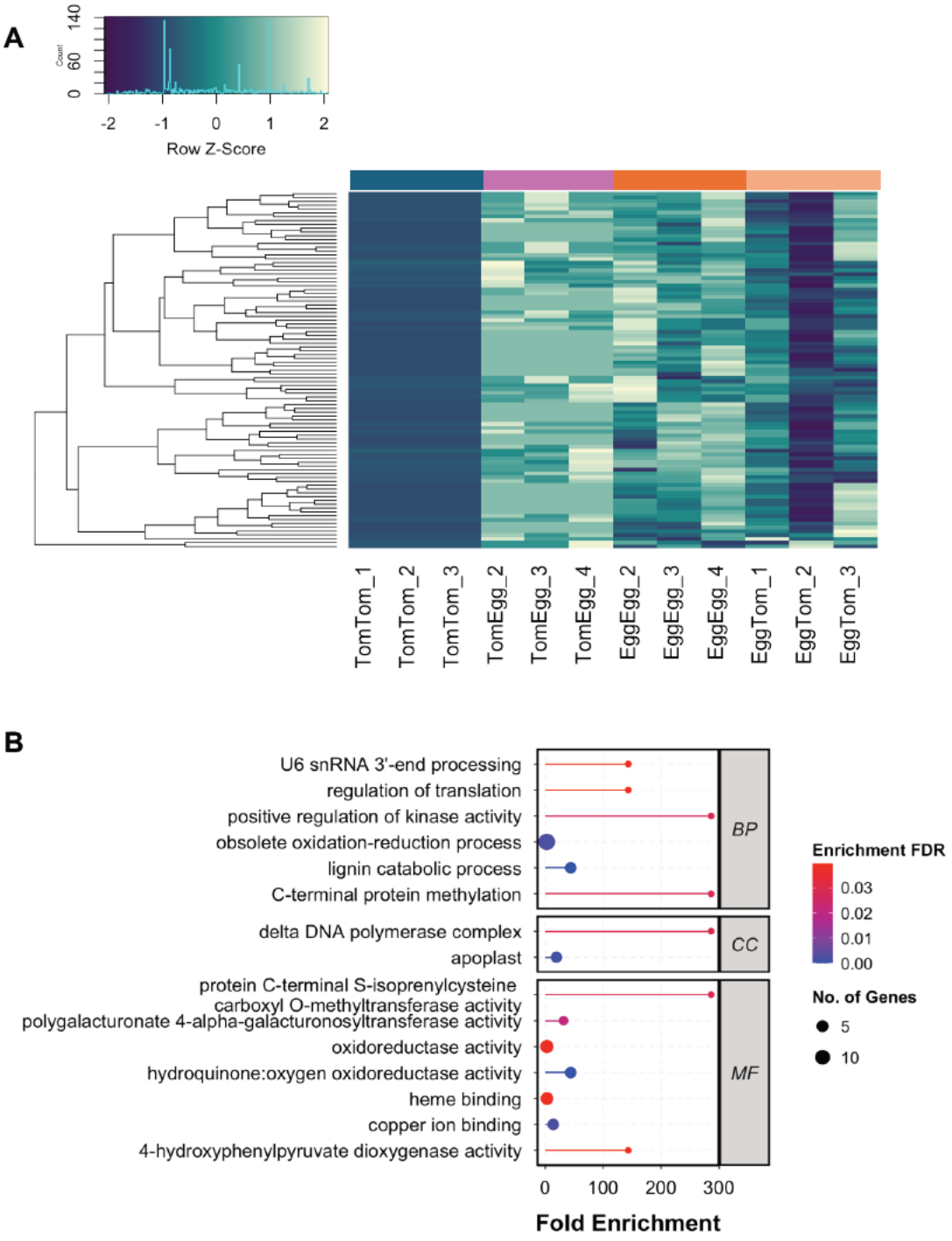


Figure 5.17. Analysis of mobile small RNAs and functional analysis of predicted targets in the genome of origin (eggplant). A) The expression level of mobile sRNAs in the tomato scions and eggplant scions of self-grafted and heterografted replicates. Raw counts were normalised by z-score based on the tissue of origin and results. B) Targets were predicted for mobile sRNAs in the eggplant genome using psRNATarget based on 2017 schema with adjusts parameters (Dai, Zhuang et al. 2018). Gene Ontology (GO) term enrichment analysis was using ShinyGO (Ge, Jung et al. 2020) was undertaken on the predicted target genes. Statistically significant terms were plotted for biological processes (BP), cellular compartments (CC) and molecular functions (MF). Colour represents the enrichment false discovery rate (FDR), the bar represents the fold enrichment, and the size of the point represents the number of genes in the population of interest.

To investigate the mechanism by which the mobile sRNAs may regulate the expression of the differentially expressed gene targets, we explored the possibility of alternative splicing events (Supplementary Figures 4.5-7). The results suggest that the sRNAs do not generate alternative splicing variants of the gene targets (Supplementary Figures 4.5-7). Similarly, we investigated the proximity of predicted target sites to DEGs in the tomato scion using a circular ideogram (Figure 5.18). The first ideogram illustrated the connections between the mobile sRNAs produced by the eggplant genome and their predicted gene targets in the tomato genome (Figure 5.18.A). The ideogram illustrates the proximity of target genes in the tomato scion to the DEGs, we know from the analysis that only 6 of the DEGs were differentially expressed and a further 2 targets were found 5 kb upstream of a DEG, but one sRNA target was found 5 k downstream of a DEG (Figure 5.18.B).

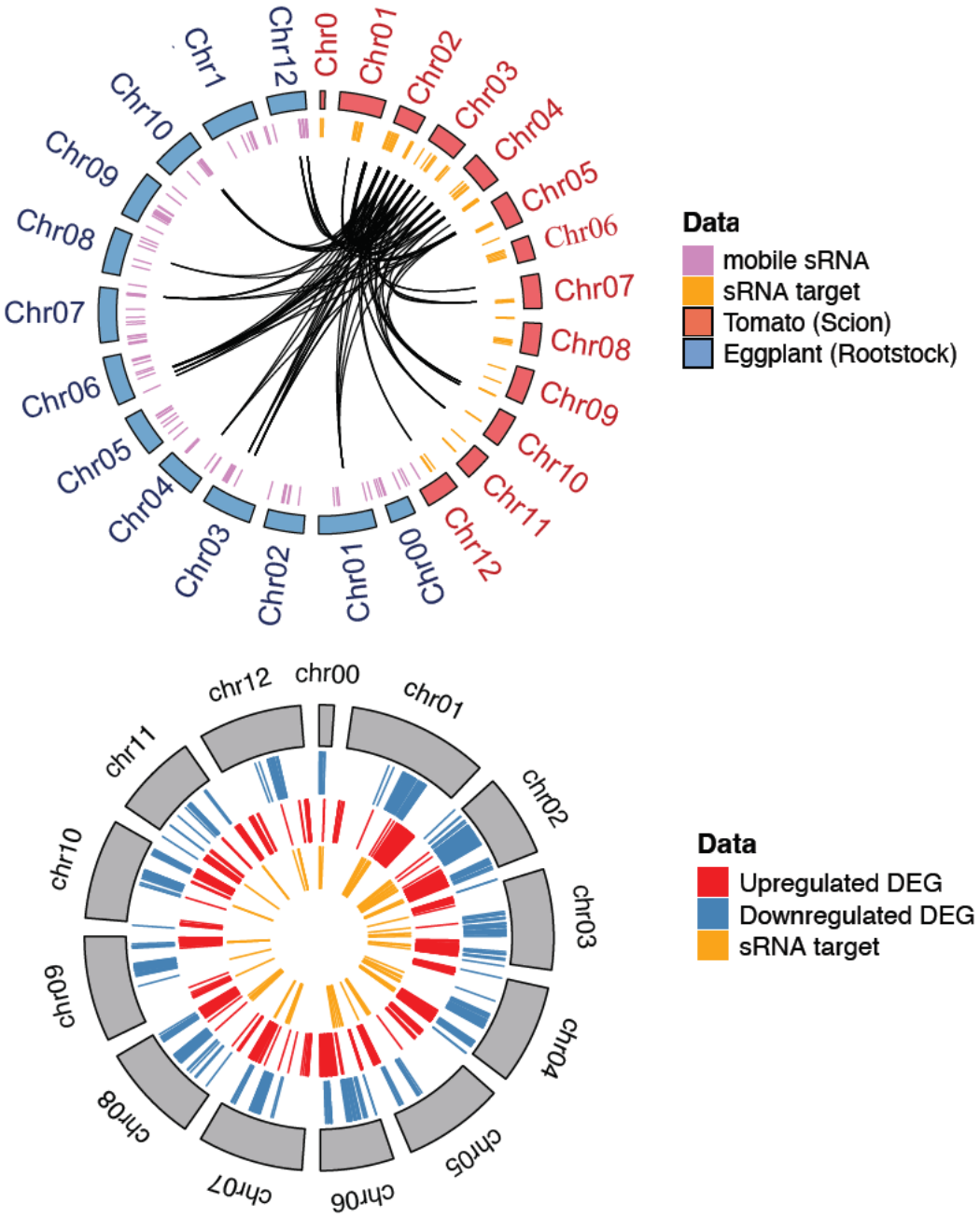


Figure 5.18. Circular ideogram illustrating genomic location of mobile sRNAs, gene targets and differentially expressed genes. From the predicted sRNA targets, we investigated the possible mechan sm by which the sRNAs may regulated target gene expression, specifically targets which were identified as differentially expressed (DE). Alignment tracks illustrating the DE gene targets (log2 fold change > 1) and the predicted sRNA binding site. A) Distribution of eggplant mobile sRNAs shown in violet and their predicted targets shown in orange. Strings connect sRNA to their target. B) The genomic location of differentially expressed genes (DEGs), whereby upregulated genes are shown in read and downregulated genes shown in blue. The predicted sRNA target genes in tomato are shown in orange.

The association between mobile RNAs and changes to scion-produced sRNA

Besides sRNAs, there are other assimilates such as hormones and proteins that can move between the roots and shoots. Different rootstock combinations can influence the uptakes of nutrients from the soil as well as hormone production and signalling which have both been associated mechanisms driving grafting-induced changes (Cohen, Edelstein et al. 2010). The latter has been investigated in numerous studies across crop families and has been associated to traits such as changes in fruit quality (Rouphael, Schwarz et al. 2010). In the tomato scions we observed changes in the tomato sRNA populations, including tomato sRNAs which were no longer located in the heterografts but present in the self-graft controls. Based on the reasoning that the eggplant rootstock could be altering the transport of other molecules, we cannot assume that the 'lost' sRNAs were produced in the tomato rootstocks and transported into the tomato scion of the control samples. However, with the utilisation of the reciprocal grafts which included eggplant self-graft controls and eggplant/tomato (scion/rootstock) heterografts we can shed further light on this hypothesis using further bioinformatic analysis. The analysis revealed that of the 334 'lost' sRNAs four were in the eggplant/tomato heterograft samples and three were located in the eggplant/eggplant self-graft controls – based on a partial overlap.

Next, we explored the crossover between mobile sRNAs and DE tomato sRNAs. There was no overlap between the gene targets predicted for the mobile sRNAs and the DE sRNAs. Yet, across the gene targets predicted for all tomato sRNAs in the self-grafts and heterografts we found that 82 targets were shared

with the targets of the mobile sRNAs (Figure 5.19). Keeping in mind that there were 95 predicted targets associated to the mobile sRNAs, this is a significantly large proportion of the eggplant sRNAs which target the same genes as the ubiquitous tomato sRNAs. Lastly, we looked at the proportion of gene target predicted for each sRNA population in relation to the total number of genes in tomato (n = 34,725). This analysis revealed that based on predicted the top 5 targets for each sRNA, the differentially expressed tomato sRNAs targeted a fractionally greater proportion of the tomato genome (0.32%) than mobile sRNAs (0.26%).

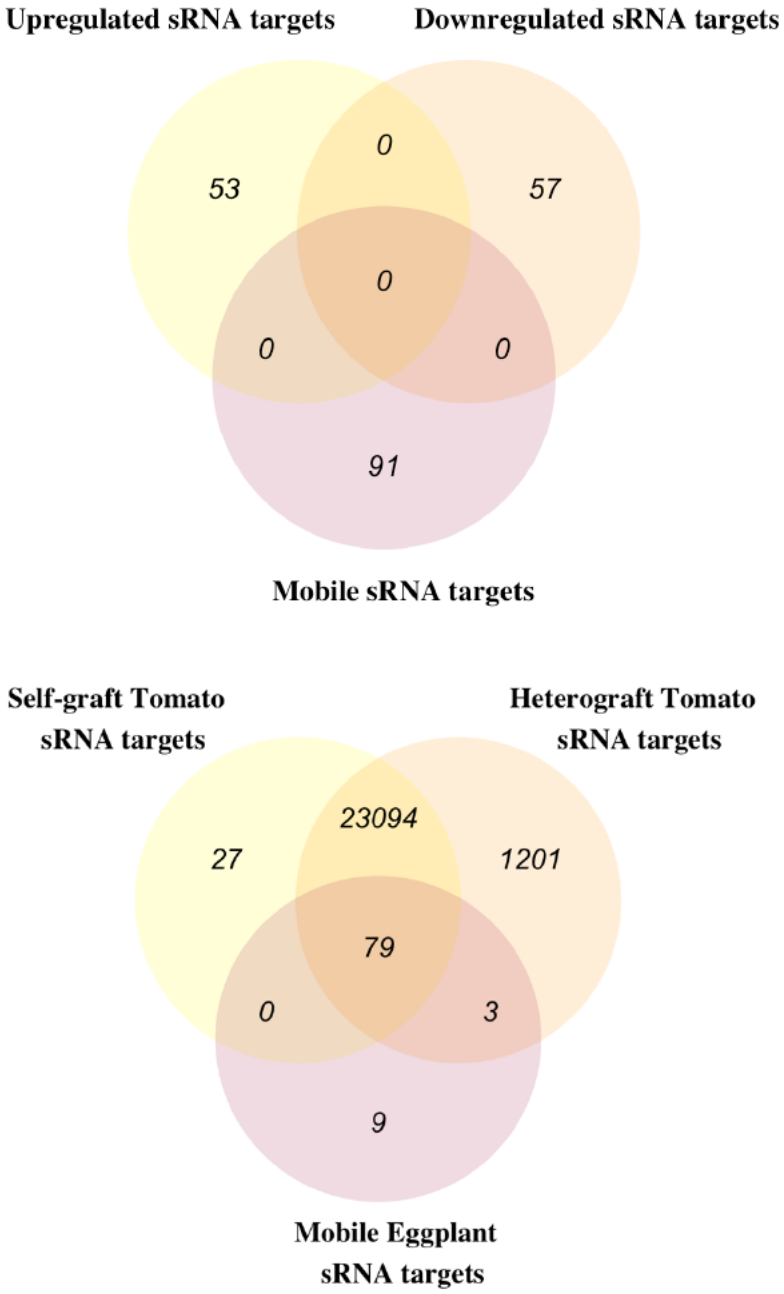


Figure 5.19. Circular ideogram showing the genomic location of differentially expressed tomato sRNAs and the predicted sRNA target genes in tomato, alongside the region of mobile sRNA biosynthesis in the eggplant genome. Differentially expressed (DE) tomato sRNAs ($p < 0.05$), where upregulated sRNAs (logFC > 0) are shown in red and downregulated sRNAs (logFC < 0) are shown in blue, are plotted alongside the predicted mobile sRNA target sites in the tomato genome, shown in purple.

Investigating root-to-shoot mobile mRNAs

Plants utilise long distance signalling to communicate between tissues to coordinate development or responses to external stimuli (Heeney and Frank 2023). mobile mRNAs, among others, are key mediators in signalling pathways (Heeney and Frank 2023). Their transport between the roots and shoots, and the concept that mRNAs may function as non-cell autonomous signalling molecules was first credited in studies that investigating phloem sap, particularly in cucurbits. Since these initial studies, vast others have demonstrated the presence of mRNAs in the translocation stream and have established this across numerous plant models (Mahajan, Bhogale et al. 2012, Luo, Huang et al. 2018, Wang, Wang et al. 2020, Davoudi, Song et al. 2022, Luo, Huang et al. 2022). In more recent years, researchers have taken advantage of technological developments such as NGS to identify population of mobile mRNAs (Kim, LeBlanc et al. 2014, Notaguchi, Higashiyama et al. 2015, Calderwood, Kopriva et al. 2016, Duan, Zhang et al. 2016, Liu, Yang et al. 2016, Luo, Huang et al. 2018, Xia, Zheng et al. 2018, Liu, Xiang et al. 2020, Wang, Wang et al. 2020, Xu, Szekely et al. 2024). Yet, these techniques are limited as it is currently impossible to identify mobile mRNAs produced by the same genotype. To combat this challenge, grafting has been employed to track mobile mRNAs that can be distinguished due to genetic polymorphisms between rootstock and scion (Tomkins, Hoerbst et al. 2022, Jeynes-Cupper and Catoni 2023). Using this approach, numerous mobile mRNA signals have been linked to physiological processes, such as defence mechanisms, morphological changes includes leaf development, and changes to crop yields (Heeney and Frank 2023).

Here, we aimed to identify putative mobile mRNAs produced by the eggplant rootstock within the leaf tissue of the tomato scion. Using *mobileRNA (Jeynes-Cupper and Catoni 2023),* we captured 46 root-to-shoot mobile mRNA transcripts consistent across all heterograft samples. GO term enrichment analysis indicated that (Figure 5.20) transcripts were enriched in processes related to *'de novo'* L-methionine biosynthetic processes, positive regulation of transcription elongation by RNA polymerase II and glycyl-tRNA aminoacylation (based on fold enrichment). These biological functions are particularly interesting given that tRNA related structures have been associated with the movement of mRNAs (Zhang, Thieme et al. 2016) and RNA polymerase II is involved in the transcription of mRNAs and small non-coding RNAs, including siRNAs and miRNAs (Kornberg 1999). In addition, L-methionine has been confirmed as a regulator of plant growth and development, particularly to enhance growth under environmental stresses such as drought (Mehak, Akram et al. 2021). Further analysis of the genes involved in L-methionine biosynthesis in the eggplant genome determined that there is only one annotated gene associated with this pathway (SMEL4.1_10g025480.1) and in our analysis we identified its transcript to be root-to-shoot mobile (Figure 5.20). This gene is homologous to the CYSTATHIONINE BETA-LYASE (CBL) gene in *Arabidopsis thaliana*, which encodes a cystathionine beta-lyase protein. This is involved in the generation of methionine required for *S*-adenosylmethionine (SAM) synthesis whereby SAM is a methyl donor for methylation (Liu, Yang et al. 2019). Hence, CBL mutants have been associated with reduced methylation (Liu, Yang et al. 2019). Plus, methionine activated glutamate receptors (calcium ion channels) can alter plant growth through alterations in stomatal opening (Kong, Hu et al. 2016). Lastly, we see an enrichment of mobile mRNA with molecular functions related to

transferase activity and GTPase activity – both of which were enriched functional roles of mobile sRNA producing-loci (Figure 5.20).

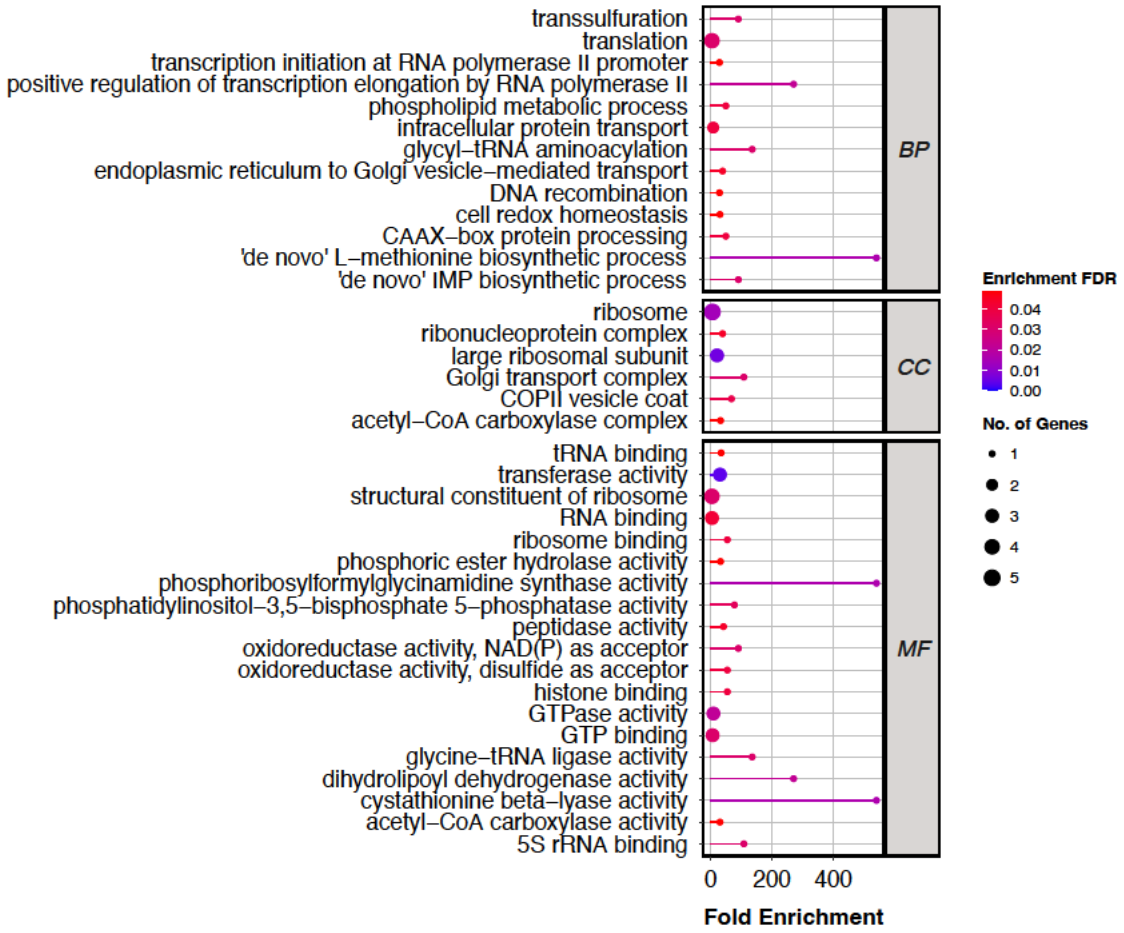


Figure 5.20. Gene Ontology (GO) term enrichment analysis of mobile eggplant mRNAs. Graft-mobile mRNAs produced in the eggplant rootstock were detected in the leaf tissues of the tomato scion from sequencing data. GO analysis was undertaken using a custom script based on the gene ontology annotations. The colour represents enrichment FDR, the dot size represents the number of genes in the pathways.

To investigate the integrity of these putative mobile transcripts we investigated their read coverage and genome mappability. Both the *mobileRNA* approach and other, users rely heavily upon the sequence polymorphisms present between the scion and rootstock genotypes. Here, more so with the *mobileRNA* approach we accept that at the alignment step we have a reduced mapping

efficiency due to the homology between the genotypes (Figure 5.21.A). The effect of homology between the scion and rootstock genomes can be estimated by calculating the genome mappability scores across annotated coding regions in the individual genomes in comparison to the merged genome. Here, we plotted the distribution of mappability across the mobile mRNAs (n = 46) in the eggplant genome (genome of origin) and in the merged genome. The results revealed that the homology of mobile transcripts to the tomato genome increased by 15% (Figure 5.21.A).

The *mobileRNA* approach discarded reads which aligned to more than one region (i.e. sequences with repetitiveness and homology). Therefore, mRNA transcripts containing regions with reduced uniqueness in comparison to other transcripts may have a lower abundance than expected since reads aligning to these repetitive regions were discarded from raw count analysis. To be mobile we expect that transcripts will exhibit read coverage across the majority of the coding region (>70%) (Figure 5.21.B). The results revealed that 13 transcripts (28%) met these criterion, and two example tracks are shown in Figure 5.21.B. Of all the mobile transcript with complete coverage, the SMEL4.1_03g031800.1.01 transcript had the highest coverage (209 read coverage). This transcript is similar to 50S ribosomal protein L2 chloroplastic (rpl2-A) in *Solanum bulbocastanum* and has been demonstrated to be a transcriptional modulator (Rippa, Cirulli et al. 2010).

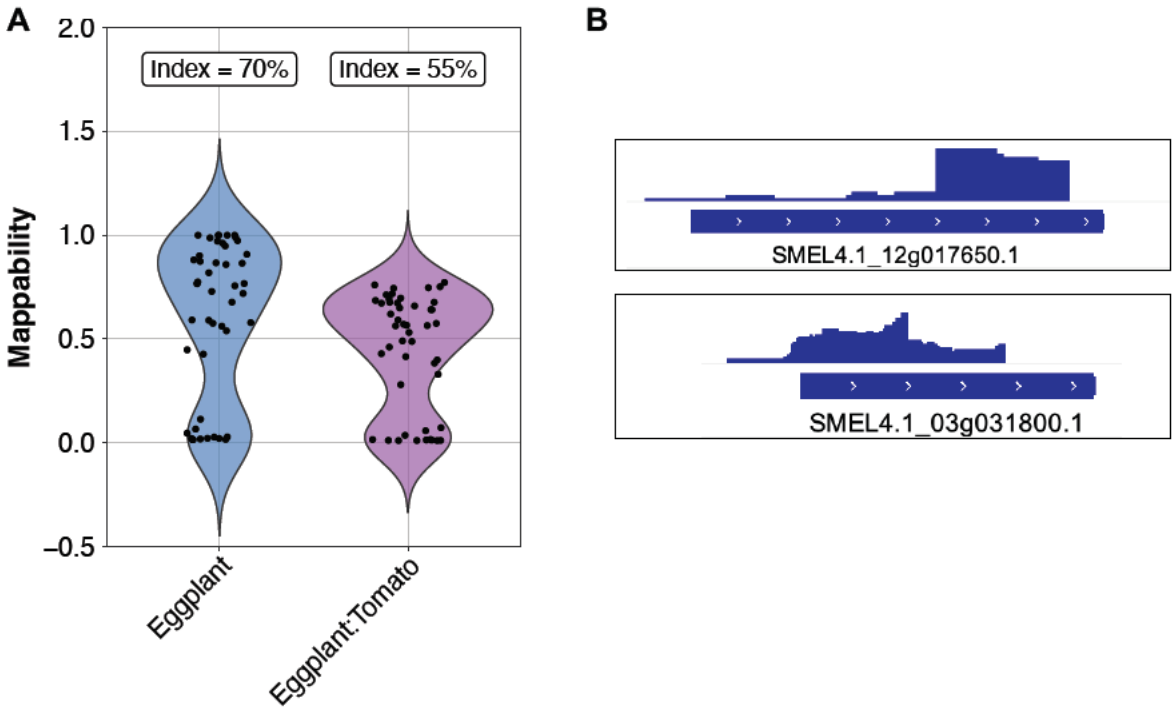


Figure 5.21. Genome mappability and genome tracks of mobile transcripts. A). Violin plot of the genome mappability of mobile transcripts in both the eggplant and merged genome reference assemblies. Each point represents a mobile transcript, and the text annotation represents the index value which is the proportion of the transcripts in the genome with a mappability above 0.5. B) The read coverage across mobile transcripts was calculated using BEDtools (Quinlan and Hall 2010). Illustrated are two transcripts with >70% read coverage.

The mechanisms which enable RNA mobility are widely debated including the mechanisms that control which mRNAs can move, how they move and the mechanisms determining their destination. Evidence from viral studies have implied that structural features facilitate mRNA mobility. For instance, RNA viruses require stem-loop structures in the 3′ untranslated regions to enable viral transmission and thus infection (Fechter, Rudinger-Thirion et al. 2001, Barends, Rudinger-Thirion et al. 2004). These structures resembled a close similarity to tRNA structures, inspiring researchers to later isolate similar TLSs in endogenous plant mobile RNAs (Zhang, Sun et al. 2009, Zhang, Thieme et al. 2016). Since this discovery further RNA modifications, including DNA cytosine methylation, have been linked to mRNA mobility (Xue, Zhao et al. 2020). Even

so, it is widely believed there could be additional interactions involved. Using RNAmotif (Macke, Ecker et al. 2001), we estimated that 5 mobile transcripts (11%) contained TLSs (SMEL410g000220, SMEL411g007560, SMEL412g011730, SMEL406g014230, SMEL408g014760). In a similar concept, the proximity of tRNA genes (1 kb upstream/downstream) to genes encoding mobile transcripts has been associated with mobility (Zhang, Sun et al. 2009, Zhang, Thieme et al. 2016). The tRNA genes in the eggplant genome were detected using ARAGORN (Laslett and Canback 2004), where we located 15 tRNA genes. However, none were in a 1 kb proximity to mobile transcripts.

Follow this, we undertook *de novo* motif analysis with *MEME* suite (Bailey, Johnson et al. 2015) to identify enrichments motifs within mobile transcripts (Figure 5.22). Using the Classic mode, we instructed MEME to have the expectation that a transcript could have any number of motif repetitions and up to 3 motifs across the analysis. The results illustrated that motif 1 was present in 23 sites (*E-value* = 1.5e-128), motif 2 was present in 216 sites (*E-value* = 1.2e-058) and motif 3 was present in 8 sites (*E-value* = 3.2e-034) (Figure 5.22). To access the functional roles of the motifs, we submitted motifs to *TomTom* to search the motifs against the JASPAR database (Rauluseviciute, Riudavets-Puig et al. 2024). This analysis found that motif 1 had a significant similarity to in the motifs found in ERF TFs in *Arabidopsis thaliana* (O'Malley, Huang et al. 2016). Similarly, motif 2 had a significant similarity to motif to GRF TFs (p = 2.40e-06) (Li 2018). Lastly, motif 3 had the closed similarity to MADS box factors in plants, specifically like the motif sound in AGL1 in *Arabidopsis thaliana* (*p* = 1.70e-03). The content of GC in transcripts can alter its stability, and within the motifs we noted a high proportion of G-C nucleotides.

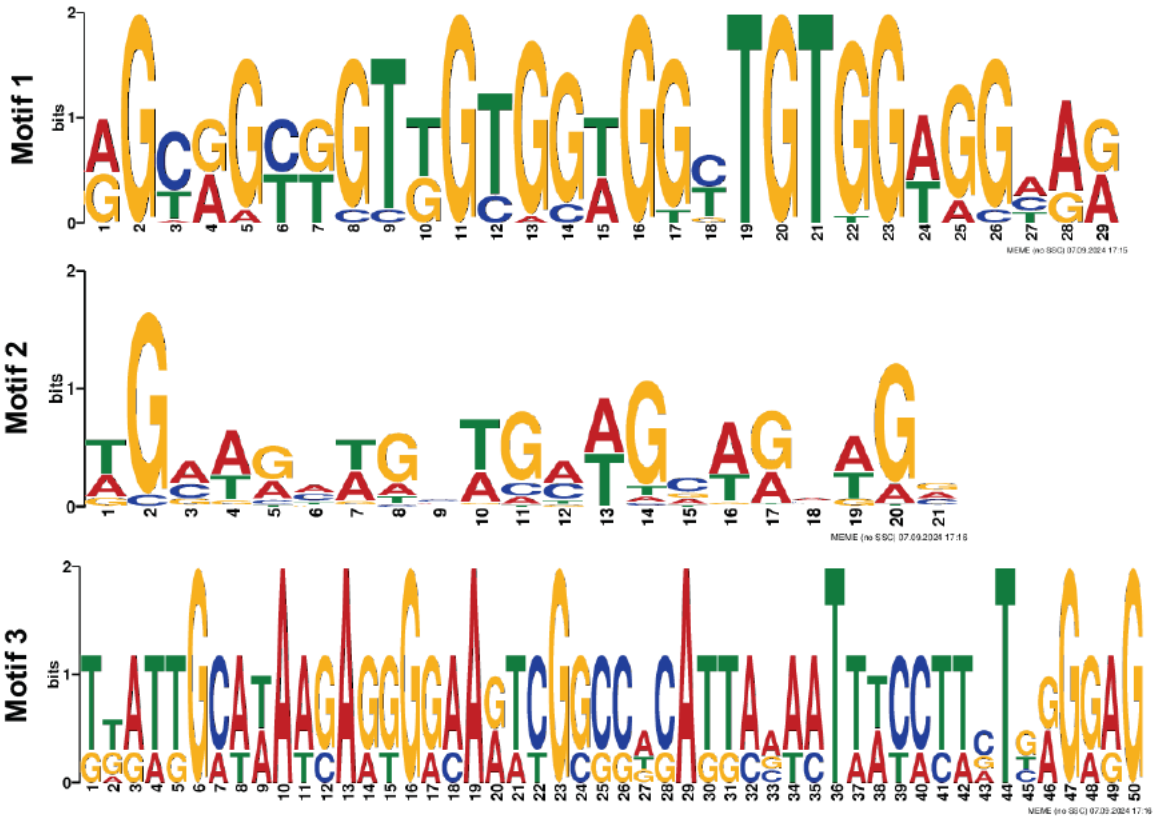


Figure 5.22.De novo motif analysis with MEME suite across mobile transcripts. MEME suite was employed to detect *de novo* motifs across the 46 mobile mRNA transcripts. Motif 1 had an E-value of 1.5e-128, Motif 2 had an E-value of 1.2e-058, and Motif 3 had an E-value of 3.2e-034.

To draw further understanding of the functional role of the mobile transcripts in the tomato scion, we investigated the expression profiles of the homologs in the tomato genome of the mobile transcript (Figure 5.23). The objective was to determine whether the mobile transcripts could have influenced the expression of endogenous gene homologs in the scion. The mobile mRNA protein sequences were BLAST (Camacho, Coulouris et al. 2009) against the tomato genome to identify possible homologs. For the 42 mobile mRNAs, we identified 67 homologs in tomato for which, three were differently expressed ($p < 0.05$) (Figure 5.23). The homologs for the mobile transcripts SMEL4.1_02g007210.1

(Solyc02g063450.4) and SMEL4.1_08g014760.1 (Solyc04g072020.3) were upregulated, whereas the homolog for the mobile transcript SMEL4.1_10g024800.1 (Solyc05g054480.3) was downregulated (Figure 5.23). We explored the function of the DE homologs and found that these genes were not well characterised in tomato. The Solyc02g063450 gene is not characterised in *Arabidopsis thaliana* but is in potato, which described it as encoding a Glycine-rich protein (PGSC0003DMG400010387). The Solyc04g072020 gene encodes a choline kinase enzyme similar to the CHOLINE KINASE 1 (CK1) gene in *Arabidopsis thaliana* which has been described as a key enzyme in multiple pathways for its role in substrate phosphorylation (Stroud, Greenberg et al. 2013), including hormone signalling, wound healing, plus, photo-morphogenesis and photoperiodic flowering (Liu, Xu et al. 2003, Dai and Xue 2010, Tan, Dai et al. 2013). Moreover, the CK1 mRNA has been described as cell-to-cell mobile (Thieme, Rojas-Triana et al. 2015). In contrast, the Solyc05g054480 gene encodes actin which is like ACTIN-11 (ACT11) in *Arabidopsis thaliana* which is involved in cytoskeleton organisation. This gene is readily utilised in experimental designs as control in RT-qPCR.

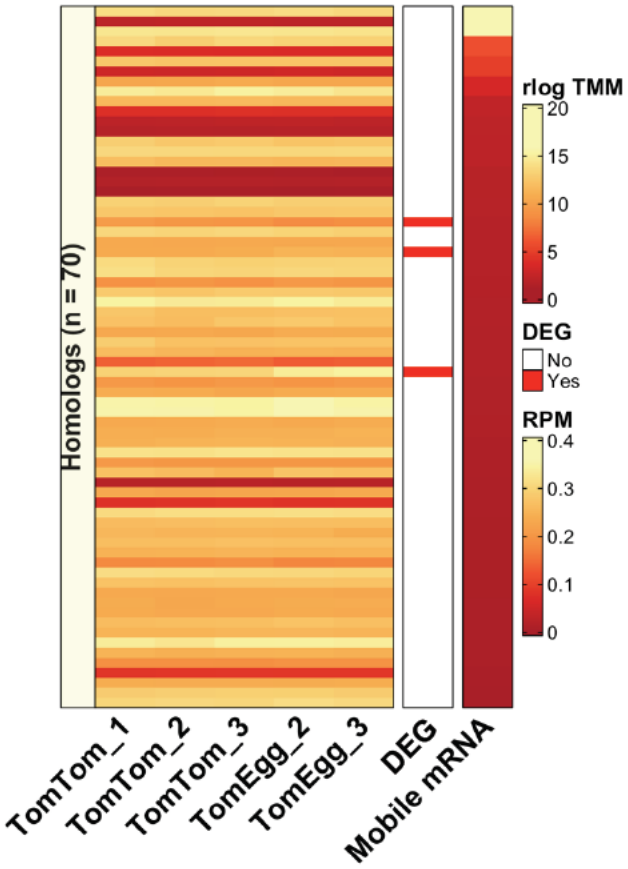


Figure 5.23. Expression profiles of the tomato homolog genes of the mobile mRNA transcripts. Graft-mobile mRNAs produced in the eggplant rootstock were detected in the leaf tissues of the tomato scion from sequencing data. Homologs were detected using BLASTp analysis (Altschul, Gish et al. 1990) and homologs were selected based percentage identity and bit score. The heatmap illustrates the expression level of tomato homologs (log transformed counts) for each replicate and ordered based on the mobile mRNA abundance (Reads Per Million, RPM). DEG heatmap represent whether the tomato homolog is differentially expressed, red signifies a differentially expressed gene.

Mobile mRNAs synthesis mobile sRNAs

Biosynthesis of sRNAs can be derived from genes (Brant and Budak 2018). Since there was an enrichment in mobile sRNA gene targets and mRNAs with a similar function, we investigate whether the mobile sRNAs could be derived from mobile mRNAs. This was an enrichment in biological functions related to GTPase regulation/activity and transferase activity in mobile sRNAs gene targets and mobile mRNAs. The data analysis was clear that the sRNA-

producing loci in the eggplant rootstock did not overlap with the mobile mRNA transcripts. However, using BLAST analysis we found a statistical enrichment of mobile sRNA sequences that matches mobile mRNA sequences. This analysis involved comparing the nucleotide sequences of the mobile sRNAs and mRNAs using BLAST (Medicine 1988, Camacho, Coulouris et al. 2009) and comparing the results to a control set which was derived from a random pool of 500 mRNA transcripts and 500 sRNA clusters from biological eggplant samples ($p < 0.05$).

5.4 Discussion

Tomato grafting is immensely popular, mainly for its ability to induce a wide range of agronomically favourable traits such as pathogen resistance, environmental stress tolerance and improved vigour. Although the intrinsic properties of rootstocks have been associated with traits such as resistance, the physiological changes and molecular mechanisms driving grafting-induced crop vigour are not as well established.

To further understand the molecular mechanisms underpinning grafting-induced traits, researchers have examined the photosynthetic capacities of heterografts. In both *Cucurbitaceae* and *Solanaceous* crops, these works have primarily demonstrated how rootstocks that introduce salt-stress tolerance can promote CO_2 assimilation in the scion which results in delayed photoinhibition and improved vigour under stress (He, Zhu et al. 2009, Huang, Bie et al. 2011, Zhen, Bie et al. 2011, Liu, Bie et al. 2012, Liu, Bie et al. 2013, Parthasarathi, Ephrath et al. 2021). However, the majority of these studies using *Solanaceous*

crops lack consistency due to a large variation in research outcomes (Venema, Dijk et al. 2008, He, Zhu et al. 2009, Parthasarathi, Ephrath et al. 2021, Ramírez-Jiménez, Marchiori et al. 2021). Here, using eggplant as a rootstock to tomato we demonstrated no change in the rate of photosynthesis or water use efficiency, but a higher TPU rate in comparison to tomato self-graft controls. These results suggest that the heterografted plants have a superior ability to process triose phosphate and allocate it to metabolic processes. This result aligned well with the observed reduction in fruit weight, yet no changes in overall fruit production in heterografts (Liu, Jia et al. 2024). Together, this suggests that the heterografts are allocating and utilising carbon stores differently to the controls. Comparable results have been shown in tomato scions with a potato rootstock in which no significant differences in photosynthetic capacity were found yet fruit had a lower average weight (Zhang and Guo 2019). Note that these previous studies did not explore TPU (Zhang and Guo 2019). Furthermore, rootstocks have been shown to alter the partitioning of carbon to different vegetative tissues in tomato (Venema, Dijk et al. 2008).

The gene expression profiles suggest that the tomato scions grafted onto eggplant have undertaken a strategic reallocation of resources resulting in adjustments to metabolic processes. The expression profiles demonstrate that through the upregulation of redox homeostasis and downregulation of glutathione catabolism, alongside reinforcing cell walls, and adapting hormonal signal transduction pathways the plant is allocating more resources to stress response mechanisms. Within the genes involved in hormone signal transduction there was an enrichment in those that either play a role in abscisic

acid (ABA) responses or auxin response. These were particularly related to negative regulation of ABA whereas the auxin related genes were positive regulators. The upregulation of hormonal signal transduction pathways and MAPK signalling pathway KEGG pathways and downregulation of secondary metabolite biosynthetic process and flavonoid biosynthesis have equally been noted in a previous tomato/eggplant transcriptome study that described the same fruit production phenotype (Liu, Jia et al. 2024). Moreover, the downregulation of flavonoid biosynthesis could be an indicator of the impacted fruit properties and fruit quality resulting in diminished fruit weight. Interestingly, in *Arabidopsis thaliana* flavonoid biosynthesis is repressed in the presence of lignin biosynthesis and auxin signalling due to altered division of resources (Xiao, Zhang et al. 2021). Overall, the reallocation of resources helps explain why we observe no change in photosynthetic capacity and the elevated TPU levels. This insinuates that the diminished fruit weight might be linked to the levels of secondary metabolites that reinforce fruit quality and the allocation of resources to cell wall modifications, such as enhanced lignin or suberin deposition.

Epigenetic mechanisms are known to play a key role in long distance signalling. The study of epigenetic modifications and sRNAs has recently been applied to elucidate the molecular mechanism driving grafting traits that cannot be explained by the rootstock's intrinsic properties. In eggplant heterografts, genome-wide hypomethylation in the CHH context has been associated with improved vigour (Cerruti, Gisbert et al. 2021). While in tomato scions grafted onto eggplant that demonstrated comparable fruit production phenotypes, there were no correlation between gene expression and DNA methylation (Liu,

Jia et al. 2024). In this analysis we did not examine DNA methylation, however, we did observe an upregulation in AGO4 and DRM1 genes which are both involved in the RdDM pathway which is driven by sRNAs to maintain or introduce *de novo* DNA methylation. Equally, we observed a greater proportion of tomato sRNAs to be upregulated instead of downregulated. These results suggests that there could be alterations to DNA methylation patterns in the heterografts in comparison to the self-grafts which could likely be regulating gene expression and transposon silencing. This would align with previous results in tomato grafting using pepper whereby hypermethylation was linked to reduced crop vigour in comparison to controls (Liu, Jia et al. 2024).

Long distance signalling between the root and shoot has been shown to be driven by hormones, RNAs and proteins. In this study, we identified mobile root-to-shoot mRNA and sRNAs in the tomato scions. Next, we aimed to predict their biological roles in the leaf tissue that could be contributing to the observed phenotype. The most interesting mobile sRNAs were those that were predicted to target DEGs. Interestingly, these six sRNAs were predicted to target upregulated genes and, specifically these included a laccase enzyme (Solyc05g052360.2) and a calcium-dependant protein kinase (Solyc12g099790.3). The gene encoding the laccase enzyme was strongly upregulated ($p < 0.05$, logFC = 7.11) and correlated to the LACCASE 12 (LAC12, AT5G05390) ortholog in *Arabidopsis thaliana* which encodes a laccase-like multicopper oxidases (LMCOs). Under normal conditions, this gene is post-transcriptionally downregulated by miR408 (Abdel-Ghany and Pilon 2008). The repressive nature of miR408 is inhibited under iron (Fe) deficiency resulting in the increase expression of LAC12. When the LAC12 repression is removed there is enhanced

lignification (Carrió-Seguí, Ruiz-Rivero et al. 2019). Further evidence has supported the involvement of LAC12 in stem lignification (Turlapati, Kim et al. 2011). The miR408 has been found to target three distinct groups of proteins, and its overexpression has been associated with improved photosynthesis (Pan, Huang et al. 2018) and with greater vegetive growth; increased leaf size, increased petiole length, increased seed size and seed weight (Gao, Feng et al. 2022). Our results demonstrated that under normal conditions the LAC12 ortholog in tomato is upregulated, thus it could be surmised that the mobile sRNAs could be interfering with miR408 silencing of the LAC12 ortholog, potentially through target mimicry (Franco-Zorrilla, Valli et al. 2007). The upregulation of the tomato LAC12 ortholog could be directing resource allocation to cell wall modifications, such as lignin biosynthesis. Or its expression could be contributing to reduction in seed size and weight, which could explain the reduced fruit weight.

We investigated whether the mobile sRNA and the tomato miR408 could be interacting to alter expression profile. BLAST analysis demonstrated that the full length of the eggplant mobile sRNA (SMchr0:31852174-31852595) matched last 6 nucleotides of the mature miRNA sequence (sly-miR408) and 16 nucleotides in the precursor sequence. This suggests a possibility interaction, including interactions between mature sequences which could affects the miRNA's functionality resulting in inhibition of modulation of its activity. For example, competition for RISC. Alternatively, due to the significant overlap with the precursor sequence this could suggest that the mobile sRNA could be affecting the stability or processing of miR408. The action of sRNAs in plants and their role in the regulation of gene expression has been well characterised,

demonstrating their specificity and multiplicity in their targets (Parent, Martinez de Alba et al. 2012, Yan and Ham 2022). That said, this has been largely characterised within a single genome - this is to say that there is a lack of studies which demonstrate the action of sRNAs that are produced by a second plant genome on another plant genome. The closest similarity is the action of plant sRNAs on defence against viral infection or parasitic plants (Kim, LeBlanc et al. 2014, Zhang, Li et al. 2019). Given the flexibility and multiplicity of sRNA action, there could be further modes of actions specifically when acting in a compatible but non-native genome. This is particularly interesting in the context of plant grafting as this joins multiple genotypes into a single plant that continues to grow, and can is routinely utilised for the cultivation of specific crops as it can introduce favourable agronomic traits (Jeynes-Cupper and Catoni 2023).

It was confounding to observe upregulation of the calcium-dependant protein kinase (Solyc12g099790.3) (CDPK) gene target of the mobile sRNAs. This gene is an ortholog of CALCIUM-DEPENDENT PROTEIN KINASE 17 (CPK17) and CALCIUM-DEPENDENT PROTEIN KINASE 34 (CPK34) which are thought to have exclusive localised expression in the pollen to regulate pollen tube growth by modulating aquaporins to maintain turgor pressure (Myers, Romanowsky et al. 2009, Gutermuth, Lassig et al. 2013, Yip Delormel and Boudsocq 2019). That being said, members of the CDPK family are known to be regulators of rapid responses that utilise calcium such as ABA-induced stomatal closure and the initiation of immune defences that includes cell modifications (Geiger, Scherzer et al. 2009, Boudsocq, Willmann et al. 2010, Geiger, Scherzer et al. 2010). This

comprises of alteration to lignification in different tissues and at different developmental stages (Matschi, Werner et al. 2013).

Additionally, of the key gene targets of the mobile sRNAs, we identified a gene that encodes the REVEILLE 1 (SlRVE1, Solyc02g036370.3) gene which is a MYB family transcription factor. This gene has been characterised as a drought-responsive gene in tomato, whereby many genes related to drought-responses have been connected to both auxin signalling and lignin biosynthesis (Choi, Lee et al. 2023). What's more, a multitude of MYB genes have been associated to the regulation of lignin and other cell wall modifications (Xiao, Zhang et al. 2021). The RVE1 gene in *Arabidopsis thaliana* can regulated auxin to modulate hypocotyl growth and overexpression can delay or inhibit seed germination (Jiang, Xu et al. 2016). In our analysis we determined that the heterograft produced lighter fruit, however, could the presence of elevated RVE1 levels regulated by a mobile sRNA indicate that a delayed germination and hence the fruit were not fully developed at the fruit collection stage. RVE1 has been characterised to play a regulatory role in the promoter of gene expression in additional gene sets (Li, Wang et al. 2022), hence, it could be investigate to understand whether SlRVE1 contributes to the regulation and reprogramming of the transcriptomic profile in the heterografts.

In plants, there have been documented cases when sRNAs have been shown to be produced from the cleavage of mRNA targets and similarly sRNAs can be synthesized from mRNA transcripts to produce secondary sRNAs (Sanan-Mishra, Abdul Kader Jailani et al. 2021, Vaucheret and Voinnet 2024). The parasitic plant, *Cuscuta campestris*, creates a natural graft with its host.

Transcripts have been observed to move from the parasitic plant into the host which then act as templated to synthesize sRNA (Shahid, Kim et al. 2018). In this study, we found a statistical enrichment in mobile sRNA within the transcript sequences of mobile mRNAs. This enrichment suggests that the mobile sRNAs could be derived from the mobile mRNAs produced by the eggplant rootstock. This is further implied by the target prediction analysis which suggests that the mobile sRNA's target genes with a similar function to the mobile mRNAs. This finding brings great intrigue and suggests a complex cascading effect induced across the graft junction between tomato and eggplant, potentially involving target mimicry (Franco-Zorrilla, Valli et al. 2007).

Overall, we have demonstrated that heterografting of tomato onto eggplant results in alterations to the plant physiology, and vigour which could be driven by gene expression changes potentially triggered by the mobilisation of eggplant sRNAs into the tomato leaves. We further suggest that the diminished fruit weight albeit without adverse effects to overall yield is strongly related to the re-allocation of carbon described by TPU. We predict that through reprogramming of hormone and RNA signal transduction pathways there is a greater allocation of carbon to stress response mechanisms including cell walls modifications. This could possibly be coupled with the reduction in flavonoid biosynthesis that could further suggest that the reduction in carbon to fruits is hampering fruit quality or seed production.

5.5 Supplementary Figures & Tables

Supplementary Table 5.1 Pre-processing data showing of messenger RNA (mRNA) sequencing data for each sample replicate for transcriptomic analysis. Samples were cleaned and aligned to the individual genome reference representing the scion genome. Samples taken from an Eggplant scion were aligned to the Eggplant genome, whereas samples taken from a Tomato scion were aligned to the Tomato genome. The Tomato genome refers to the *Solanum lycopersium* version SL4.0 and Annotation ITAG4.0 reference (Tomato Genome Consortium 2012). The Eggplant genome to *Solanum melongena* version Version 4.1 reference (Barchi, Rabanus-Wallace et al. 2021). mRNA sequencing samples were generated by Illumina sequencing, 20M raw reads.

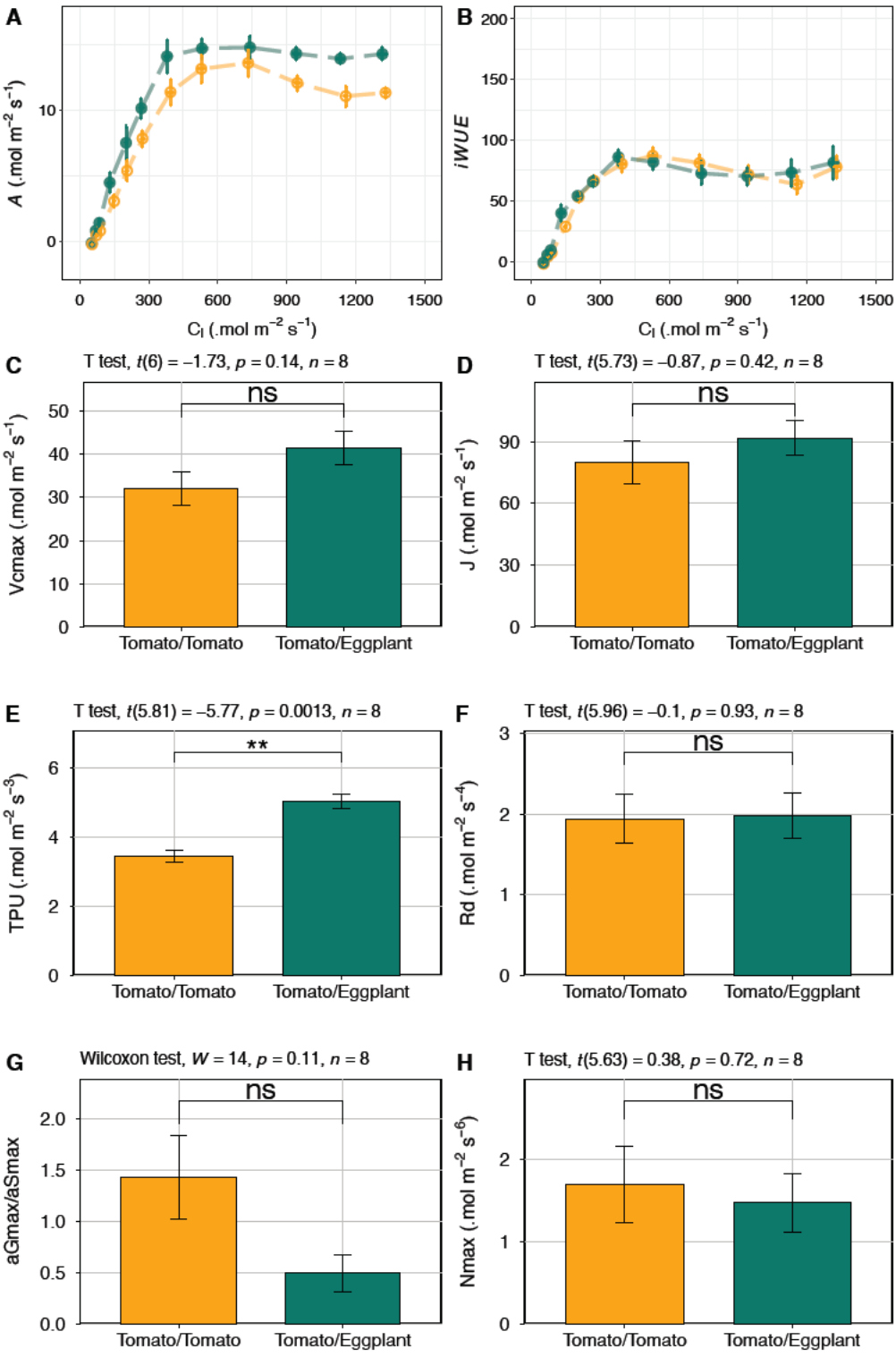
Condition	Sample	Clean reads	Mapped reads	Unmapped reads
Heterograft	TomEgg_1	146,943,384	131,393,413	46,288,516
Heterograft	TomEgg_2	142,315,884	169,737,651	5,496,351
Heterograft	TomEgg_3	148,075,894	170,162,677	6,198,104
Heterograft	TomEgg_4	136,531,960	169,395,421	4,731,095
Self-graft	TomTom_1	102,409,586	127,226,376	1,882,927
Self-graft	TomTom_2	142,521,776	170,297,642	2,703,911
Self-graft	TomTom_3	143,282,966	172,562,875	5,692,565

Supplementary Table 5.2. Pre-processing data showing of messenger RNA (mRNA) sequencing data for each sample replicate for mobile mRNA analysis. Samples were cleaned and aligned to a merged genome containing the Tomato genome and the Eggplant genome**.** The Tomato genome refers to the *Solanum lycopersium* version SL4.0 and Annotation ITAG4.0 reference (Tomato Genome Consortium 2012). The Eggplant genome to *Solanum melongena* version Version 4.1 reference (Barchi, Rabanus-Wallace et al. 2021). mRNA sequencing samples were generated by Illumina sequencing, 20M raw reads.

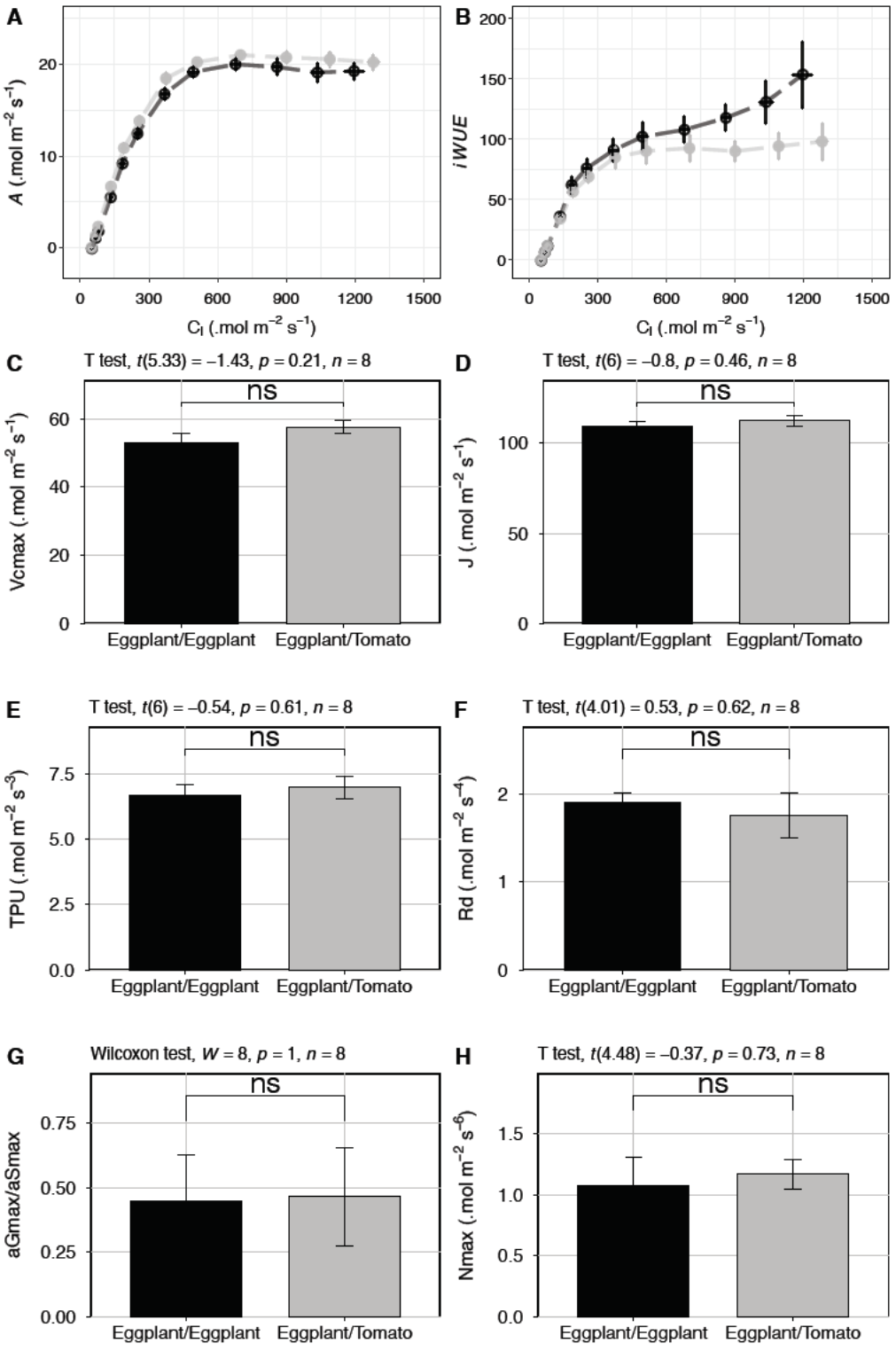
Condition	Sample	Cleaned reads	Total Unique reads	Mapped to Tomato	Mapped to Eggplant	Suppressed multimappers
Heterograft	TomEgg_1	146,943,384	128,010,212	84,641,419	43,459,395	18,933,172
Heterograft	TomEgg_2	142,315,884	125,394,842	125,316,965	108,656	16,921,042
Heterograft	TomEgg_3	148,075,894	131,252,100	131,203,568	69,440	16,823,794
Heterograft	TomEgg_4	136,531,960	119,654,987	119,526,870	151,295	16,876,973
Self-graft	TomTom_1	102,409,586	90,841,576	90,821,843	36,452	11,568,010
Self-graft	TomTom_2	142,521,776	129,125,765	129,099,781	47,363	13,396,011
Self-graft	TomTom_3	143,282,966	125,666,267	125,585,021	116,347	17,616,699

Supplementary Table 5.3. Pre-processing data showing of small RNA (sRNA) sequencing data for each sample replicate. Samples were cleaned and aligned to a merged genome containing the Tomato genome and the Eggplant genome. The Tomato genome refers to the *Solanum lycopersium* version SL4.0 and Annotation ITAG4.0 reference (Tomato Genome Consortium 2012). The Eggplant genome to *Solanum melongena* version Version 4.1 reference (Barchi, Rabanus-Wallace et al. 2021). sRNA sequencing samples were generated by Illumina sequencing, 20M raw reads.

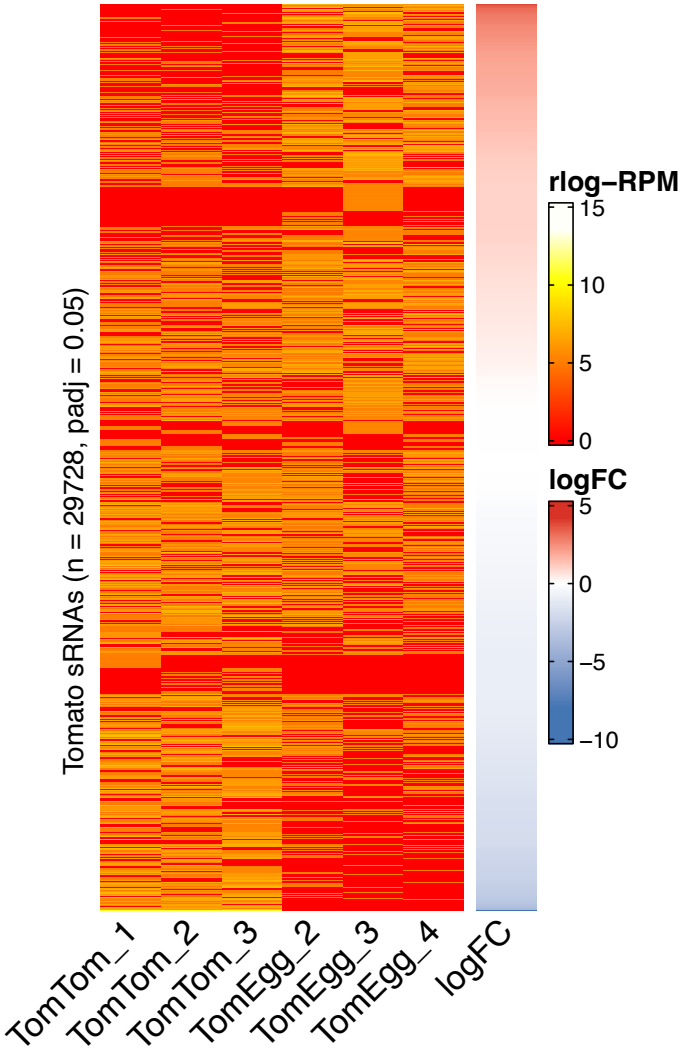
Sample	Scion	Rootstock	Raw_reads	Cleaned Reads	Mapped Reads	Unmapped Reads	Mapped to Tomato	Mapped to Eggplant	Supressed multimappers
EggEgg_1	Eggplant	Eggplant	27,306,988	25,562,388	6,725,599	2,585,232	54,354	6,671,245	16,251,557
EggEgg_2	Eggplant	Eggplant	33,361,196	28,573,684	5,334,448	2,411,995	77,467	5,256,981	20,827,241
EggEgg_3	Eggplant	Eggplant	24,969,770	23,251,713	5,020,557	2,170,698	44,506	4,976,051	16,060,458
EggEgg_4	Eggplant	Eggplant	32,532,803	30,051,391	6,654,274	2,691,652	52,348	6,601,926	20,705,465
EggTom_1	Eggplant	Tomato	24,003,218	21,803,258	3,974,612	1,825,379	49,717	3,924,895	16,003,267
EggTom_2	Eggplant	Tomato	22,898,841	17,402,443	2,548,930	1,472,570	53,195	2,495,735	13,380,943
EggTom_3	Eggplant	Tomato	23,252,886	21,827,421	6,407,060	2,290,063	36,682	6,370,378	13,130,298
TomEgg_1	Tomato	Eggplant	31,583,471	27,939,854	5,869,224	2,029,964	3,878,027	1,991,197	20,040,666
TomEgg_2	Tomato	Eggplant	39,457,394	34,749,638	5,955,418	2,193,842	5,703,668	251,750	26,600,378
TomEgg_3	Tomato	Eggplant	25,387,829	21,218,102	4,171,841	1,393,771	4,031,710	140,131	15,652,490
TomEgg_4	Tomato	Eggplant	32,559,353	27,683,984	5,600,751	1,792,270	5,426,633	174,118	20,290,963
TomTom_1	Tomato	Tomato	37,396,601	31,575,367	5,430,762	1,999,324	5,220,002	210,760	24,145,281
TomTom_2	Tomato	Tomato	35,221,220	30,622,742	5,497,009	1,862,833	5,326,027	170,982	23,262,900
TomTom_3	Tomato	Tomato	31,806,876	29,731,758	5,695,196	2,040,746	5,576,558	118,638	21,995,816



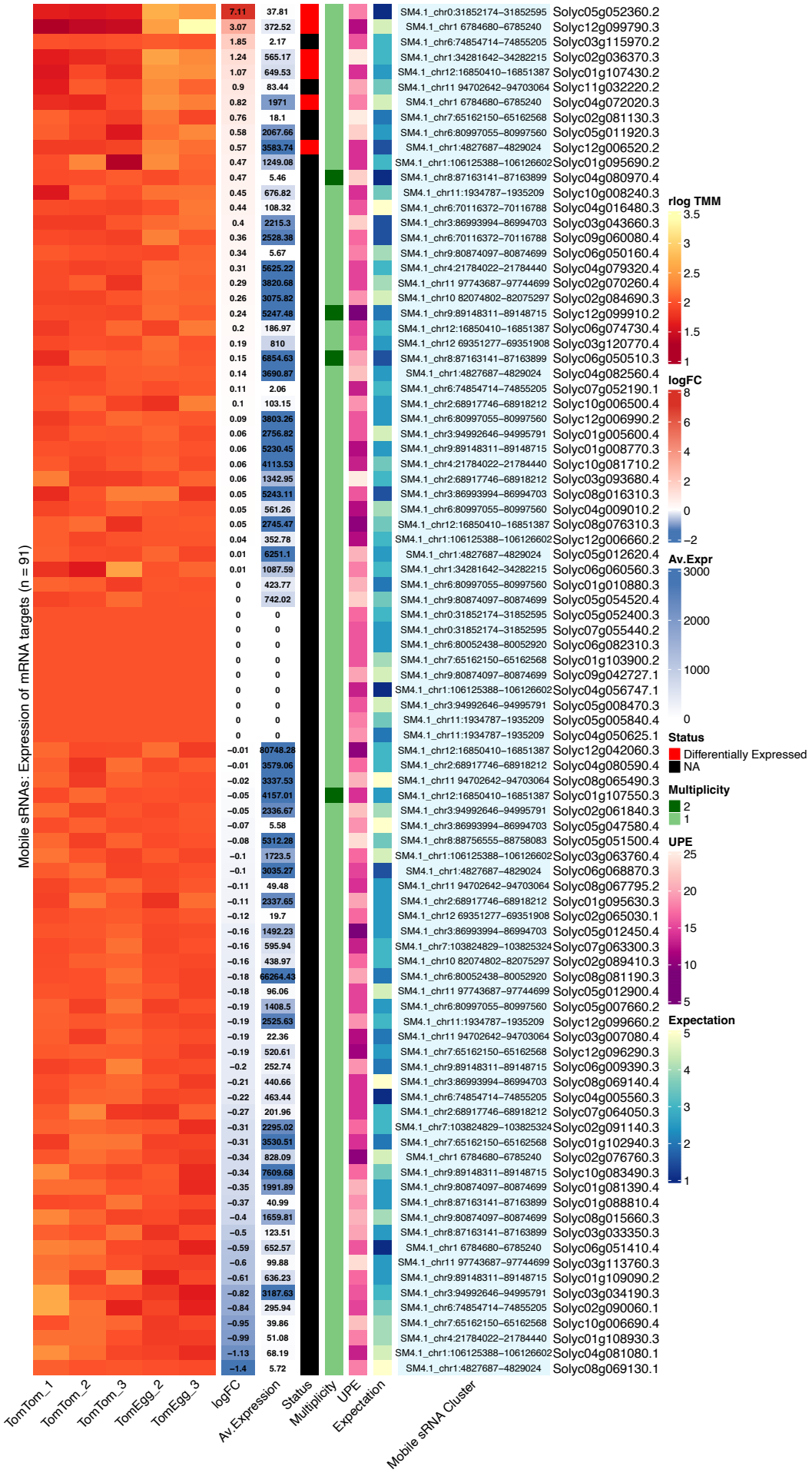
Supplementary Figure 5.5.1. Chlorophyll fluorescence imaging of tomato self-graft controls and tomato/eggplant heterografts. Error bars represent standard error. A) Photosynthesis as a function of internal carbon dioxide concentration (C_i). B) Intrinsic water use efficiency (iWUE) as a function of internal carbon dioxide concentration. C) Maximum efficiency of Rubisco carboxylase activity in photosystem II. D) Non photochemical quenching (NPQ).C) Triose phosphate utilisation. E) Dark respiration rate (Rd). F) Sum of alphaGmax and alphaSmax. G) Maximum photosynthetic rate.



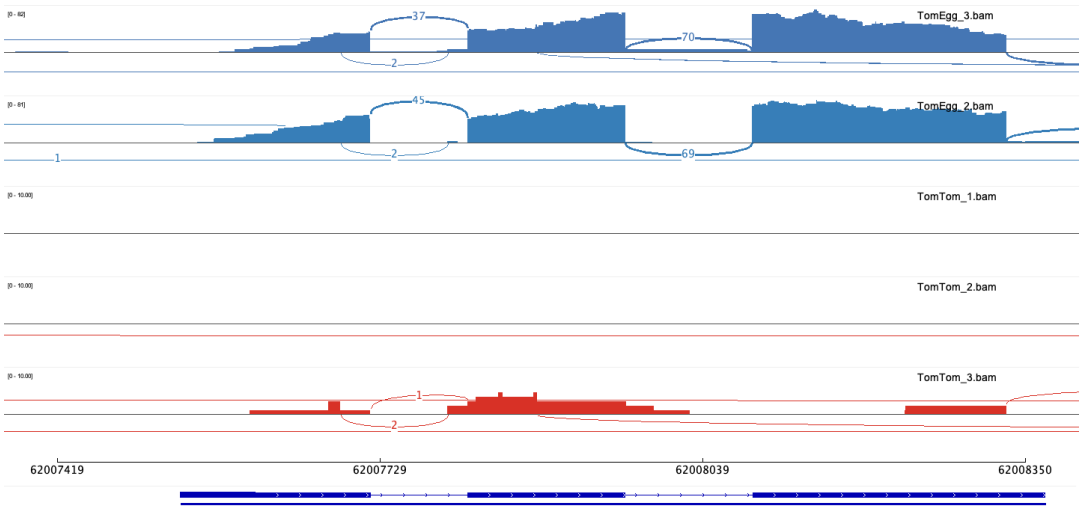
Supplementary Figure 5.5.2. Chlorophyll fluorescence imaging of eggplant self-graft controls and eggplant/ tomato heterografts. Error bars represent standard error. A) Photosynthesis as a function of internal carbon dioxide concentration (C_i). B) Intrinsic water use efficiency (iWUE) as a function of internal carbon dioxide concentration. C) Maximum efficiency of Rubisco carboxylase activity in photosystem II. D) Non photochemical quenching (NPQ).C) Triose phosphate utilisation. E) Dark respiration rate (Rd). F) Sum of alphaGmax and alphaSmax. G) Maximum photosynthetic rate.



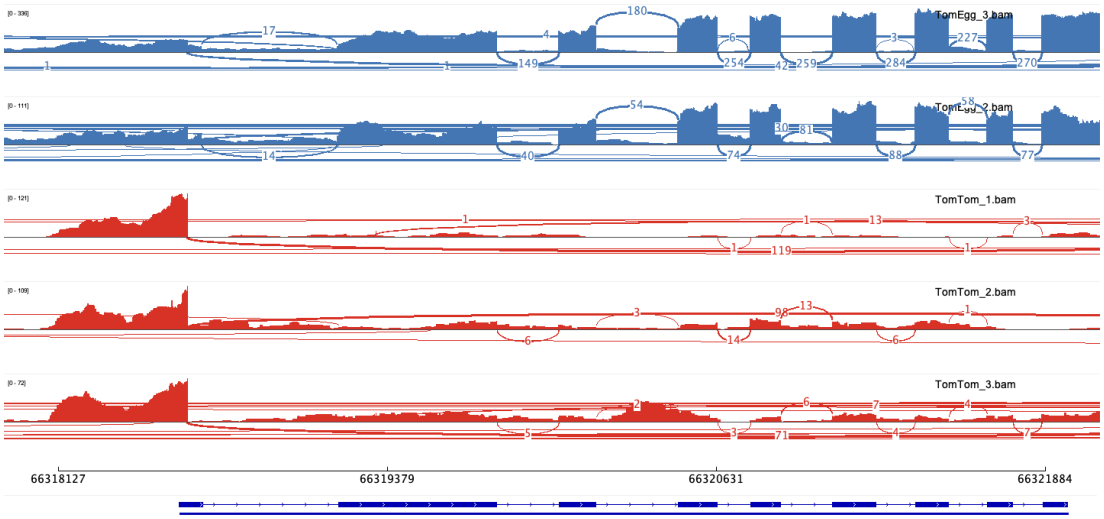
Supplementary Figure 5.5.3. Expression profiles of the total population of all differentially expressed tomato sRNAs (p < 0.05) produced by in the scion. Heatmap showing the relative rlog-transformed RPM values of differentially expressed tomato sRNA (*p* < 0.05) ordered by the log2 fold change (logFC). Each column represents a replicate whereby "TomTom" replicates are control sample and "TomEgg" represents are heterograft samples. Each row represents a tomato sRNA (*n* = 29,728). The gradient bars on the below show the expression level for rlog RPM values and the column for logFC represents the log2 fold change.


Mobile sRNAs: Expression of mRNA targets (n = 91)
TomTom_1
TomTom_2
TomTom_3
TomEgg_2
TomEgg_3
logFC
Av.Expression
Status
Multiplicity
UPE
Expectation
Mobile sRNA Cluster
rlog TMM
3.5
3
2.5
2
1.5
1
logFC
8
6
4
2
0
−2
Av.Expr
3000
2000
1000
0
Status
Differentially Expressed
NA
Multiplicity
2
1
UPE
25
20
15
10
5
Expectation
5
4
3
2
1

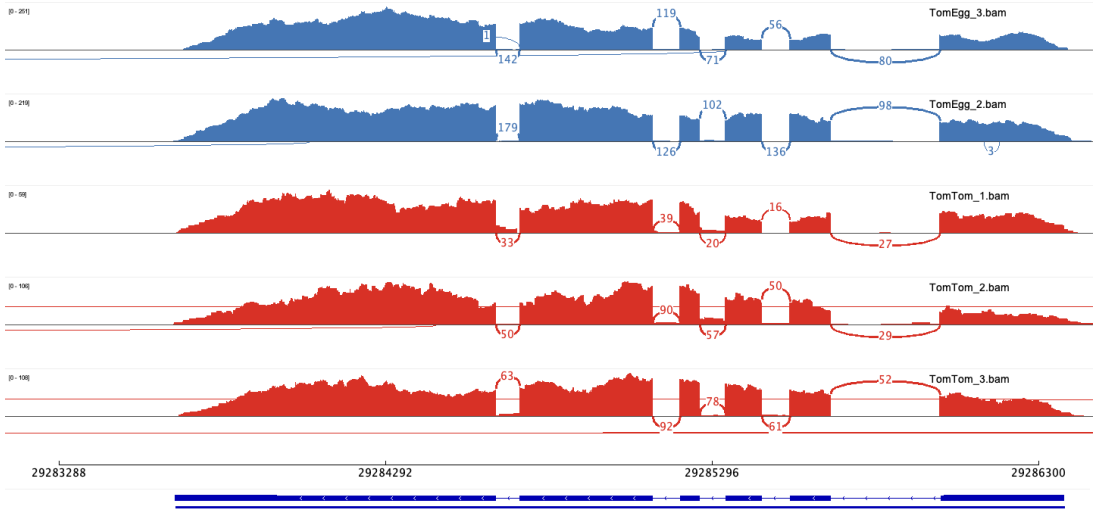
Supplementary Figure 5.5.4. Expression profiles of the predicted gene targets in the tomato scion of mobile sRNAs. Heatmap showing the relative rlog-transformed TMM values of differentially expressed target genes ($p < 0.05$) ordered by the log2 fold change (logFC). Each column represents a replicate, and each row represents a tomato sRNA ($n = 6$). The gradient bars on the below show the expression level for rlog TMM values. The column for logFC represents the log2 fold change, and the Av. Expression column represents the average expression value (rlog) across the experimental design. The UPE represents the maximum accessibility energy to unpair the sRNA from the target site and where the Expectation represents the penalty for mismatches between the sRNA and target site.



Supplementary Figure 5.5.5. Sashimi plot of coverage across the Solyc05g0523602 transcript, a key predicted gene target for a putative mobile sRNA. Sashimi plot of differential alternative splicing (DAS) of the Solyc05g0523602 gene transcript for self-graft (TomTom) samples shown in red and heterograft (TomEgg) samples shown in blue. Each shows the read coverage with the junction reads plotted as arcs with the indicated junction read counts.



Supplementary Figure 5.5.6. Sashimi plot of coverage across the Solyc12g099790 transcript, a key predicted gene target for a putative mobile sRNA. Sashimi plot of differential alternative splicing (DAS) of the Solyc12g099790 gene transcript for self-graft (TomTom) samples shown in red and heterograft (TomEgg) samples shown in blue. Each shows the read coverage with the junction reads plotted as arcs with the indicated junction read counts.



Supplementary Figure 5.5.7. Sashimi plot of coverage across the Solyc02g036370 transcript, a key predicted gene target for a putative mobile sRNA. Sashimi plot of differential alternative splicing (DAS) of the Solyc02g036370 gene transcript for self-graft (TomTom) samples shown in red and heterograft (TomEgg) samples shown in blue. Each shows the read coverage with the junction reads plotted as arcs with the indicated junction read counts.

CHAPTER 6: GENERAL DISCUSSION

Plant grafting is a fundamental research tool; assisting numerous discoveries, but most notably systemic signalling pathways in plants (Melnyk 2017). Plant communication between cells and tissues utilizes complex networks of proteins, hormones and RNAs and, in a non-linear manner, utilize both post-transcriptional and post-translational regulatory mechanism to achieve a coordinate response throughout the plant (Yoo, Kragler et al. 2004, Zhang, Kollwig et al. 2014, Kehr, Morris et al. 2022) (Figure 6.1). RNAs can act in a non-autonomous manner to activate further signalling and development in recipient cells or tissues (Lucas, Yoo et al. 2001). Therefore, determining where mobile RNA originate from and where they interact, and under what conditions are important for further elucidation of their roles in plant signal transduction (Tomkins, Hoerbst et al. 2022).

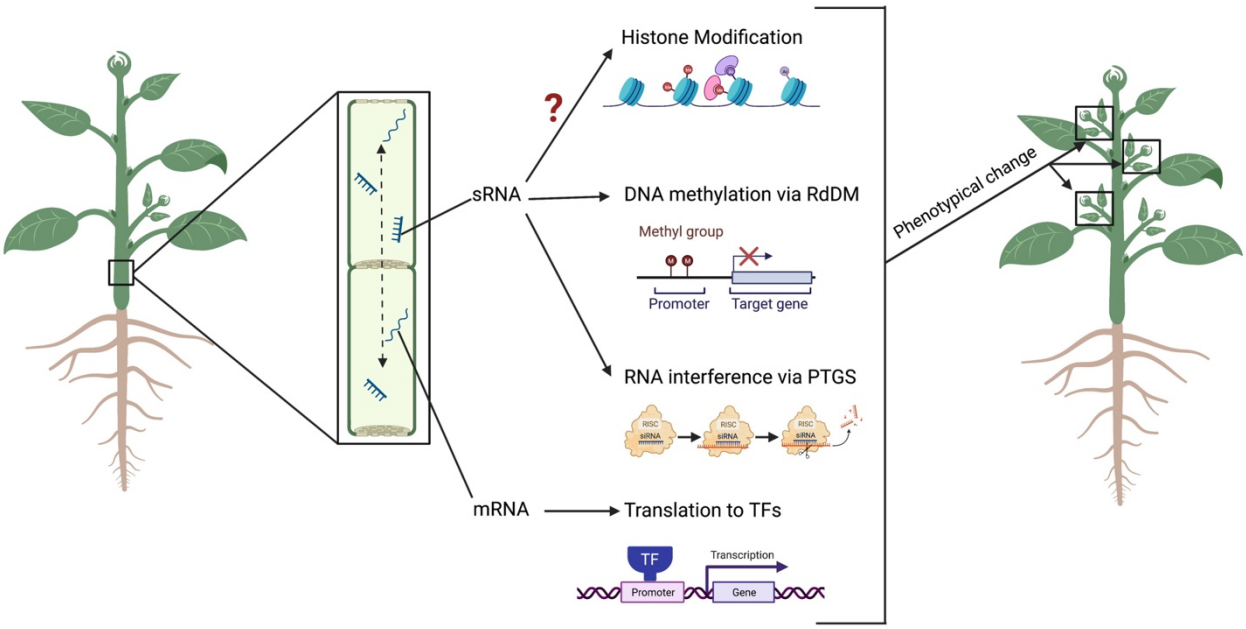


Figure 6.1. Figure taken from Jeynes-Cupper and Catoni (2023) demonstrating the movement of RNAs between the roots and shoots and their interactions driving epigenetic modifications and lead to phenotypical changes. In recipient tissues, sRNAs can introduce variation to DNA methylation patters through the RNA-directed DNA Methylation (RdDM) pathway and can alter expression through post-transcriptional gene silencing (PTGS). Mobile mRNAs are thought to translation into transcription factors (TFs) to modulate expression patterns. The diagram also illustrated histone modifications driven by sRNA, however, this interaction has not yet demonstrated in grafting experiment

Considering technological advancements, it is possible to undertaken genome-wide identification of putative mobile RNAs and experimental validations to confirm their presence. Using these techniques researchers have captured mobile mRNAs and identified their essential roles in physiological and developmental processes (Kim, Canio et al. 2001, Haywood, Yu et al. 2005, Banerjee, Chatterjee et al. 2006, Kitagawa, Wu et al. 2022). More recently, systemic sRNA signalling has been demonstrated to initiate transcriptional gene silencing through in recipient tissues and demonstrating their capacity to introduce epigenetic variation across graft junctions (Molnar, Melnyk et al. 2010, Lewsey, Hardcastle et al. 2016). To detect mobile molecules, researchers utilize heterografting to combine plants from distinct genotypes, for instance, if an RNA originating from the rootstock is found within the shoot, then this

could be interpretated as a mobile molecule that has moved across the graft junction. However, this interpretation is dependent on the ability to distinguish the RNAs produced by the shoots and roots.

The detection of mobile RNA is not without its challenges. Numerous papers have discussed how previous studies utilizing sequencing technologies to detect mobile RNAs, deploy varying bioinformatic pipelines. Possibly as a result, most studies demonstrate variability between experiments with little overlap in their results (Kehr, Morris et al. 2022, Tomkins, Hoerbst et al. 2022, Paajanen, Tomkins et al. 2024). These previous pipelines follow a similar workflow that aims to leverage sequence polymorphisms between the genotypes to distinguish the origin of RNAs. These pipelines commonly use independent single-reference mapping approaches and downstream selection or variant calling methods and additional statistical testing to discriminate noise from biological polymorphisms (Xia, Zheng et al. 2018, Wang, Wang et al. 2020, Rubio, Stammitti et al. 2022, Tomkins, Hoerbst et al. 2022, Paajanen, Tomkins et al. 2024). To combat these challenges, we developed an alternative method to standardize the detection of mobile RNAs; essentially the detection of RNA expression in multiple genotypes within a sample.

Advanced alignment tools have been developed to place sequencing reads to the best location within a reference genome. To do so, they optimize both speed and accuracy, and the most advanced algorithms consider the presence of technical and experimental sequencing errors, plus, the presence of structural variants that introduce further variation between the reads and the reference genome (Kim 2019). These alignment algorithms assume that all or most of the sequencing reads are assembled in the given reference genome, hence, the

deploy advanced statistical testing to determine the best location for a read within the genome. This approach has been specifically designed for standard sequencing experiments where only a single genotype is considered, and hence is not optimal for situations whereby more than one genotype is present. To optimize the utilization of alignment algorithms, here, we introduce the *mobileRNA* method that employs a genome reference contains the genetic sequences from both the shoot and root genotypes – i.e. a merged genome. We theorized that by supplying the alignment algorithms with all the information at the time of alignment, they can make the best possible decision to determine the origin of a read.

To quantitatively evaluate the *mobileRNA* method, we synthesized blended synthetic datasets and benchmarked the method against previously used pipelines. Synthetic datasets are artificially constructed and commonly lack a true reflection of real biological context (Lähnemann, Köster et al. 2020). Therefore, blended datasets were designed to capture a greater level of natural data noise by utilizing real biological datasets to both generate simulated mobile RNAs and as a base to inject the simulated mobile RNAs. This approach allowed us to regulate true positives while allowing us to benchmark for false negatives and false positives. The blended datasets were not only designed to simulate known grafting combinations but also to access the effects of homology between the shoot and root genotypes. From the analysis, we determined that the *mobileRNA* method outperformed comparable methods by significantly reducing the amount of data noise while increasing the confidence in detected mobile RNAs. However, the homology between the two genomes plays the largest role in the ability to detect mobile molecules. Therefore, to

assist users and allow them to predict the proportion of detectable mobile RNAs between two genotype we propose the use of a genome mappability score. In instances where the two genome references show high homology, we expect the *mobileRNA* method to underestimate the proportion of mobile RNAs within the graft system.

Tomatoes are one of the most economically important crops in the world, with more than 170.7 million tons produced globally in 2014 (Singh, Kumar et al. 2017). To cultivated tomatoes, grafting is extensively used for soil-less production in the Netherlands and USA (Lee 1994). By developing rootstocks using wild and modern *solanaceous* varieties, breeds can introduce a wide range of favourable crop traits to tomato including abiotic and biotic stress tolerance and improved vigour in non-stress conditions (Colla, Pérez-Alfocea et al. 2017). The mechanisms that introduce grafting related traits have been extensively explored in *solanaceous* and other families including woody trees and *cucurbits*. While many traits have been associated with the intrinsic properties of the rootstock, traits such as crop vigour are not as easily explained. So far, several studies have indicated the involvement of complex RNA signalling mechanisms that may regulate gene expression and trigger physiological changes in the scion (Molnar, Melnyk et al. 2010, Melnyk, Molnar et al. 2011, Avramidou, Kapazoglou et al. 2015, Lewsey, Hardcastle et al. 2016, Cerruti, Gisbert et al. 2021, Li, Wang et al. 2021, Rubio, Stammitti et al. 2022). Despite the recent surge in genome-scale identification studies that characterize mobile RNAs as well as studies that characterize DNA methylation changes in the scion, there lacks studies which associate mobile RNAs with alterations to transcriptomic regulation that contribute to grafting-induced traits (Cerruti, Gisbert et al. 2021,

Li, Wang et al. 2021, Jeynes-Cupper and Catoni 2023). Here, we undertook tomato grafting experiments and assessed changes in crop vigour. The grafting traits illustrated key changes in fruit quality and fruit weight, while no changes in overall production. In Chapter 5, we accessed the photosynthetic ability of the heterografted plants in comparison to the self-grafted, and identified a significantly enhance TPU in heterografted plants with an eggplant rootstock. Employing the newly devised *mobileRNA* approach, we detected mobile mRNAs and sRNAs in the scions of tomato heterografted plants that demonstrated unique grafting-induced traits. With transcriptomic analysis we detected a key upregulation in cell wall biosynthesis, remodelling and metabolism across all heterograft conditions. Interestingly, depending on the rootstock different biochemical pathways were upregulated which indicated that different alterations to the cell wall for each condition. Modifications to cell wall components have previously been observed in grafted plants, and such modifications can impact growth, development and alter traits such as abiotic and biotic stress tolerance (Boerjan, Ralph et al. 2003, Choi, Lee et al. 2023). We were able to detect mobile sRNAs and mRNAs which could be playing into this regulation. For instance, in Chapter 5 we suggest that mobile mRNAs produced by the eggplant rootstock could be degraded or used as template to synthesis the mobile sRNAs (Figure 6.2). In the phenylpropanoid pathway, responsible for synthesizing lignin (a key component in cell walls and fruits), is regulated at both the transcriptional and post-transcriptional level (Boerjan, Ralph et al. 2003, Zhang, Yang et al. 2021). In fact, we identified a key mobile sRNA which could be interfering with this post-transcriptional regulation of this pathway. These results, although only a snippet, illustrate the type of molecular

complexity of the rootstock-scion interactions identified in the overall results in the heterografting experiments.

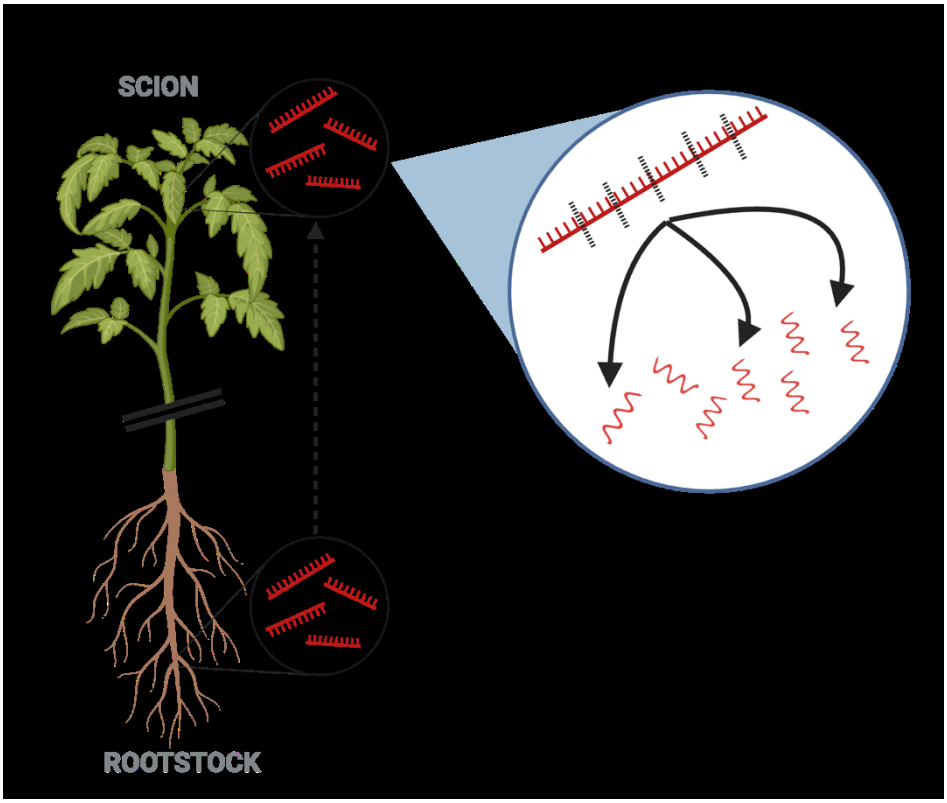


Figure 6.2. Over-simplified schematic diagram of the proposed interaction between mobile mRNAs and sRNAs in the tomato scions grafted onto eggplant rootstocks. Based on the results we hypothesis that mobile mRNAs travel from the eggplant rootstock into the tomato scion and sRNAs are produced from their sequences. See chapter 5 for more details. Created using BioRender.com.

Research considerations & future work

The detection of mobile RNAs in heterografting experiments presents several challenges. Firstly, to date distinguishing the origin of RNAs produced by the same genotype is currently impossible using genome-scale approaches. In other terms, there is no reliable method to distinguish endogenous RNAs produced by one tissue and identified within another tissue of the same genotype. This limitation restricts our ability to access the role of mobile transcripts in systemic signalling to coordinate growth and development. Secondly, a large proportion

of plant sRNAs originate from repetitive regions, including TEs (Vaucheret and Voinnet 2024). The sRNAs spawned from TEs include 24-nt siRNAs which are involved in the RdDM pathway which can mediate *de novo* DNA methylation (Vaucheret and Voinnet 2024). The repetitive nature of these short read sequences prevents their detection via existing methods, including *mobileRNA*. This is because these reads will likely align ambiguous to sequences in both the scion and rootstock genomes, making it impossible to determine their true origin. Hence, the *mobileRNA* approach discards reads that align to multiple locations within the merged genome, ultimately to avoid misinterpretation of their origin. As a result, methods are unable to efficiently and unambiguously detect these classes of mobile sRNAs, despite their potential significance in epigenetic regulation, and responses to stress and developmental cues (Vaucheret and Voinnet 2024). This limitation underscores a broader concern where we may likely incur bias and skewed results, namely towards those lacking extremely repetitive regions.

Several studies have demonstrated that reference-based alignment outperform reference-free approaches, and the increased availability of assembled genomes from different organisms has promoted the generation of advanced mapping algorithms (Langmead, Trapnell et al. 2009, Kim, Paggi et al. 2019). The quality of genome assemblies can influence the identification of mobile RNAs. In our analysis we indicated that the use of a long read-assisted *de novo* assembly could more efficiently detect mobile RNA than a SNPs-only based assembly. This outcome implied that the quality of the reference genomes influences the detection of mobile RNAs. This association has been evaluated in a recent study that re-analysed existing heterografting experiments to detect mobile mRNAs

(Paajanen, Tomkins et al. 2024) which also described the genome complexity to also play a significant role (Paajanen, Tomkins et al. 2024). These outcomes highlight the need for high-quality reference genomes, and the limitations posed by draft or incomplete genome references may hinder research objective. In the past 20 years, more than 1,000 plant genomes have been published and year-on-year the assemblies and annotations are readily improved (Sun, Shang et al. 2022). Fundamental experimental research, using models such as *Arabidopsis thaliana*, has characterized the functions and roles of thousands of genes (Sun, Shang et al. 2022). Despite these advancements, many genes in key crops have not been functionally characterized to the same degree as others in model species (Edwards, Batley et al. 2013). In Chapters 4 and 5, we characterized key putative gene targets for mobile sRNA action, however, most of these genes lacked a functional characterization, or were poorly described in literature. This limitation makes it challenging to draw inference regarding the molecular mechanisms involving mobile signalling. Further investigation into the roles of annotated genes in key crops would provide further clues as to the regulatory mechanisms underpinning grafting-traits.

In Chapter 4, we investigated tomato heterografting with commercial rootstocks provided by ENZA ZADEN. This experimental design had several key limitations. Firstly, to detect root-to-shoot mobile RNAs in these grafting combinations the bioinformatic pipeline relies highly on the genetic variation between the scion and rootstock genomes. The available genome assemblies do not include vast commercial lines such as the ones utilized in this study. Breeding schemes employ modern techniques such as quantitative trait loci (QTL) mapping and hybridization to develop commercial lines with

economically valuable traits. Consequently, this can impact their genetic landscape, making it challenging to estimate the proportion of the genome derived from different parents/lineage. To detect root-to-shoot mobile RNAs, we have utilized the *S. habrochaites* genome to represent the tomato hybrid rootstock lines. This reference genome was employed since a large proportion of the genetic origin in the rootstocks is expected to derive from *S. habrochaites*. Due to the hybrid nature of the rootstocks, the sole use of the *S. habrochaites* genome may not capture the full extent of the mobile transcripts – likely underestimating their presence. On the other hand, to represent the scion genotype we utilized the `Heinz` cultivar genome reference, which has its own limitations. Mobile mRNA transcripts from the rootstock could be produced from gene fragments that originate from modern tomato lines, matching the scion's genetic background. Hence, alignment of the sequencing reads to the `Heinz` genome reference may inadvertently assign mobile mRNA expression to the scion transcriptome profile. Thus, mobile mRNA transcript abundance may contribute to the relative gene expression levels in the scion. Consequently, we may observe gene upregulation, when in fact their endogenous levels are lower. The lack of distinguishability between mobile and endogenous transcripts could result in improper understanding of the molecular mechanisms underpinning grafting-induced traits.

In contract, limitations to this analysis also arose due to the greenhouse conditions. In the Netherlands, soil-free tomato cultivation is primarily employed alongside grafting (Lee 1994). Our experimental design followed this practice whereby the grafted plants were grown on wool block, supplied with a nutrient-fortified water and grown upwards along a guide string (Lee 1994, Singh, Kumar et al. 2017). Tomato plants will grow upwards following the

guide string to its set height before trailing back down. The height of the guide string determines the length of the season; the plants cannot withstand the pressures from hanging downwards for an extended period. Unfortunately, within our experiment, the guide string was set too low for our crop, resulted in a truncated growing season. Based on the existing data provided by ENZA ZADEN, the tomato grafts demonstrate the greatest difference in vigour after a further 1-2 months since the end of our experiment. This limitation impacted our ability to show the greatest difference in grafting-induced phenotypes provided by the RS-1 and RS-2 rootstocks.

So far, several studies in *Arabidopsis thaliana* have demonstrated the involvement of sRNA signalling and their ability to trigger physiological changes across the graft junction (Molnar, Melnyk et al. 2010, Bai, Kasai et al. 2011, Melnyk, Molnar et al. 2011, Thieme, Rojas-Triana et al. 2015, Lewsey, Hardcastle et al. 2016). This includes inducing DNA methylation changes in the recipient tissues through the RdDM pathway (Lewsey, Hardcastle et al. 2016, Zhang, Lang et al. 2018). Since these findings, studies utilizing crop grafting have characterized DNA methylation changes in the scion in response to heterografting, for which some have been associated with grafting-induced traits including vigour (Wu, Wang et al. 2013, Avramidou, Kapazoglou et al. 2015, Cao, Yu et al. 2016, Cerruti, Gisbert et al. 2021, Rubio, Stammitti et al. 2022). Yet, these studies do not investigate the shoot-root interactions and the molecular signalling pathways that could be regulating the genome-wide DNA methylation alterations in the scion. In the experimental studies in Chapters 4 and 5 we identified changes in the transcriptomic profiles of genes associated with epigenetic regulation. Bisulfite sequencing (BS-seq) could be undertaken

on DNA samples from these experiments to analyses whether genome-wide cytosine DNA methylation changes occur in the scion in response to heterografting. Since we have analysed the changes in sRNAs in the scion, connecting these with DNA methylation changes could help shed further light on the molecular mechanism involved in traits in tomato.

Final concluding remarks

To summaries, these results emphasize that grafting-induced traits involve complex interactions between the scion and the rootstock. The results highlighted that elucidating these interactions is not without its challenges, and bioinformatic methods must take into consideration a wide range of assumptions including homology, sequencing errors, and read depth. Here, this contribution presents the *mobileRNA* method that outperforms previously described methods for the detection of mobile RNAs using NGS data taken from heterografting experiments. This method was applied to detect mobile RNAs in heterografting experiments in *solanaceous* species to investigate whether mobile RNAs are involved in grafting-induced traits, specifically changes in vigour. Indeed, we located mobile mRNAs and sRNAs produced by the rootstock genotype in the leaves of the scion. Interestingly, we found that less than 10% of putative mobile transcripts contained structural features associated with mobility, such as TLSs, which suggests that other endogenous mechanisms play the largest role in RNA trafficking selectivity. From the collective results, heterografting inadvertently induces changes in genes involved in stress response pathways. To facilitate these changes, it is likely that mobile mRNAs could play a more important role than previously described. Here, we provide putative evidence to suggest that mobile mRNAs could be the

source of rootstock-encoded sRNAs in the scion. For which, these sRNAs might play a key role in regulating resource allocation to alter the patterns of secondary metabolite production. Despite these promising results, further validation is required, and our outcomes underscore the current limitations within the field. Here, we contribute improvements in our understanding of grafting-induced traits and the underpinning molecular mechanisms in *Solanaceous* crops, while demonstrating the importance of elucidating RNA signalling pathways in plant.

CHAPTER 7: APPENDICES

Supplementary Material 7.1. List of photosynthetic-related genes. A curated list of genes in Arabidopsis was acquired from Dr. Robyn Emmerson (R Emmerson 2022). Reciprocal protein sequences analysis was conducted to identify orthologs in tomato (*Solanum lycopersicum*) and eggplant (*Solanum melongena*) genomes.

Arabidopsis Gene ID	Tomato Gene ID	Eggplant Gene ID
AT1G01060	Solyc10g005080.3.1	SMEL4.1_04g000690.1.01
AT1G01060	Solyc10g005080.3.1	SMEL4.1_04g000700.1.01
AT1G01720	Solyc11g017470.2.1	SMEL4.1_04g010980.1.01
AT1G01720	Solyc06g060230.3.1	SMEL4.1_06g015730.1.01
AT1G02340	NA	NA
AT1G05085	NA	NA
AT1G08540	Solyc01g081490.3.1	SMEL4.1_01g020120.1.01
AT1G09530	Solyc01g102300.3.1	SMEL4.1_01g001850.1.01
AT1G10120	Solyc04g077480.3.1	SMEL4.1_04g018520.1.01
AT1G14920	Solyc01g059950.1.1	NA
AT1G14920	Solyc01g059960.1.1	SMEL4.1_01g028070.1.01
AT1G15820	Solyc01g105030.3.1	NA
AT1G15820	Solyc01g105050.3.1	NA
AT1G18330	Solyc03g098320.3.1	SMEL4.1_03g021470.1.01
AT1G19350	Solyc04g079980.3.1	SMEL4.1_05g018690.1.01
AT1G19350	Solyc12g089040.2.1	SMEL4.1_05g018690.1.01
AT1G19350	Solyc04g079980.3.1	SMEL4.1_04g020890.1.01
AT1G19350	Solyc12g089040.2.1	SMEL4.1_04g020890.1.01
AT1G26260	Solyc01g010135.1.1	SMEL4.1_01g034510.1.01
AT1G26260	Solyc05g010610.3.1	SMEL4.1_10g016510.1.01
AT1G26945	Solyc04g005660.3.1	NA
AT1G26945	Solyc05g007210.2.1	SMEL4.1_10g019710.1.01
AT1G27730	Solyc01g107170.2.1	NA
AT1G29160	Solyc02g076850.2.1	SMEL4.1_02g010630.1.01
AT1G32060	Solyc08g076220.3.1	SMEL4.1_08g019600.1.01
AT1G32230	Solyc08g076420.3.1	SMEL4.1_08g019810.1.01
AT1G32230	Solyc06g066330.3.1	NA
AT1G32230	Solyc08g005270.3.1	SMEL4.1_08g002870.1.01
AT1G32330	Solyc08g076590.3.1	NA
AT1G32330	Solyc08g005170.3.1	SMEL4.1_08g002790.1.01
AT1G32640	NA	NA
AT1G42960	Solyc12g094630.2.1	SMEL4.1_05g019370.1.01
AT1G42960	Solyc04g082640.3.1	SMEL4.1_04g022710.1.01

AT1G43670	Solyc04g071340.3.1	SMEL4.1_04g013740.1.01
AT1G43670	Solyc04g071340.3.1	SMEL4.1_05g022830.1.01
AT1G43670	Solyc12g056530.2.1	SMEL4.1_05g022830.1.01
AT1G43670	Solyc12g056530.2.1	SMEL4.1_04g013740.1.01
AT1G44446	Solyc06g060310.3.1	SMEL4.1_06g015630.1.01
AT1G44446	Solyc11g012850.2.1	SMEL4.1_12g005900.1.01
AT1G44446	Solyc06g060310.3.1	SMEL4.1_06g015660.1.01
AT1G44446	Solyc11g012850.2.1	SMEL4.1_06g015630.1.01
AT1G44446	Solyc11g012850.2.1	SMEL4.1_06g015660.1.01
AT1G44446	Solyc06g060310.3.1	SMEL4.1_12g005900.1.01
AT1G49190	Solyc04g008050.3.1	SMEL4.1_11g019670.1.01
AT1G51600	NA	NA
AT1G64860	Solyc06g072710.3.1	SMEL4.1_06g024380.1.01
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AT1G66350	Solyc10g086370.2.1	SMEL4.1_10g019250.1.01
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AT1G67090	Solyc02g085950.3.1	SMEL4.1_02g022990.1.01
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AT1G67090	Solyc02g085950.3.1	SMEL4.1_02g022980.1.01
AT1G67090	Solyc03g034220.3.1	SMEL4.1_02g022960.1.01
AT1G67090	Solyc02g063150.3.1	SMEL4.1_02g022980.1.01
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AT1G76100	Solyc04g082010.1.1	NA
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AT1G80280	Solyc03g119990.3.1	SMEL4.1_03g031350.1.01

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AT2G05070	Solyc07g047850.3.1	SMEL4.1_07g015640.1.01
AT2G20180	Solyc06g008030.3.1	NA
AT2G20570	Solyc07g053630.3.1	SMEL4.1_07g018900.1.01
AT2G20570	Solyc10g008160.3.1	NA
AT2G25180	NA	NA
AT2G25930	Solyc11g070100.2.1	SMEL4.1_12g017860.1.01
AT2G25930	Solyc12g095900.2.1	SMEL4.1_05g019410.1.01
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AT2G26150	Solyc08g062960.3.1	SMEL4.1_08g012690.1.01
AT2G27050	Solyc01g009170.3.1	SMEL4.1_08g016940.1.01
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AT2G40080	Solyc06g051660.1.1	NA
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AT2G42220	Solyc03g053110.3.1	NA
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AT2G46830	Solyc10g005080.3.1	SMEL4.1_04g000700.1.01
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AT2G46970	NA	NA
AT2G47400	Solyc06g009630.1.1	NA
AT2G47400	Solyc01g079470.3.1	SMEL4.1_01g023530.1.01
AT3G01500	Solyc02g086820.3.1	SMEL4.1_02g029690.1.01
AT3G03450	Solyc10g086370.2.1	SMEL4.1_10g019250.1.01
AT3G03450	Solyc11g011260.1.1	SMEL4.1_11g000560.1.01
AT3G04550	Solyc11g006060.1.1	SMEL4.1_11g004450.1.01
AT3G06483	Solyc01g057210.3.1	SMEL4.1_01g029070.1.01
AT3G06483	Solyc01g057210.3.1	SMEL4.1_05g022270.1.01
AT3G06483	Solyc12g098930.2.1	SMEL4.1_05g022270.1.01
AT3G07340	Solyc06g083170.3.1	SMEL4.1_06g029290.1.01
AT3G08940	Solyc09g014520.3.1	NA
AT3G13960	NA	NA
AT3G16857	Solyc01g065540.3.1	NA
AT3G16857	Solyc05g054390.3.1	SMEL4.1_05g004070.1.01
AT3G17609	NA	NA
AT3G20770	Solyc01g009170.3.1	SMEL4.1_08g016940.1.01
AT3G20770	Solyc06g073720.2.1	SMEL4.1_06g025350.1.01
AT3G20770	Solyc06g073730.2.1	SMEL4.1_06g025350.1.01
AT3G20770	Solyc06g073720.2.1	SMEL4.1_06g025340.1.01
AT3G20770	Solyc06g073730.2.1	SMEL4.1_06g025340.1.01
AT3G20770	Solyc06g073720.2.1	SMEL4.1_08g016940.1.01
AT3G20770	Solyc06g073730.2.1	SMEL4.1_08g016940.1.01
AT3G21175	NA	NA
AT3G22170	Solyc07g043270.3.1	SMEL4.1_07g013360.1.01
AT3G26650	Solyc02g020940.3.1	SMEL4.1_11g021380.1.01
AT3G26650	Solyc04g009030.3.1	SMEL4.1_11g021380.1.01
AT3G27690	Solyc07g047850.3.1	SMEL4.1_02g012440.1.01
AT3G27690	Solyc12g006140.2.1	NA
AT3G27690	Solyc07g047850.3.1	SMEL4.1_02g012460.1.01
AT3G27690	Solyc07g047850.3.1	SMEL4.1_07g015640.1.01
AT3G53920	Solyc08g065970.3.1	SMEL4.1_08g013910.1.01
AT3G54620	NA	NA
AT3G55370	NA	NA
AT3G55800	Solyc05g052600.3.1	SMEL4.1_05g001040.1.01
AT3G56940	Solyc10g077040.2.1	SMEL4.1_10g027120.1.01
AT3G56940	Solyc10g077040.2.1	SMEL4.1_00g007430.1.01
AT3G59060	Solyc07g043580.3.1	SMEL4.1_00g005860.1.01
AT3G62090	NA	NA

AT3G62410	Solyc01g079470.3.1	SMEL4.1_01g023530.1.01
AT3G62410	Solyc06g009630.1.1	NA
AT4G04330	NA	NA
AT4G05180	Solyc02g079950.3.1	NA
AT4G15090	Solyc08g060840.1.1	NA
AT4G16780	Solyc06g060830.3.1	SMEL4.1_06g016060.1.01
AT4G16780	Solyc08g007270.3.1	SMEL4.1_08g001890.1.01
AT4G16780	Solyc08g078300.3.1	SMEL4.1_08g024110.1.01
AT4G23750	Solyc08g081960.2.1	SMEL4.1_08g026460.1.01
AT4G25560	Solyc03g025870.3.1	SMEL4.1_03g016190.1.01
AT4G25560	Solyc01g009645.1.1	NA
AT4G26150	Solyc07g038160.3.1	NA
AT4G27430	Solyc07g063350.3.1	SMEL4.1_07g022840.1.01
AT4G27440	Solyc07g054210.3.1	NA
AT4G27440	Solyc10g006900.3.1	NA
AT4G27440	Solyc12g013710.2.1	NA
AT4G27600	Solyc03g097210.3.1	SMEL4.1_03g019870.1.01
AT4G31920	NA	NA
AT4G32800	Solyc06g066540.1.1	SMEL4.1_06g019300.1.01
AT4G34530	Solyc01g109700.3.1	SMEL4.1_01g004860.1.01
AT4G36730	Solyc02g085610.3.1	SMEL4.1_02g023240.1.01
AT4G36730	Solyc02g062950.3.1	NA
AT5G02200	NA	NA
AT5G02810	Solyc10g086000.2.1	SMEL4.1_10g020160.1.01
AT5G03720	NA	NA
AT5G11260	Solyc08g061130.3.1	SMEL4.1_08g010690.1.01
AT5G11670	Solyc08g066360.3.1	SMEL4.1_05g024490.1.01
AT5G11670	Solyc08g066360.3.1	SMEL4.1_05g012760.1.01
AT5G11670	Solyc08g066360.3.1	SMEL4.1_08g014070.1.01
AT5G13730	Solyc01g087690.2.1	SMEL4.1_01g021050.1.01
AT5G20730	Solyc07g042260.3.1	SMEL4.1_07g012550.1.01
AT5G24120	Solyc03g007370.3.1	SMEL4.1_03g018810.1.01
AT5G24470	Solyc03g081240.3.1	SMEL4.1_03g019390.1.01
AT5G28770	NA	NA
AT5G35210	Solyc11g066780.2.1	SMEL4.1_12g016220.1.01
AT5G35210	Solyc06g074640.2.1	SMEL4.1_06g025730.1.01
AT5G35490	NA	NA
AT5G37190	NA	NA
AT5G38410	Solyc02g063150.3.1	SMEL4.1_02g022990.1.01
AT5G38410	Solyc02g063150.3.1	SMEL4.1_02g006850.1.01
AT5G38410	Solyc03g034220.3.1	SMEL4.1_02g006850.1.01

AT5G38410	Solyc02g063150.3.1	SMEL4.1_02g022960.1.01
AT5G38410	Solyc02g085950.3.1	SMEL4.1_02g006850.1.01
AT5G38410	Solyc03g034220.3.1	SMEL4.1_02g022960.1.01
AT5G38410	Solyc03g034220.3.1	SMEL4.1_02g022980.1.01
AT5G38410	Solyc02g085950.3.1	SMEL4.1_02g022960.1.01
AT5G38410	Solyc02g085950.3.1	SMEL4.1_02g022980.1.01
AT5G38410	Solyc02g085950.3.1	SMEL4.1_02g022990.1.01
AT5G38410	Solyc03g034220.3.1	SMEL4.1_03g003530.1.01
AT5G38410	Solyc02g085950.3.1	SMEL4.1_03g003530.1.01
AT5G38410	Solyc02g063150.3.1	SMEL4.1_02g022980.1.01
AT5G38410	Solyc03g034220.3.1	SMEL4.1_02g022990.1.01
AT5G38420	Solyc02g063150.3.1	SMEL4.1_02g006850.1.01
AT5G38420	Solyc02g085950.3.1	SMEL4.1_02g022980.1.01
AT5G38420	Solyc02g085950.3.1	SMEL4.1_02g022990.1.01
AT5G38420	Solyc03g034220.3.1	SMEL4.1_03g003530.1.01
AT5G38420	Solyc02g085950.3.1	SMEL4.1_02g022960.1.01
AT5G38420	Solyc03g034220.3.1	SMEL4.1_02g006850.1.01
AT5G38420	Solyc02g063150.3.1	SMEL4.1_02g022990.1.01
AT5G38420	Solyc02g063150.3.1	SMEL4.1_02g022960.1.01
AT5G38420	Solyc03g034220.3.1	SMEL4.1_02g022980.1.01
AT5G38420	Solyc03g034220.3.1	SMEL4.1_02g022960.1.01
AT5G38420	Solyc02g063150.3.1	SMEL4.1_02g022980.1.01
AT5G38420	Solyc03g034220.3.1	SMEL4.1_02g022990.1.01
AT5G38420	Solyc02g085950.3.1	SMEL4.1_02g006850.1.01
AT5G38420	Solyc02g085950.3.1	SMEL4.1_03g003530.1.01
AT5G38430	Solyc02g063150.3.1	SMEL4.1_02g006850.1.01
AT5G38430	Solyc02g085950.3.1	SMEL4.1_02g006850.1.01
AT5G38430	Solyc03g034220.3.1	SMEL4.1_02g022990.1.01
AT5G38430	Solyc02g063150.3.1	SMEL4.1_02g022980.1.01
AT5G38430	Solyc02g085950.3.1	SMEL4.1_02g022980.1.01
AT5G38430	Solyc02g085950.3.1	SMEL4.1_02g022960.1.01
AT5G38430	Solyc03g034220.3.1	SMEL4.1_03g003530.1.01
AT5G38430	Solyc02g063150.3.1	SMEL4.1_02g022960.1.01
AT5G38430	Solyc03g034220.3.1	SMEL4.1_02g006850.1.01
AT5G38430	Solyc02g063150.3.1	SMEL4.1_02g022990.1.01
AT5G38430	Solyc02g085950.3.1	SMEL4.1_02g022990.1.01
AT5G38430	Solyc03g034220.3.1	SMEL4.1_02g022960.1.01
AT5G38430	Solyc02g085950.3.1	SMEL4.1_03g003530.1.01
AT5G38430	Solyc03g034220.3.1	SMEL4.1_02g022980.1.01
AT5G39610	Solyc02g088180.3.1	SMEL4.1_02g028410.1.01
AT5G44190	Solyc07g053630.3.1	SMEL4.1_07g018900.1.01

AT5G44190	Solyc10g008160.3.1	NA
AT5G46110	Solyc10g008980.3.1	SMEL4.1_04g004570.1.01
AT5G48150	Solyc06g035620.3.1	NA
AT5G48150	Solyc12g005340.2.1	SMEL4.1_10g005270.1.01
AT5G48150	Solyc07g063940.2.1	SMEL4.1_07g023610.1.01
AT5G48490	Solyc01g066910.3.1	NA
AT5G48560	Solyc06g083170.3.1	SMEL4.1_06g029290.1.01
AT5G51110	NA	NA
AT5G54270	Solyc12g011450.2.1	NA
AT5G54270	Solyc07g063600.3.1	NA
AT5G56860	Solyc07g038160.3.1	NA
AT5G60100	NA	NA
AT5G61380	Solyc06g069697.1.1	SMEL4.1_06g022360.1.01
AT5G61380	Solyc03g115770.3.1	SMEL4.1_03g026990.1.01
AT5G62000	Solyc03g118290.3.1	SMEL4.1_03g029420.1.01
AT5G62000	Solyc12g042077.1.1	SMEL4.1_05g012510.1.01
AT5G62000	Solyc12g042077.1.1	SMEL4.1_03g029420.1.01
AT5G62000	Solyc03g118290.3.1	SMEL4.1_05g012510.1.01

Supplementary Material 7.2. Table of differentially expressed genes between self-grafted and heterografted conditions: Tomato/Eggplant heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Gene ID	baseMean	log2FoldChange	pvalue	padj	expression
Solyc01g005257.1	694.3815942	-0.894165806	2.65E-05	0.001499716	downregulated
Solyc01g005530.3	423.5984066	-0.762172735	0.00159912	0.037247496	downregulated
Solyc01g006320.4	373.4540669	-1.234040294	0.001721735	0.03931265	downregulated
Solyc01g006890.3	1171.135941	-0.770198189	0.000336974	0.01130828	downregulated
Solyc01g006950.3	123.5891472	-2.44672467	0.00049477	0.015277916	downregulated
Solyc01g007960.3	33.5718275	-1.69505156	0.002348126	0.048731613	downregulated
Solyc01g008930.4	1650.837497	-0.687756213	0.002400984	0.049544011	downregulated
Solyc01g009930.3	74.89073575	-3.573495333	1.09E-05	0.0007544	downregulated
Solyc01g010060.2	54.16311835	-2.751838202	2.43E-06	0.0002072	downregulated
Solyc01g057770.3	1336.087588	-0.922062448	0.001541568	0.036406329	downregulated
Solyc01g058720.4	1630.349849	-1.688092517	2.06E-08	3.03E-06	downregulated
Solyc01g067740.3	7467.396398	-1.745522225	2.99E-12	8.61E-10	downregulated
Solyc01g068410.4	12.6341932	-3.395782536	0.00142629	0.034399021	downregulated
Solyc01g074000.3	1876.717515	-1.10371207	0.00035316	0.011764567	downregulated
Solyc01g079180.4	179.0617515	-1.529865598	0.000283538	0.010096707	downregulated
Solyc01g079240.3	6058.994462	-0.781322006	0.000758747	0.020869215	downregulated

Solyc01g079600.4	335.0619684	-0.690382856	0.002106323	0.045102321	downregulated
Solyc01g080700.4	956.6331029	-0.727025694	0.001757986	0.039939688	downregulated
Solyc01g086640.2	302.7987925	-1.622166809	0.000218363	0.008186438	downregulated
Solyc01g086730.4	66.21257399	-2.372344213	0.000352561	0.011761861	downregulated
Solyc01g087970.3	2061.717283	-0.615034129	0.000728095	0.020221981	downregulated
Solyc01g088400.4	630.8271101	-1.652624144	6.42E-05	0.003055346	downregulated
Solyc01g089890.3	236.333614	-1.686296006	0.000398261	0.012935023	downregulated
Solyc01g090340.3	7078.161954	-0.557417813	0.001599363	0.037247496	downregulated
Solyc01g091240.4	1110.702417	-0.745691341	0.00162954	0.037753775	downregulated
Solyc01g091590.3	39.56940547	-2.069753817	0.00032894	0.01117067	downregulated
Solyc01g094020.3	1060.530714	-0.667266545	0.000700107	0.019636707	downregulated
Solyc01g094850.3	26.35158838	-2.625651677	3.75E-05	0.001995026	downregulated
Solyc01g096140.3	20.22258553	-4.575922518	2.65E-05	0.001499716	downregulated
Solyc01g096510.2	115.1159714	-2.869177136	2.00E-07	2.31E-05	downregulated
Solyc01g096940.4	1587.879574	-1.033012512	0.000676365	0.019108573	downregulated
Solyc01g097000.3	855.0792973	-1.038711073	2.40E-06	0.000205363	downregulated
Solyc01g099030.4	373.4264473	-1.218777421	9.52E-05	0.004308637	downregulated
Solyc01g102350.3	2780.709783	-0.855088816	0.000536135	0.016005835	downregulated
Solyc01g103660.4	195.1246574	-1.090271757	0.00030275	0.010549342	downregulated
Solyc01g105310.3	374.9089297	-3.661963438	6.78E-10	1.34E-07	downregulated
Solyc01g105350.3	752.6533766	-4.28518416	6.69E-06	0.000495475	downregulated
Solyc01g107020.4	613.0137795	-0.683556955	0.001083495	0.027972647	downregulated
Solyc01g108000.3	312.9211681	-0.874955609	0.000257121	0.009319015	downregulated
Solyc01g108210.4	819.8145953	-1.439066518	4.31E-06	0.000335402	downregulated
Solyc01g108330.2	320.3737677	-1.099228317	3.76E-07	4.11E-05	downregulated
Solyc01g108530.3	911.052751	-0.822492647	0.002256069	0.047371193	downregulated
Solyc01g108560.4	195.7081256	-0.968115719	0.000174612	0.006909149	downregulated
Solyc01g108610.3	761.054201	-1.275126587	4.96E-05	0.002472103	downregulated
Solyc01g109250.2	249.640532	-1.682207598	4.81E-05	0.002426739	downregulated
Solyc01g109670.3	92.59012772	-3.520477326	9.89E-07	9.48E-05	downregulated
Solyc01g109690.1	3792.858891	-1.552875674	0.000807167	0.021961718	downregulated
Solyc01g109880.3	2749.456887	-1.932970346	9.82E-05	0.00440071	downregulated
Solyc01g109950.4	201.4769931	-1.494867533	0.000165093	0.006691581	downregulated
Solyc01g110060.3	1381.207054	-0.852166464	0.001865562	0.041833967	downregulated
Solyc01g111070.3	25.14298739	-1.971388469	0.002047318	0.044482958	downregulated
Solyc01g111100.5	441.3839147	-1.115771719	1.30E-07	1.56E-05	downregulated
Solyc01g111810.3	461.4290042	-0.697931961	0.001178279	0.029644863	downregulated
Solyc01g111840.3	326.1717456	-1.187993797	1.78E-05	0.001113841	downregulated
Solyc01g111970.4	68.46539851	-2.098998975	6.46E-07	6.68E-05	downregulated
Solyc02g014860.3	364.3038284	-1.928196802	0.002075747	0.044742782	downregulated
Solyc02g030480.4	2149.369884	-0.956623701	2.25E-05	0.001334766	downregulated

Solyc02g031730.1	12.31636204	-5.461537797	0.001032599	0.026852846	downregulated
Solyc02g037490.1	42.43392014	-1.902965539	0.001894007	0.042269098	downregulated
Solyc02g037550.3	107.4319602	-3.12022003	4.80E-09	8.33E-07	downregulated
Solyc02g037555.1	40.06614066	-2.656904675	1.34E-05	0.000894294	downregulated
Solyc02g061990.3	344.8559626	-2.011455229	1.51E-12	4.62E-10	downregulated
Solyc02g065060.3	484.0959606	-2.12468766	1.80E-08	2.73E-06	downregulated
Solyc02g065230.3	213.4990313	-1.191334755	4.20E-06	0.000328986	downregulated
Solyc02g065240.3	1299.844715	-1.119242787	2.85E-05	0.001590328	downregulated
Solyc02g065610.3	463.9989212	-1.213035912	0.000207372	0.007826059	downregulated
Solyc02g067040.3	91.55818088	-1.258288906	0.001630197	0.037753775	downregulated
Solyc02g067360.3	1247.864198	-0.654401944	0.001004773	0.026340469	downregulated
Solyc02g067660.4	1063.916225	-1.07462275	0.001773531	0.040212434	downregulated
Solyc02g067730.2	60.99070645	-2.856969319	0.000325119	0.011107341	downregulated
Solyc02g067890.3	2080.003409	-1.131936465	5.91E-06	0.000447345	downregulated
Solyc02g068680.1	44.16408856	-1.632009961	0.001544202	0.036430656	downregulated
Solyc02g069060.4	91.77934874	-2.023532627	0.000223944	0.008340612	downregulated
Solyc02g069250.4	332.785889	-1.601122086	3.45E-05	0.001871595	downregulated
Solyc02g069690.1	415.0364134	-0.882122956	0.000295422	0.010373547	downregulated
Solyc02g070040.1	88.18446329	-1.263662066	0.001432258	0.034506334	downregulated
Solyc02g070580.1	1326.909568	-0.881477785	0.000162849	0.006618559	downregulated
Solyc02g070670.4	2233.285659	-0.73099836	5.16E-05	0.002567436	downregulated
Solyc02g071080.3	564.3182857	-1.562977892	2.70E-07	2.99E-05	downregulated
Solyc02g071090.3	1045.743618	-2.220789484	3.04E-09	5.39E-07	downregulated
Solyc02g071110.3	1177.783336	-0.895567811	0.000752684	0.020752712	downregulated
Solyc02g076730.3	430.7384875	-1.097303224	0.001115707	0.02857694	downregulated
Solyc02g076750.3	675.6441807	-1.118866177	0.000144271	0.00601413	downregulated
Solyc02g077060.2	17.7441489	-3.344374144	0.000602226	0.017535701	downregulated
Solyc02g077330.3	2006.677727	-1.486971501	4.57E-05	0.002321974	downregulated
Solyc02g077970.4	19.44637964	-3.74755218	7.59E-05	0.003535748	downregulated
Solyc02g078130.3	40.56180849	-2.185509784	1.15E-05	0.000789556	downregulated
Solyc02g078400.3	13226.57447	-2.122566919	3.46E-06	0.000279022	downregulated
Solyc02g078480.3	1562.69342	-0.724586169	0.000102811	0.004570708	downregulated
Solyc02g079490.3	663.491949	-1.877791616	2.31E-05	0.001350551	downregulated
Solyc02g079590.3	951.7479698	-1.081728134	0.000356937	0.011855625	downregulated
Solyc02g079600.3	223.2425939	-1.414489472	0.001251224	0.03103337	downregulated
Solyc02g080010.2	1081.601983	-1.135478278	0.001435973	0.034522613	downregulated
Solyc02g080110.3	238.9225495	-1.005424888	0.002144624	0.045749964	downregulated
Solyc02g081340.3	280.2631339	-3.038906268	1.61E-20	1.41E-17	downregulated
Solyc02g081360.4	84.75715243	-1.316171121	0.002084856	0.044779271	downregulated
Solyc02g082150.1	111.0904315	-1.657518698	0.000532707	0.015924443	downregulated
Solyc02g082450.3	204.8519444	-1.188343432	0.002317816	0.048271936	downregulated

Solyc02g083620.3	355.0068726	-0.768099313	0.002171153	0.046256575	downregulated
Solyc02g083860.3	682.623177	-2.120274065	1.96E-08	2.93E-06	downregulated
Solyc02g085020.4	472.3022366	-3.245815278	2.50E-37	1.42E-33	downregulated
Solyc02g085830.4	225.899341	-2.010169853	0.00150018	0.035651388	downregulated
Solyc02g086770.3	184.34845	-0.978236248	0.000157519	0.006448071	downregulated
Solyc02g086840.3	1864.980881	-0.923999726	7.45E-06	0.000540557	downregulated
Solyc02g086960.2	472.2573776	-0.817605708	0.002200727	0.046553374	downregulated
Solyc02g087330.3	1147.575198	-0.941531025	0.000503635	0.01542441	downregulated
Solyc02g087350.3	65.83670747	-1.887619222	0.000764299	0.020996504	downregulated
Solyc02g087430.4	1441.598535	-0.601057037	0.002178197	0.046256575	downregulated
Solyc02g089620.3	7128.306736	-4.479784831	1.46E-05	0.000959622	downregulated
Solyc02g089630.3	90.92257632	-4.795837934	1.37E-10	2.99E-08	downregulated
Solyc02g089980.3	854.5778316	-0.72029736	0.001437711	0.034527851	downregulated
Solyc02g090150.1	93.47946669	-1.090618588	0.001280798	0.031457792	downregulated
Solyc02g090540.4	142.9695535	-2.643227792	8.86E-06	0.000627093	downregulated
Solyc02g091690.3	159.3131681	-1.589290802	0.000874783	0.023491963	downregulated
Solyc02g091830.3	218.0408292	-1.16776403	0.002314952	0.048271936	downregulated
Solyc02g092670.1	10974.06635	-1.265105304	2.28E-05	0.001343108	downregulated
Solyc02g092680.1	80.28153951	-1.419349537	0.001712341	0.03917692	downregulated
Solyc02g092770.3	552.4232101	-1.504119223	5.11E-08	6.79E-06	downregulated
Solyc02g092790.3	8001.401693	-1.592609086	0.000452272	0.014169554	downregulated
Solyc02g093050.3	998.2555371	-1.008266141	0.000662653	0.018891918	downregulated
Solyc02g093230.4	329.7449837	-0.907273911	0.000111506	0.004871732	downregulated
Solyc02g093350.3	517.4150802	-0.815474155	0.00056827	0.016810585	downregulated
Solyc02g093550.3	2424.656003	-0.840696133	0.002305318	0.048182624	downregulated
Solyc02g094300.4	1915.135448	-0.905015985	0.000987603	0.026012393	downregulated
Solyc03g005340.4	4338.515431	-0.773041164	0.00027838	0.009928594	downregulated
Solyc03g006220.4	559.9388716	-1.211761208	2.84E-09	5.09E-07	downregulated
Solyc03g007770.3	5002.433202	-1.361317103	0.002400332	0.049544011	downregulated
Solyc03g007890.3	520.5486813	-1.543888721	9.25E-05	0.004219106	downregulated
Solyc03g025190.4	296.3873134	-2.843774988	7.86E-19	5.58E-16	downregulated
Solyc03g031420.1	303.7427515	-0.94729848	8.39E-05	0.003881752	downregulated
Solyc03g033360.3	219.5769204	-0.881851912	0.001105816	0.028387598	downregulated
Solyc03g033410.4	2164.424574	-1.452422319	1.21E-08	1.91E-06	downregulated
Solyc03g033420.4	1424.373155	-0.637826122	0.001087074	0.02803317	downregulated
Solyc03g044010.4	1464.320406	-0.521330614	0.002178225	0.046256575	downregulated
Solyc03g044300.3	123.3614308	-1.515511808	1.51E-05	0.000984706	downregulated
Solyc03g044600.2	704.3451945	-1.19058667	0.00050376	0.01542441	downregulated
Solyc03g053020.4	1769.406028	-0.961059064	0.000388615	0.012703525	downregulated
Solyc03g053060.3	24.91361205	-4.870334215	0.000306179	0.010611632	downregulated
Solyc03g078150.3	531.3322509	-1.153363568	2.37E-06	0.000204163	downregulated

Solyc03g078780.3	391.9650562	-1.015598164	0.000110035	0.004826012	downregulated
Solyc03g082370.1	96.79306603	-2.131837491	0.00028432	0.010108702	downregulated
Solyc03g082420.3	50.41186696	-2.150668001	0.000439349	0.013914331	downregulated
Solyc03g093550.1	508.6830454	-0.889047675	2.08E-05	0.001262682	downregulated
Solyc03g093560.1	187.2708145	-1.283411459	0.001217219	0.030422452	downregulated
Solyc03g095180.3	1130.974397	-1.660529868	0.00200869	0.043796005	downregulated
Solyc03g097050.3	510.1616501	-0.774996235	0.000331673	0.01123111	downregulated
Solyc03g097230.1	260.4087233	-1.700774559	0.001406276	0.033952378	downregulated
Solyc03g097570.3	120.9433862	-1.770762026	0.000513779	0.015625897	downregulated
Solyc03g097600.3	405.937325	-2.175995749	3.27E-05	0.001784678	downregulated
Solyc03g097840.3	324.1011741	-1.449262038	0.001675202	0.038560189	downregulated
Solyc03g111360.3	84.20970366	-1.124295444	0.002210107	0.0466968	downregulated
Solyc03g111530.4	90.889053	-1.294712238	0.000602816	0.017535701	downregulated
Solyc03g111620.1	175.9498152	-1.670682295	0.000144684	0.006020296	downregulated
Solyc03g111680.3	959.996962	-0.697764871	0.000414464	0.013285335	downregulated
Solyc03g112300.3	521.0576403	-1.250226158	0.00040101	0.012977974	downregulated
Solyc03g114800.1	298.5391647	-1.306394173	9.02E-05	0.004133286	downregulated
Solyc03g115200.3	2605.301712	-1.45123228	6.32E-06	0.000472196	downregulated
Solyc03g115930.3	201.2674992	-1.987104193	0.000158341	0.006470054	downregulated
Solyc03g115950.3	286.5725822	-1.091864689	0.000499708	0.015404175	downregulated
Solyc03g116460.4	1405.233808	-1.654262942	2.75E-05	0.001540329	downregulated
Solyc03g116700.4	886.66268	-1.746054081	0.000334672	0.011271448	downregulated
Solyc03g117560.3	724.8687154	-1.135318665	0.000467309	0.014571412	downregulated
Solyc03g117570.3	108.8569285	-1.38721769	0.000706582	0.019745194	downregulated
Solyc03g118130.3	14527.65553	-0.899018585	0.002300316	0.048122356	downregulated
Solyc03g119250.4	610.5098506	-1.231934122	0.000889772	0.023810053	downregulated
Solyc03g121070.3	2287.023555	-0.79076848	0.001994988	0.043664862	downregulated
Solyc03g122360.3	512.7567919	-1.596854863	1.08E-07	1.32E-05	downregulated
Solyc04g005100.3	1508.949748	-1.098323949	0.000169443	0.006777414	downregulated
Solyc04g007800.4	925.3191843	-1.567602185	0.002192289	0.046467487	downregulated
Solyc04g008330.1	2815.835619	-1.416628404	8.58E-07	8.47E-05	downregulated
Solyc04g008650.4	499.7817471	-0.966921666	0.000125831	0.005411061	downregulated
Solyc04g008870.3	265.2359836	-1.618937099	1.73E-06	0.000157463	downregulated
Solyc04g015360.3	424.9680771	-0.880184994	0.001709201	0.039144505	downregulated
Solyc04g016200.1	468.4040452	-1.539866555	0.000254513	0.009251658	downregulated
Solyc04g025530.3	83.1898892	-2.205264251	2.65E-06	0.000221748	downregulated
Solyc04g040130.1	283.231973	-2.269057589	0.000186238	0.007282512	downregulated
Solyc04g049340.3	661.1750951	-0.922564765	4.19E-05	0.002194779	downregulated
Solyc04g054500.3	499.1669674	-2.064637145	0.001498379	0.035651388	downregulated
Solyc04g054760.3	262.3309781	-2.089446049	4.26E-13	1.45E-10	downregulated
Solyc04g055200.3	3636.42614	-0.879977581	0.001986713	0.04356769	downregulated

Solyc04g056370.3	84.24931663	-1.104085102	0.00223432	0.047001394	downregulated
Solyc04g058205.1	17.96269543	-3.356036106	0.000186648	0.007285987	downregulated
Solyc04g064880.4	51.72245142	-3.418908103	2.61E-05	0.00149272	downregulated
Solyc04g072070.3	158.199992	-3.378666891	7.12E-09	1.17E-06	downregulated
Solyc04g072780.4	7563.89913	-0.805142955	0.000372059	0.012286058	downregulated
Solyc04g072790.2	61.00457574	-2.50206364	2.49E-06	0.000212246	downregulated
Solyc04g074050.4	421.2750061	-1.093446999	0.001845027	0.041502157	downregulated
Solyc04g074440.1	192.2315555	-0.915941839	0.001507669	0.03575442	downregulated
Solyc04g074680.1	68.61175591	-2.914363279	0.000308333	0.010662135	downregulated
Solyc04g076290.3	613.5271555	-0.619386179	0.001015727	0.026555018	downregulated
Solyc04g076950.3	645.6319574	-1.224259312	3.04E-05	0.001669613	downregulated
Solyc04g077380.2	119.3437761	-1.681757903	3.80E-05	0.002012677	downregulated
Solyc04g078460.3	2549.85233	-2.427570038	1.28E-11	3.15E-09	downregulated
Solyc04g078660.2	96.61483483	-1.450850544	0.001742426	0.039665515	downregulated
Solyc04g078750.3	5756.665503	-1.313637334	1.87E-05	0.001151949	downregulated
Solyc04g078860.4	177.6109066	-1.451083826	2.19E-06	0.000191077	downregulated
Solyc04g079250.3	247.8070178	-2.397220854	6.59E-05	0.003126528	downregulated
Solyc04g079360.1	20.19399856	-2.287070288	0.001258549	0.031147035	downregulated
Solyc04g079760.4	633.8041884	-3.239103946	4.19E-08	5.66E-06	downregulated
Solyc04g079910.4	170.0348288	-1.640105762	0.001136559	0.028883094	downregulated
Solyc04g080740.1	1285.610984	-1.289769097	1.23E-06	0.000114983	downregulated
Solyc04g081810.4	461.7062907	-1.098672393	1.86E-05	0.001150487	downregulated
Solyc04g081890.1	352.6181167	-1.435780895	0.001643942	0.038033312	downregulated
Solyc04g082140.3	5368.173381	-0.786385938	0.001808446	0.040876442	downregulated
Solyc04g082950.4	827.8085707	-0.838567078	4.17E-06	0.000327546	downregulated
Solyc04g150111.1	2706.945443	-0.693147513	0.00070839	0.019771383	downregulated
Solyc05g005540.4	1168.588292	-1.160762385	0.000333726	0.011271448	downregulated
Solyc05g005810.4	110.3365711	-1.002193578	0.00191021	0.042505714	downregulated
Solyc05g006510.2	557.5875473	-1.294304555	0.001767189	0.040108649	downregulated
Solyc05g006800.2	431.2742205	-1.193687991	2.81E-06	0.00023165	downregulated
Solyc05g006810.4	182.6227111	-1.263466189	0.001940753	0.042946595	downregulated
Solyc05g006855.1	155.0502765	-3.305736113	1.01E-07	1.25E-05	downregulated
Solyc05g006870.3	388.8115065	-2.235758462	6.88E-06	0.000505917	downregulated
Solyc05g007800.4	456.1181777	-0.739193527	0.000368276	0.012196579	downregulated
Solyc05g009470.4	26408.48547	-0.788560988	5.37E-05	0.002628097	downregulated
Solyc05g009480.1	17.31255471	-4.351623218	0.001811813	0.040876442	downregulated
Solyc05g009490.3	193.5764319	-2.112567566	0.0004146	0.013285335	downregulated
Solyc05g010320.4	2592.134941	-1.402119769	5.77E-05	0.002785574	downregulated
Solyc05g011890.1	4427.925996	-0.656976486	0.001231267	0.030672308	downregulated
Solyc05g012600.3	5798.749407	-0.544333281	0.001296933	0.031785351	downregulated
Solyc05g015800.3	971.1990036	-2.056584541	0.000108385	0.004762868	downregulated

Solyc05g015850.4	42.19508858	-2.683336462	0.000206648	0.00781169	downregulated
Solyc05g050350.2	173.2930385	-2.004529661	0.002020604	0.044013517	downregulated
Solyc05g051880.4	64.61329803	-4.233532809	2.12E-12	6.18E-10	downregulated
Solyc05g052920.4	4147.383017	-0.740313468	0.002221963	0.046828184	downregulated
Solyc05g053330.3	69.56989603	-3.080792643	0.001155427	0.029264385	downregulated
Solyc05g054090.3	446.4129614	-1.814277847	3.91E-06	0.000309642	downregulated
Solyc05g054480.3	558.7257671	-1.026617117	0.001033029	0.026852846	downregulated
Solyc05g054820.1	99.90949526	-1.839132692	0.000523716	0.015759347	downregulated
Solyc06g005150.3	2886.188917	-0.753156865	0.001882568	0.042096517	downregulated
Solyc06g007130.5.1	1207.248716	-1.026246917	3.94E-08	5.41E-06	downregulated
Solyc06g008760.1	3778.046784	-1.391077984	3.83E-06	0.000304907	downregulated
Solyc06g009190.4	3871.330963	-0.759448796	0.001446294	0.034660705	downregulated
Solyc06g009510.1	83.97255844	-1.36373842	0.000260828	0.009409003	downregulated
Solyc06g035960.3	694.8666858	-1.899067429	0.000196996	0.007560071	downregulated
Solyc06g036130.4	1076.969677	-0.995478839	0.00041993	0.013418272	downregulated
Solyc06g050350.3	445.6017312	-1.121907206	2.03E-06	0.000178864	downregulated
Solyc06g050900.3	2110.332023	-0.87330434	0.000667611	0.018935662	downregulated
Solyc06g051460.4	3321.801423	-0.819888575	0.001653635	0.038179799	downregulated
Solyc06g051830.3	578.0374776	-0.947026925	0.000410651	0.013233432	downregulated
Solyc06g060470.1	29.09704188	-3.062365767	0.000254216	0.009251658	downregulated
Solyc06g060570.3	264.5571512	-1.739007923	3.64E-06	0.000291833	downregulated
Solyc06g062420.4	74.02037855	-2.539757338	0.001224244	0.030530833	downregulated
Solyc06g062430.3	161.8298834	-2.876199001	1.05E-05	0.000732454	downregulated
Solyc06g062920.3	71.4169958	-3.665504337	6.80E-07	6.96E-05	downregulated
Solyc06g064610.1	399.5392846	-1.583052239	0.000303864	0.01057194	downregulated
Solyc06g066700.1	1795.264205	-1.898384399	0.000103006	0.004570708	downregulated
Solyc06g066800.2	1051.047888	-0.720717259	0.000670911	0.019005531	downregulated
Solyc06g068990.4	246.3508133	-1.022759214	1.33E-05	0.00089233	downregulated
Solyc06g069580.3	929.1411666	-0.651411377	0.001126062	0.028781574	downregulated
Solyc06g069740.1	54.77292726	-1.801043382	0.002178553	0.046256575	downregulated
Solyc06g071150.4	86.74021253	-1.815218554	0.000893261	0.023875302	downregulated
Solyc06g073560.4	178.0692991	-1.234178414	0.001933168	0.042849962	downregulated
Solyc06g074000.1	3171.643575	-1.115513976	4.23E-06	0.000330573	downregulated
Solyc06g074240.3	95.5511591	-1.992204538	1.11E-05	0.000767755	downregulated
Solyc06g074390.3	1801.630309	-0.795660679	0.000934269	0.024767391	downregulated
Solyc06g074790.2	2457.476009	-0.970689353	0.001023123	0.026656349	downregulated
Solyc06g075090.4	1009.49546	-0.994738202	0.000238024	0.008778685	downregulated
Solyc06g075280.3	103.4131557	-1.527860623	0.000257187	0.009319015	downregulated
Solyc06g075510.4	705.5570536	-1.313968782	0.000511103	0.015565354	downregulated
Solyc06g076300.3	598.3426328	-1.149828084	1.90E-06	0.00016959	downregulated
Solyc06g076570.4	368.549177	-0.727902078	0.002398468	0.049544011	downregulated

Solyc06g082030.3	77.61003499	-1.521113981	0.001854489	0.041673717	downregulated
Solyc06g082070.3	399.877514	-1.476802582	2.30E-10	4.98E-08	downregulated
Solyc06g082860.4	230.8297336	-0.857649654	0.001365245	0.033173257	downregulated
Solyc06g084460.4	1440.672503	-0.661123758	0.000414283	0.013285335	downregulated
Solyc07g005370.4	10924.57465	-0.82137006	4.18E-05	0.002194701	downregulated
Solyc07g005440.1	6339.912577	-0.743587416	0.000168149	0.006749425	downregulated
Solyc07g005760.3	12601.14707	-0.806400337	0.000287375	0.010153776	downregulated
Solyc07g005860.3	1745.506397	-0.641789733	0.00032753	0.011147824	downregulated
Solyc07g006370.1	2479.55992	-2.479679776	3.94E-20	3.20E-17	downregulated
Solyc07g006420.1	245.5751592	-2.468776242	2.60E-05	0.001491747	downregulated
Solyc07g007590.1	873.9889566	-0.689919604	0.000222484	0.008299862	downregulated
Solyc07g008620.1	388.4600484	-1.72581436	0.001008171	0.026387825	downregulated
Solyc07g008670.3	1362.442004	-0.767213469	1.19E-05	0.00081487	downregulated
Solyc07g014590.4	2317.401984	-0.525977915	0.00145852	0.034880113	downregulated
Solyc07g014730.3	313.6543434	-1.247090887	0.000301877	0.010535075	downregulated
Solyc07g039570.3	67.42982685	-3.342408405	8.43E-08	1.07E-05	downregulated
Solyc07g040710.3	30.50877855	-3.937636792	4.23E-05	0.002207632	downregulated
Solyc07g045460.3	408.3190189	-1.552284003	2.05E-07	2.33E-05	downregulated
Solyc07g047890.4	169.7794004	-0.938759889	0.00051831	0.015696468	downregulated
Solyc07g049280.3	401.4971872	-0.934590325	0.000419338	0.013418221	downregulated
Solyc07g052100.4	67.68851427	-1.139640428	0.002192577	0.046467487	downregulated
Solyc07g052150.4	34.36317191	-4.504253061	0.000312578	0.010727268	downregulated
Solyc07g052970.3	675.354181	-0.914425437	0.000379444	0.01247551	downregulated
Solyc07g052980.3	7011.112564	-2.374788066	1.81E-07	2.11E-05	downregulated
Solyc07g053120.4	1475.421906	-1.618534649	6.70E-06	0.000495475	downregulated
Solyc07g053240.3	29.77040656	-3.515205243	1.79E-05	0.001115353	downregulated
Solyc07g053820.3	109.4043495	-1.113776616	0.000808275	0.021965554	downregulated
Solyc07g054450.4	451.6450769	-1.263354622	8.88E-07	8.73E-05	downregulated
Solyc07g055050.3	6992.360782	-0.785222118	0.000756767	0.020839975	downregulated
Solyc07g055750.4	30.96729714	-1.748303276	0.002320215	0.048271936	downregulated
Solyc07g056060.4	181.2650841	-0.922646681	0.000428763	0.013642958	downregulated
Solyc07g056510.3	64.50316144	-5.540778983	4.36E-10	9.18E-08	downregulated
Solyc07g062100.4	182.3397014	-0.985995442	0.000299382	0.010480202	downregulated
Solyc07g062260.3	712.3934154	-0.594706445	0.001160291	0.029322188	downregulated
Solyc07g062930.3	405.5832771	-1.288900742	0.001222866	0.030529992	downregulated
Solyc07g064650.3	223.4272602	-2.29676031	6.87E-05	0.003220268	downregulated
Solyc07g065460.1	172.3896854	-1.365881718	0.002357855	0.048876006	downregulated
Solyc07g065820.3	1994.281167	-0.755001608	0.000609995	0.01767663	downregulated
Solyc07g066020.2	1647.147742	-1.141053036	0.000312246	0.010727268	downregulated
Solyc08g005610.3	246.7131515	-1.300058016	0.000235071	0.008698018	downregulated
Solyc08g005880.4	474.6501796	-1.675459157	5.75E-10	1.16E-07	downregulated

Solyc08g006330.3	332.6492245	-1.061071963	0.001971221	0.04326974	downregulated
Solyc08g008270.4	2727.500726	-0.597547448	0.002049987	0.044482958	downregulated
Solyc08g008480.4	281.1828081	-1.463567976	0.000492562	0.015245948	downregulated
Solyc08g013840.3	2781.713579	-1.10339307	4.29E-05	0.00223001	downregulated
Solyc08g014130.3	1569.273898	-0.827292469	1.19E-06	0.000112648	downregulated
Solyc08g023510.3	17.09518332	-4.951452737	0.000155911	0.006393739	downregulated
Solyc08g028780.1	79.17865164	-1.38671498	0.000437576	0.013903904	downregulated
Solyc08g029000.3	282.4246521	-2.365445543	0.000870928	0.02341612	downregulated
Solyc08g060920.4	578.53235	-1.197658152	0.000438786	0.013914331	downregulated
Solyc08g061270.1	1418.783204	-1.402581601	1.63E-05	0.001046348	downregulated
Solyc08g061480.3	538.792346	-1.912106954	1.61E-05	0.001035133	downregulated
Solyc08g067340.4	150.9942665	-3.227681609	3.47E-05	0.00187263	downregulated
Solyc08g068600.3	98.48039938	-1.635026326	0.000138024	0.005785543	downregulated
Solyc08g068610.3	24.59372588	-3.8631797	0.000197987	0.007578041	downregulated
Solyc08g068680.4	92.54140002	-2.023341454	0.000704248	0.01970421	downregulated
Solyc08g068710.1	185.0341811	-1.796394053	1.17E-06	0.000110466	downregulated
Solyc08g068770.3	400.81658	-1.361884508	0.00017217	0.006862322	downregulated
Solyc08g074620.3	149.1820546	-1.803989751	5.58E-10	1.13E-07	downregulated
Solyc08g075550.4	61.2027175	-3.273537224	0.000327025	0.011147824	downregulated
Solyc08g075570.4	143.079957	-2.976651472	3.69E-05	0.001969086	downregulated
Solyc08g076050.4	359.0745613	-1.268402472	0.000501864	0.01542441	downregulated
Solyc08g077480.4	2510.641497	-1.335035735	4.16E-11	9.74E-09	downregulated
Solyc08g077760.3	132.2930894	-1.37758417	0.001867144	0.041833967	downregulated
Solyc08g078090.1	1538.357883	-1.388194443	0.000675757	0.019108573	downregulated
Solyc08g078520.4	473.0239148	-1.05046517	1.21E-05	0.00082627	downregulated
Solyc08g078650.3	40.97321912	-2.26610961	0.001399915	0.033834753	downregulated
Solyc08g079090.4	4407.125446	-0.962442254	0.000369489	0.01221894	downregulated
Solyc08g079830.4	4234.278162	-1.577260677	1.95E-13	6.90E-11	downregulated
Solyc08g080040.4	361.6673316	-1.179550632	5.56E-05	0.002715487	downregulated
Solyc08g080530.1	15.06615381	-4.682595824	0.001093523	0.028153775	downregulated
Solyc08g080770.3	74.46425289	-1.853461248	0.00011763	0.005090357	downregulated
Solyc08g082130.3	304.9521938	-1.314057858	0.00192201	0.042684401	downregulated
Solyc08g082160.3	555.4540922	-1.602761548	9.68E-05	0.004354139	downregulated
Solyc08g150124.1	33.5043913	-4.038357396	3.25E-08	4.53E-06	downregulated
Solyc09g007110.3	2283.520905	-0.859090581	1.58E-05	0.00101991	downregulated
Solyc09g007240.3	1384.461834	-0.641286946	0.001192574	0.029905165	downregulated
Solyc09g007760.4	7830.883379	-1.18932148	0.001017417	0.026568627	downregulated
Solyc09g007910.4	2584.228726	-1.534346336	1.50E-06	0.000138393	downregulated
Solyc09g008060.4	518.2711955	-0.948078504	0.000170001	0.00678781	downregulated
Solyc09g009530.4	1678.921539	-0.964715002	0.000131043	0.005596174	downregulated
Solyc09g009550.4	138.3946364	-1.285224009	0.001175316	0.029603098	downregulated

Solyc09g010230.2	367.860596	-1.000685946	4.69E-06	0.000363313	downregulated
Solyc09g010980.1	67.46816834	-2.047821079	0.001355248	0.033009831	downregulated
Solyc09g011140.4	7415.31055	-0.613019861	0.000262362	0.009446262	downregulated
Solyc09g011540.2	5.484399178	-5.73977993	0.002211618	0.0466968	downregulated
Solyc09g011550.3	33.60835178	-2.927463875	0.00019169	0.007419071	downregulated
Solyc09g011860.4	135.2281275	-1.643067268	5.18E-05	0.002568189	downregulated
Solyc09g014990.4	558.4600732	-1.53093555	0.000508423	0.015525345	downregulated
Solyc09g059170.3	730.384063	-1.093287425	5.22E-06	0.000403509	downregulated
Solyc09g064440.4	2573.383033	-0.636248588	0.000526047	0.015808544	downregulated
Solyc09g064630.3	13079.50751	-1.166374881	0.000557302	0.016518828	downregulated
Solyc09g065100.3	96.55904366	-1.66042049	0.000445383	0.013995376	downregulated
Solyc09g065660.4	185.0323629	-2.803010227	6.63E-09	1.12E-06	downregulated
Solyc09g065870.4	1024.229261	-0.851177879	1.56E-05	0.001011078	downregulated
Solyc09g072810.3	347.5289143	-1.325606037	0.000306324	0.010611632	downregulated
Solyc09g073030.4	89.72846593	-1.500849712	0.000141895	0.005925953	downregulated
Solyc09g074230.4	1573.842215	-1.682016901	2.64E-05	0.001499716	downregulated
Solyc09g074300.1	776.7951473	-0.956931992	0.001266901	0.031272998	downregulated
Solyc09g074350.1	115.2786107	-1.373562793	0.00033538	0.011271448	downregulated
Solyc09g074430.4	293.9520211	-1.522164113	1.83E-06	0.000164776	downregulated
Solyc09g074470.3	356.7243285	-1.221913047	0.000378496	0.012462382	downregulated
Solyc09g075420.3	862.5189083	-0.808339004	0.000478498	0.014830822	downregulated
Solyc09g075470.2	889.7825372	-0.834206929	8.64E-05	0.003981686	downregulated
Solyc09g082210.4	1173.982305	-0.60137156	0.000883523	0.023670699	downregulated
Solyc09g082660.3	268.6770463	-3.039947141	3.85E-19	2.82E-16	downregulated
Solyc09g083110.3	616.7372224	-0.617268609	0.002348744	0.048731613	downregulated
Solyc09g083360.3	29.01447557	-2.108655476	0.000373857	0.012327529	downregulated
Solyc09g083380.4	3200.382009	-0.872882572	0.000528833	0.015871275	downregulated
Solyc09g089910.1	27.97704145	-3.961991347	9.32E-05	0.004241958	downregulated
Solyc09g090630.3	119.1930917	-2.890864926	1.84E-08	2.77E-06	downregulated
Solyc09g090680.3	729.713315	-1.084065173	0.001135109	0.028878548	downregulated
Solyc09g090760.4	89.39110508	-1.198028412	0.000767905	0.021023087	downregulated
Solyc09g091050.4	1406.990294	-0.616391983	0.000398544	0.012935023	downregulated
Solyc09g091510.3	977.7363844	-2.539824013	2.12E-08	3.09E-06	downregulated
Solyc09g097890.2	1616.818515	-1.278722671	2.31E-06	0.000199893	downregulated
Solyc09g098080.4	48.62471559	-4.635137811	2.78E-05	0.001552851	downregulated
Solyc10g005400.3	7677.579526	-1.253978114	3.32E-05	0.00180612	downregulated
Solyc10g006920.3	50.91398247	-1.648764906	0.001954203	0.042994365	downregulated
Solyc10g007560.2	49.83324962	-3.088480804	0.000155602	0.006392622	downregulated
Solyc10g007570.4	153.4367862	-3.165630891	5.62E-06	0.000431359	downregulated
Solyc10g008247.1	56.75821019	-1.33423562	0.00092899	0.024656216	downregulated
Solyc10g011740.3	1350.696688	-0.765059528	0.001157511	0.029284517	downregulated

Solyc10g038080.3	495.5425559	-0.912000681	0.000635194	0.018243963	downregulated
Solyc10g052470.1	495.0316597	-1.602693883	5.59E-05	0.002723862	downregulated
Solyc10g052490.2	2015.961651	-1.77057563	8.38E-07	8.31E-05	downregulated
Solyc10g054100.3	2724.372911	-0.930970353	3.62E-05	0.0019336	downregulated
Solyc10g074540.1	1804.958643	-1.277342879	0.001686946	0.038777907	downregulated
Solyc10g076480.2	204.7901229	-2.222611286	0.000132751	0.005654513	downregulated
Solyc10g076820.2	270.5640834	-1.35016272	4.46E-05	0.002278566	downregulated
Solyc10g076900.3	189.700476	-1.191477297	0.000105758	0.004674556	downregulated
Solyc10g078220.2	68.00268575	-2.540245288	0.000314726	0.01078472	downregulated
Solyc10g078240.2	1728.555117	-0.713437656	0.00061588	0.017801745	downregulated
Solyc10g078440.2	477.916493	-1.333171381	0.000348789	0.011670298	downregulated
Solyc10g078550.4	3604.7589	-1.305717566	1.67E-06	0.000152641	downregulated
Solyc10g078580.1	10147.77243	-1.52790309	3.47E-05	0.00187263	downregulated
Solyc10g079210.2	62.05162182	-1.378031574	0.000540823	0.016124618	downregulated
Solyc10g079930.1	563.0427822	-1.325724452	0.00019637	0.007552263	downregulated
Solyc10g080360.1	1684.609327	-1.078246572	0.000310482	0.010687635	downregulated
Solyc10g081420.2	1542.153305	-0.714369022	0.000729105	0.020225316	downregulated
Solyc10g082060.1	37.81318243	-2.416487327	0.000185637	0.007271527	downregulated
Solyc10g083440.2	771.4150535	-1.440662203	3.72E-06	0.000297316	downregulated
Solyc10g083970.1	7415.613808	-0.514428563	0.001570162	0.036775779	downregulated
Solyc10g084170.1	109.6945286	-1.057548288	0.000806084	0.021961708	downregulated
Solyc10g084180.2	2488.638352	-0.903718945	3.84E-06	0.000304907	downregulated
Solyc10g084230.2	570.0160733	-1.496720079	0.001947818	0.042994365	downregulated
Solyc10g085010.3	372.4326734	-1.990135094	8.93E-05	0.004098176	downregulated
Solyc10g085860.1	54.50908817	-2.256042516	0.000125994	0.005411061	downregulated
Solyc10g085920.3	1075.991661	-0.62763072	0.001396573	0.033789935	downregulated
Solyc10g086250.2	803.3041389	-2.725465579	3.96E-08	5.41E-06	downregulated
Solyc10g086270.2	54.81020622	-3.37776179	8.00E-10	1.54E-07	downregulated
Solyc11g006420.2	872.8838611	-0.89824487	5.95E-05	0.002862398	downregulated
Solyc11g007500.2	32.72995972	-3.62438431	0.000136551	0.005755664	downregulated
Solyc11g007890.2	98.31735547	-1.852934448	0.001933237	0.042849962	downregulated
Solyc11g007940.2	259.3041234	-1.128311363	3.21E-05	0.001759795	downregulated
Solyc11g008720.3	203.3777954	-0.907531586	0.00162983	0.037753775	downregulated
Solyc11g010670.1	246.5106915	-2.252673755	9.07E-07	8.80E-05	downregulated
Solyc11g010790.1	158.8074255	-1.085093064	8.37E-05	0.003881752	downregulated
Solyc11g011380.2	7351.021794	-1.365229799	1.26E-06	0.000117119	downregulated
Solyc11g011580.2	13.31352414	-3.511265243	0.000602033	0.017535701	downregulated
Solyc11g012690.3	1608.289059	-0.992370015	0.000298549	0.010467188	downregulated
Solyc11g013110.2	5343.239864	-0.882359689	0.000666773	0.018935529	downregulated
Solyc11g027830.2	3576.952549	-0.717908513	0.001323977	0.032343474	downregulated
Solyc11g040040.2	1339.42677	-0.752906236	0.000509521	0.015538008	downregulated

Solyc11g045520.2	143.1585512	-1.576074913	0.000725024	0.020161358	downregulated
Solyc11g045530.3	129.5045841	-1.186309498	0.002336865	0.048573866	downregulated
Solyc11g062440.2	2945.995336	-1.580976075	6.76E-17	3.57E-14	downregulated
Solyc11g066390.2	19495.73697	-4.385906013	1.37E-35	5.18E-32	downregulated
Solyc11g066430.2	2742.68508	-1.26292298	6.50E-06	0.000484278	downregulated
Solyc11g066580.3	271.896999	-3.725547902	3.03E-30	6.26E-27	downregulated
Solyc11g068880.2	383.9262005	-1.961906716	0.001395499	0.033789935	downregulated
Solyc11g069260.2	1064.289747	-0.718324156	0.001111668	0.028505625	downregulated
Solyc11g069290.2	2947.434045	-0.652479312	0.00011387	0.004965483	downregulated
Solyc11g069960.2	2063.044155	-1.127399136	0.001819754	0.041014871	downregulated
Solyc11g071730.3	450.3328102	-0.99728607	0.000443116	0.013982171	downregulated
Solyc11g071960.2	215.6357804	-1.787789845	2.77E-06	0.000229992	downregulated
Solyc12g007045.1	130.2647762	-2.279402625	4.46E-05	0.002278566	downregulated
Solyc12g009190.2	164.9140004	-1.980475161	0.002272042	0.047618563	downregulated
Solyc12g009770.2	611.9428053	-2.021695198	0.000743559	0.020550999	downregulated
Solyc12g038970.3	1600.547833	-0.728921154	0.000605784	0.017585193	downregulated
Solyc12g042890.2	400.0256839	-1.955511881	0.002069565	0.044694332	downregulated
Solyc12g042950.2	5716.393706	-1.219296325	6.40E-05	0.003055179	downregulated
Solyc12g044240.3	104.3306767	-1.662264375	1.48E-05	0.000968729	downregulated
Solyc12g049030.1	231.744612	-3.522554936	4.52E-07	4.80E-05	downregulated
Solyc12g049350.2	65.50501425	-3.308377278	1.95E-06	0.000173391	downregulated
Solyc12g049550.2	530.6615816	-0.834866627	0.000408386	0.013179166	downregulated
Solyc12g055710.1	69.96743861	-1.798761168	0.001269145	0.031272998	downregulated
Solyc12g056600.3	1186.966863	-0.576270588	0.002142222	0.045749964	downregulated
Solyc12g057080.2	2081.933172	-1.687337751	1.44E-14	6.30E-12	downregulated
Solyc12g088170.2	473.1694182	-3.271093759	2.84E-23	3.39E-20	downregulated
Solyc12g088300.2	243.2445016	-1.751709029	9.62E-05	0.00433788	downregulated
Solyc12g088390.1	116.9611722	-1.8880128	2.63E-05	0.001499346	downregulated
Solyc12g088820.2	1592.518276	-1.089708269	1.21E-06	0.000113789	downregulated
Solyc12g098500.2	1162.095186	-0.953379927	0.00049494	0.015277916	downregulated
Solyc12g098590.3	577.6301565	-3.787588071	2.17E-46	4.92E-42	downregulated
Solyc12g099160.2	555.6367307	-0.974494679	0.000391002	0.012741617	downregulated
Solyc12g099500.2	479.5422798	-1.005730209	0.001574166	0.036831586	downregulated
Solyc12g100240.1	77.21147004	-3.274255396	0.000274087	0.009837251	downregulated
Solyc12g100250.3	41.8636311	-3.674507662	0.00022995	0.008550318	downregulated
Solyc12g150113.1	679.5927237	-0.683426305	0.000405538	0.013105864	downregulated
Solyc00g028960.1	14.55860298	7.570895144	1.64E-07	1.92E-05	upregulated
Solyc00g500259.1	50.77842098	1.855703084	0.000183126	0.007185558	upregulated
Solyc01g005210.4	3771.844233	0.972956075	2.17E-05	0.001297174	upregulated
Solyc01g005240.4	3005.060061	1.122296881	5.39E-07	5.66E-05	upregulated
Solyc01g005440.4	7772.43445	1.255158802	1.72E-05	0.001091293	upregulated

Solyc01g006290.4	11695.67955	1.582140959	3.43E-06	0.000277673	upregulated
Solyc01g009170.4	6158.862525	0.84353265	0.00195401	0.042994365	upregulated
Solyc01g010480.3	10922.82172	1.512012084	0.00032289	0.011047783	upregulated
Solyc01g010500.3	24.96264322	2.495579895	0.000451881	0.014169554	upregulated
Solyc01g028807.1	1048.792172	3.658525382	8.73E-18	5.36E-15	upregulated
Solyc01g058260.4	3280.152378	0.827605672	0.000173964	0.006909149	upregulated
Solyc01g060260.4	10.56052518	3.193807087	0.001480752	0.035300328	upregulated
Solyc01g066290.2	237.3438252	1.151527888	0.002103791	0.045090584	upregulated
Solyc01g067300.3	67.14806744	2.41879043	0.000515365	0.015653167	upregulated
Solyc01g067440.4	329.7216337	2.631548736	3.69E-19	2.80E-16	upregulated
Solyc01g067460.3	753.9725806	2.79931488	2.23E-13	7.78E-11	upregulated
Solyc01g068520.1	8.229095302	4.785222931	0.0008062	0.021961708	upregulated
Solyc01g079350.3	2048.363037	0.611547984	0.000715837	0.019930273	upregulated
Solyc01g079530.4	297.5181447	1.417174655	4.42E-05	0.002268995	upregulated
Solyc01g080020.2	1083.278831	3.305212233	0.000467563	0.014571412	upregulated
Solyc01g080410.3	867.2810859	1.193905258	0.001904492	0.042461379	upregulated
Solyc01g080480.4	73.65014955	1.924897527	1.68E-06	0.000153235	upregulated
Solyc01g081600.3	30.78438359	7.677859433	2.73E-07	3.01E-05	upregulated
Solyc01g087800.2	1986.356922	1.562619598	0.000306406	0.010611632	upregulated
Solyc01g087810.2	1136.782285	2.077505926	8.60E-17	4.44E-14	upregulated
Solyc01g087840.3	144.8466005	2.172440656	8.54E-09	1.38E-06	upregulated
Solyc01g088300.3	56.53745408	2.127499995	7.70E-06	0.000555395	upregulated
Solyc01g090460.3	114.0780767	1.353661163	0.001946855	0.042994365	upregulated
Solyc01g090760.4	103.2408149	1.541406633	0.001688074	0.038777907	upregulated
Solyc01g091000.4	24.884196	1.991311879	0.001516985	0.035937835	upregulated
Solyc01g094790.3	4622.161298	0.821274024	0.000119766	0.005172928	upregulated
Solyc01g094915.1	59.42681255	1.844235643	0.000645668	0.018474729	upregulated
Solyc01g095100.4	185.5145309	0.937979652	0.001268404	0.031272998	upregulated
Solyc01g095260.1	7.706454213	4.178460143	0.001556828	0.036652398	upregulated
Solyc01g095750.2	121.8576549	3.649144657	2.08E-14	8.58E-12	upregulated
Solyc01g096630.3	1408.052636	0.806088649	7.54E-06	0.000545548	upregulated
Solyc01g096880.4	1142.840788	1.804212401	9.84E-14	3.67E-11	upregulated
Solyc01g097280.2	80.54922808	1.642801712	2.00E-06	0.000177598	upregulated
Solyc01g098190.3	2576.305977	0.73486011	1.26E-05	0.000856994	upregulated
Solyc01g098400.3	149.7724836	2.724410891	5.25E-05	0.002589704	upregulated
Solyc01g099150.5.1	108.7000264	1.279027337	3.80E-05	0.002012677	upregulated
Solyc01g099160.4	266.823971	1.613607968	8.82E-06	0.000626076	upregulated
Solyc01g099840.3	15171.54765	1.508082216	5.88E-06	0.000446502	upregulated
Solyc01g099910.4	1531.750469	0.928005941	2.15E-05	0.001297174	upregulated
Solyc01g099970.4	1968.121634	0.792683435	0.00242047	0.049868942	upregulated
Solyc01g101195.1	7.406520113	6.592043935	0.000247638	0.009045144	upregulated

Solyc01g101220.3	26.3757619	5.22462003	4.57E-09	7.98E-07	upregulated
Solyc01g102270.2	407.7156678	0.932050685	0.000859286	0.023130463	upregulated
Solyc01g102290.3	1159.449354	1.015487955	6.73E-05	0.003169995	upregulated
Solyc01g102300.3	964.2482654	0.880337535	0.001910222	0.042505714	upregulated
Solyc01g103060.4	22.87181847	5.299848251	6.25E-08	8.16E-06	upregulated
Solyc01g103970.4	315.6881454	1.171664023	1.05E-07	1.29E-05	upregulated
Solyc01g104100.3	28.49508255	2.325497839	0.002199639	0.046553374	upregulated
Solyc01g104950.4	20178.86179	1.011415964	0.000101185	0.004517364	upregulated
Solyc01g105430.4	239.3594999	2.304311416	0.000556581	0.016518828	upregulated
Solyc01g105767.1	274.9061142	5.388642583	1.20E-44	1.37E-40	upregulated
Solyc01g105770.2	334.1624856	5.710550702	3.75E-25	5.68E-22	upregulated
Solyc01g106620.2	1751.654756	2.03279589	3.20E-06	0.000260338	upregulated
Solyc01g106820.3	859.8643742	2.627785241	1.77E-05	0.001113841	upregulated
Solyc01g106920.4	51.89113765	6.991964574	4.33E-12	1.20E-09	upregulated
Solyc01g107190.3	2840.311831	2.47579246	2.68E-13	9.23E-11	upregulated
Solyc01g107430.2	649.5318799	1.072596699	5.73E-05	0.00276923	upregulated
Solyc01g108300.3	2266.946979	1.31891364	2.21E-06	0.000192196	upregulated
Solyc01g108630.3	19903.43649	0.898253541	5.25E-05	0.002589704	upregulated
Solyc01g108710.3	131.9098353	7.551054168	0.000639331	0.018339599	upregulated
Solyc01g108900.4	220.1560725	1.175852394	0.000137284	0.005766119	upregulated
Solyc01g108910.4	1101.586695	1.478708981	0.000657753	0.018796829	upregulated
Solyc01g109500.4	1221.42984	1.330083659	0.001536927	0.036372343	upregulated
Solyc01g109700.3	6144.162827	1.521364404	0.000276165	0.009895133	upregulated
Solyc01g110000.3	3134.114102	3.100077067	1.86E-13	6.70E-11	upregulated
Solyc01g110590.4	133.4485464	1.520728833	0.000102314	0.004557778	upregulated
Solyc01g110660.4	136.3602251	1.143984418	0.001604229	0.037304488	upregulated
Solyc01g111320.3	1403.145495	0.549257049	0.000944945	0.024992091	upregulated
Solyc01g111380.3	793.5322997	0.738891225	0.001877396	0.042022217	upregulated
Solyc01g111880.4	105.2578549	2.617650996	6.77E-13	2.23E-10	upregulated
Solyc02g005606.1	42.68534201	2.76556372	4.03E-07	4.32E-05	upregulated
Solyc02g014730.3	17.44548073	3.563344904	2.40E-05	0.001396325	upregulated
Solyc02g036370.3	565.1687969	1.23591977	2.43E-07	2.74E-05	upregulated
Solyc02g063410.3	139.93318	3.101909405	5.52E-13	1.84E-10	upregulated
Solyc02g063450.4	22924.88956	2.535869297	2.98E-24	3.98E-21	upregulated
Solyc02g067800.4	5.819739196	6.244248921	0.000915685	0.024388557	upregulated
Solyc02g068040.3	444.8222564	2.222235012	7.40E-06	0.000538885	upregulated
Solyc02g068080.3	2952.933607	1.801959209	7.01E-10	1.37E-07	upregulated
Solyc02g068170.1	81.48567664	3.62014279	9.01E-11	2.03E-08	upregulated
Solyc02g069180.4	1158.716769	0.691655003	0.00230835	0.048201662	upregulated
Solyc02g069730.3	17.89314994	3.988257216	1.05E-05	0.000733681	upregulated
Solyc02g070180.3	122.0148932	2.502883518	2.71E-06	0.000226741	upregulated

Solyc02g072150.3	1853.030963	1.194702556	0.000107762	0.004744664	upregulated
Solyc02g076630.1	22.95877711	7.247198928	7.72E-08	9.96E-06	upregulated
Solyc02g076660.3	727.2397539	1.450958748	2.05E-05	0.001244412	upregulated
Solyc02g077590.1	478.4913679	1.819764982	1.62E-08	2.50E-06	upregulated
Solyc02g077880.3	4777.618366	3.969464114	2.16E-05	0.001297174	upregulated
Solyc02g078020.3	614.5174605	1.64815591	4.98E-15	2.26E-12	upregulated
Solyc02g078150.4	97.18237858	3.985060592	3.12E-08	4.37E-06	upregulated
Solyc02g078160.3	149.4772352	2.389676669	9.38E-13	3.05E-10	upregulated
Solyc02g078450.3	990.2740188	1.854277478	2.04E-08	3.02E-06	upregulated
Solyc02g078550.3	1807.302924	0.626633502	0.000187672	0.007300897	upregulated
Solyc02g078720.4	689.828643	0.803356504	0.002216634	0.046759242	upregulated
Solyc02g079500.4	417.1037298	0.855468723	0.001569212	0.036775779	upregulated
Solyc02g079960.3	917.2965486	0.841533613	5.64E-05	0.002741486	upregulated
Solyc02g079980.3	303.9165194	1.869571002	0.000147968	0.006119262	upregulated
Solyc02g080200.4	1807.081371	1.926070302	4.06E-05	0.002138277	upregulated
Solyc02g080220.3	436.1895251	1.911908967	1.99E-11	4.80E-09	upregulated
Solyc02g081150.1	2678.707112	0.68988079	0.000812922	0.02206545	upregulated
Solyc02g082060.2	2672.165448	1.539050459	7.07E-07	7.14E-05	upregulated
Solyc02g082080.1	3130.072581	1.026058338	0.00181009	0.040876442	upregulated
Solyc02g082850.3	1117.007801	1.204583025	1.60E-07	1.88E-05	upregulated
Solyc02g083280.4	8145.184078	1.523649315	6.85E-06	0.000504955	upregulated
Solyc02g083835.1	2104.951659	1.916974097	2.03E-07	2.32E-05	upregulated
Solyc02g084570.4	2422.348635	0.649250168	0.001128092	0.028781574	upregulated
Solyc02g084640.4	1310.601492	0.598005147	0.001966159	0.043200353	upregulated
Solyc02g084790.3	19.65926112	5.616017686	1.53E-05	0.000990818	upregulated
Solyc02g084840.3	172.0773291	1.138482312	5.35E-05	0.002623402	upregulated
Solyc02g085300.4	2359.670463	1.456675549	1.09E-12	3.45E-10	upregulated
Solyc02g085610.4	290.6106681	0.838483311	0.001257064	0.031144204	upregulated
Solyc02g085760.2	15491.55954	1.055761955	1.75E-05	0.001099939	upregulated
Solyc02g085770.4	2919.291465	1.717834008	8.63E-08	1.09E-05	upregulated
Solyc02g086452.1	2640.049166	0.903996444	0.000522673	0.015748821	upregulated
Solyc02g086454.1	3574.270603	0.919220257	0.000182984	0.007185558	upregulated
Solyc02g086456.1	941.9864998	0.924071955	0.000192403	0.007434038	upregulated
Solyc02g086458.1	13693.41209	0.787047508	3.02E-05	0.001666032	upregulated
Solyc02g087870.3	2442.491785	1.241444825	1.21E-07	1.46E-05	upregulated
Solyc02g088730.2	363.0127116	1.054725651	3.92E-07	4.26E-05	upregulated
Solyc02g089030.1	191.978718	1.197147356	0.002085255	0.044779271	upregulated
Solyc02g089160.3	437.9738501	1.730026458	0.000610996	0.017683068	upregulated
Solyc02g089500.4	441.5831334	1.251383303	0.000629588	0.01812877	upregulated
Solyc02g089510.3	869.4475213	1.244146886	4.54E-05	0.002311099	upregulated
Solyc02g089520.2	241.6981596	1.284955191	8.54E-06	0.000608104	upregulated

Solyc02g089720.3	446.7208268	1.385637345	2.11E-08	3.09E-06	upregulated
Solyc02g090210.3	61.33427545	7.230452859	1.73E-14	7.26E-12	upregulated
Solyc02g090530.4	956.1016732	0.57221718	0.001171391	0.029536987	upregulated
Solyc02g090850.3	3295.548543	0.485813221	0.001788171	0.040503942	upregulated
Solyc02g092150.3	552.7511617	0.802885834	8.59E-05	0.003966817	upregulated
Solyc02g092260.3	648.0265659	0.623465662	0.000993067	0.026112837	upregulated
Solyc02g092480.4	2818.416721	0.781211686	3.57E-05	0.001915299	upregulated
Solyc02g092490.3	724.9725494	1.312738247	1.11E-11	2.78E-09	upregulated
Solyc02g092550.3	1290.527577	1.261350498	0.000591726	0.017368771	upregulated
Solyc02g092820.4	39.16905668	2.273036792	0.001695154	0.038901219	upregulated
Solyc02g093580.4	119.6366154	2.582479964	6.50E-12	1.68E-09	upregulated
Solyc02g094180.3	16.69185679	4.204192892	2.37E-05	0.001381702	upregulated
Solyc02g150135.1	100.8305088	1.268159498	0.000570122	0.016821562	upregulated
Solyc02g150146.1	357.397012	0.942012051	5.76E-06	0.000438831	upregulated
Solyc03g005090.4	5200.628078	0.870357085	2.12E-07	2.40E-05	upregulated
Solyc03g005210.4	78.63557602	6.113246774	7.67E-18	4.84E-15	upregulated
Solyc03g005450.3	920.5292203	1.611999764	1.00E-06	9.54E-05	upregulated
Solyc03g005820.3	1235.510879	0.801432666	0.000520967	0.015718253	upregulated
Solyc03g006360.3	55.88908639	8.546134613	1.08E-09	2.03E-07	upregulated
Solyc03g006380.4	332.6487136	0.797474083	0.000473058	0.014702322	upregulated
Solyc03g006410.3	843.0457369	1.353846479	0.002421121	0.049868942	upregulated
Solyc03g006490.3	1119.467263	3.523590228	0.000167967	0.006749425	upregulated
Solyc03g006700.3	211.2906685	2.388331303	6.00E-10	1.20E-07	upregulated
Solyc03g006880.3	3757.536381	0.728461959	0.000988102	0.026012393	upregulated
Solyc03g025290.3	1462.455896	0.619919956	0.002232288	0.047001394	upregulated
Solyc03g025380.3	188.3252251	1.672779765	1.44E-05	0.000951108	upregulated
Solyc03g025430.1	314.3972735	1.694372294	0.002113954	0.045223099	upregulated
Solyc03g026370.1	34.58134476	2.02807373	0.000203902	0.007759553	upregulated
Solyc03g032060.1	588.4710427	0.870140656	0.000260913	0.009409003	upregulated
Solyc03g034000.3	322.6142901	2.524471583	1.97E-21	1.94E-18	upregulated
Solyc03g034380.1	36.86425497	1.864585994	0.000128232	0.005496811	upregulated
Solyc03g043740.4	197.2365524	1.729775711	2.54E-06	0.000215104	upregulated
Solyc03g044790.3	67.69087293	1.82566714	0.000188062	0.007303544	upregulated
Solyc03g063100.2	26.87552519	3.294639601	1.16E-06	0.000110462	upregulated
Solyc03g082620.4	9389.57302	1.095815701	0.000335141	0.011271448	upregulated
Solyc03g083440.4	4514.986543	1.805736596	1.36E-08	2.13E-06	upregulated
Solyc03g083910.5	6247.753848	0.535449959	0.001050475	0.027181949	upregulated
Solyc03g083960.3	4221.388658	0.72696816	0.00077941	0.021282958	upregulated
Solyc03g093140.3	2937.187133	0.765046224	0.000389268	0.012706593	upregulated
Solyc03g095310.3	686.8382585	1.854452447	7.25E-09	1.18E-06	upregulated
Solyc03g095650.3	3451.162305	1.764904202	5.71E-05	0.00276923	upregulated

Solyc03g095980.3	87.20804925	1.161941384	0.002247843	0.047242139	upregulated
Solyc03g096390.3	1142.654249	0.918876085	0.001185447	0.029759304	upregulated
Solyc03g096545.1	24.55619399	3.346259452	0.001646887	0.038062691	upregulated
Solyc03g096670.3	424.2773579	1.17446337	0.000942117	0.024946343	upregulated
Solyc03g096740.4	431.1766164	0.894284319	0.00059967	0.017511455	upregulated
Solyc03g096760.1	645.881017	1.874907864	0.000167803	0.006749425	upregulated
Solyc03g097120.3	772.8154648	0.844484302	4.18E-05	0.002194701	upregulated
Solyc03g097500.3	104.5722475	4.846856395	3.63E-25	5.68E-22	upregulated
Solyc03g097940.3	195.6500338	0.982062107	0.000551917	0.016412313	upregulated
Solyc03g098070.3	193.3157949	1.132074523	0.000843063	0.022774725	upregulated
Solyc03g098240.3	193.3634741	2.25249653	1.51E-11	3.68E-09	upregulated
Solyc03g098320.4	4311.396706	0.950558804	0.00085463	0.023058247	upregulated
Solyc03g098480.1	31.83225802	2.04400248	0.001318274	0.03223882	upregulated
Solyc03g098790.3	322.5358543	5.974478789	1.47E-06	0.000136022	upregulated
Solyc03g098795.1	742.3916032	5.680554043	0.000205201	0.007769949	upregulated
Solyc03g111310.3	927.2014499	1.507859169	0.000133489	0.005668685	upregulated
Solyc03g111690.4	10805.08866	0.959172775	0.000972398	0.025688266	upregulated
Solyc03g112060.3	9518.488321	1.206940175	1.97E-05	0.001198374	upregulated
Solyc03g112200.1	3704.999722	1.047952307	0.000327776	0.011147824	upregulated
Solyc03g112210.1	788.211571	1.156077073	2.78E-06	0.000229992	upregulated
Solyc03g113280.3	10271.58317	0.556239701	0.000530919	0.015912852	upregulated
Solyc03g113620.3	5888.764403	0.915854509	0.000691342	0.01941482	upregulated
Solyc03g113680.4	2983.018504	0.76599658	1.57E-05	0.001015656	upregulated
Solyc03g113690.1	89.53015406	3.121476014	3.14E-07	3.45E-05	upregulated
Solyc03g114705.1	27.74558802	2.746642528	0.001673646	0.038560189	upregulated
Solyc03g115650.4	4050.595023	1.05644313	0.000734547	0.020326633	upregulated
Solyc03g116590.3	1262.573907	0.851667403	3.07E-05	0.001686689	upregulated
Solyc03g116630.3	1274.295416	1.482648688	1.18E-10	2.60E-08	upregulated
Solyc03g116640.4	207.5217536	0.732722288	0.00214426	0.045749964	upregulated
Solyc03g116680.3	1973.125668	1.016843055	0.000301283	0.010530519	upregulated
Solyc03g117420.4	4480.697687	1.426162809	0.000285663	0.010127441	upregulated
Solyc03g117540.4	690.3562106	1.047693554	4.95E-05	0.002469926	upregulated
Solyc03g118300.1	438.8329601	1.072136777	0.002029938	0.044174475	upregulated
Solyc03g118970.3	2140.31828	0.602338037	0.000308986	0.010668471	upregulated
Solyc03g119060.3	3766.566747	0.947066003	2.94E-05	0.001626379	upregulated
Solyc03g119200.4	196.0856576	2.195492306	1.86E-12	5.49E-10	upregulated
Solyc03g119300.4	1844.070946	0.713533103	0.00058868	0.017301695	upregulated
Solyc03g119540.3	13519.45944	0.73120017	6.87E-05	0.003220268	upregulated
Solyc03g119720.4	1062.626236	1.274271958	3.55E-05	0.001908256	upregulated
Solyc03g119760.3	2614.96403	0.908261992	0.001236627	0.030772091	upregulated
Solyc03g119770.4	170.2713645	1.985457959	9.21E-07	8.90E-05	upregulated

Solyc03g119910.4	84.90356277	1.450204551	4.27E-05	0.002223805	upregulated
Solyc03g119930.1	3853.024923	1.975810213	1.16E-15	5.49E-13	upregulated
Solyc03g121090.4	810.2379552	1.636850156	0.000709871	0.019788403	upregulated
Solyc03g121250.3	208.9619314	0.922590644	0.000994513	0.026120612	upregulated
Solyc03g121300.2	2341.569666	0.679993881	0.001703752	0.039059063	upregulated
Solyc03g121400.1	867.9031433	0.686395807	0.000235026	0.008698018	upregulated
Solyc03g121920.3	1400.032879	0.696937903	0.001893468	0.042269098	upregulated
Solyc04g005250.4	209.5576389	1.594783954	4.03E-07	4.32E-05	upregulated
Solyc04g007170.3	833.3802648	0.969055932	6.26E-06	0.000470448	upregulated
Solyc04g007210.3	4543.394994	0.893773463	0.000442093	0.013969285	upregulated
Solyc04g007290.4	453.9955526	1.503076741	0.000532129	0.015924443	upregulated
Solyc04g007690.3	517.9207818	0.865266501	0.001625282	0.037753775	upregulated
Solyc04g007810.1	45.63658754	3.002906369	1.45E-08	2.26E-06	upregulated
Solyc04g008020.3	2793.221854	0.695495651	0.000152689	0.006284302	upregulated
Solyc04g008050.4	1615.32965	1.009501858	1.79E-06	0.000161625	upregulated
Solyc04g009900.4	3719.883307	1.943739579	6.53E-08	8.48E-06	upregulated
Solyc04g011600.4	31.73788809	5.856866105	2.14E-09	3.90E-07	upregulated
Solyc04g011780.1	17.06871725	7.801490042	5.70E-08	7.53E-06	upregulated
Solyc04g011790.1	112.8807489	5.902443451	0.00051779	0.015696468	upregulated
Solyc04g011800.1	208.7104416	10.44875324	3.11E-17	1.72E-14	upregulated
Solyc04g011810.1	115.8976275	10.56377894	1.21E-17	7.26E-15	upregulated
Solyc04g011820.1	69.32317184	5.477005313	5.43E-20	4.25E-17	upregulated
Solyc04g011830.1	179.1394939	7.647344849	0.001268443	0.031272998	upregulated
Solyc04g011840.1	133.6205374	10.7686433	1.44E-18	9.92E-16	upregulated
Solyc04g011850.1	38.09281805	8.957046807	5.64E-12	1.49E-09	upregulated
Solyc04g011860.1	73.779483	6.113125341	5.99E-14	2.31E-11	upregulated
Solyc04g011870.1	159.9041431	5.504316901	1.07E-14	4.75E-12	upregulated
Solyc04g011880.1	774.4021264	2.632794443	9.86E-06	0.000691649	upregulated
Solyc04g011940.3	5.494546139	6.162730932	0.000769924	0.021049217	upregulated
Solyc04g014280.1	8.061533725	6.714971515	7.30E-05	0.003414515	upregulated
Solyc04g014290.1	96.18735409	7.114394649	1.17E-21	1.21E-18	upregulated
Solyc04g014310.1	93.39153405	6.567891605	3.77E-20	3.17E-17	upregulated
Solyc04g014320.1	140.1579193	5.646263843	9.10E-24	1.15E-20	upregulated
Solyc04g014330.1	137.2614544	6.278049214	4.39E-05	0.002259223	upregulated
Solyc04g014350.1	133.1154645	5.840094958	2.76E-32	8.97E-29	upregulated
Solyc04g014770.1	46.37260662	3.680103337	1.14E-07	1.38E-05	upregulated
Solyc04g016190.1	7.407620348	4.752719707	0.002319331	0.048271936	upregulated
Solyc04g017690.3	6431.513086	1.116116231	1.69E-05	0.001076627	upregulated
Solyc04g051420.3	32.57133074	2.202499652	0.000130871	0.005596174	upregulated
Solyc04g052990.1	21.97186226	2.410082008	0.000234603	0.008698018	upregulated
Solyc04g053000.1	52.23748512	1.861203923	6.28E-05	0.003010775	upregulated

Solyc04g053110.1	137.9530173	6.024588806	2.12E-30	5.34E-27	upregulated
Solyc04g055257.1	7.802854876	5.660634076	0.001449348	0.034697304	upregulated
Solyc04g056310.3	4.483589059	5.870540144	0.002361127	0.048899224	upregulated
Solyc04g056340.4	1230.45522	0.951638043	5.87E-08	7.71E-06	upregulated
Solyc04g058100.3	98.75715149	1.669536541	3.31E-05	0.001805233	upregulated
Solyc04g063380.3	763.2795769	0.988404763	0.000445202	0.013995376	upregulated
Solyc04g064550.1	1430.441548	0.681375377	0.001464574	0.034988063	upregulated
Solyc04g071070.2	395.8501133	2.884513452	6.48E-14	2.45E-11	upregulated
Solyc04g071083.1	139.1860229	4.07337204	1.80E-08	2.73E-06	upregulated
Solyc04g071120.3	490.5922066	1.903950791	1.43E-05	0.000949153	upregulated
Solyc04g071890.3	672.0194728	1.489425148	1.49E-05	0.00097093	upregulated
Solyc04g071900.4	1061.024903	1.363408346	0.000689848	0.019396847	upregulated
Solyc04g072020.3	1970.995677	0.81938178	0.000293162	0.010310125	upregulated
Solyc04g072700.4	100.9921234	2.416097957	0.000110586	0.004840871	upregulated
Solyc04g072760.3	620.9431482	1.799107891	6.13E-11	1.39E-08	upregulated
Solyc04g072810.4	1937.452163	0.754326187	0.000878177	0.023555258	upregulated
Solyc04g072890.4	541.6467494	1.311344069	2.93E-05	0.001625636	upregulated
Solyc04g073990.3	1407.11536	1.242213908	1.17E-10	2.60E-08	upregulated
Solyc04g074400.1	98.30875204	6.473582768	0.001718512	0.039278544	upregulated
Solyc04g076020.3	1541.68423	0.73333977	0.002174564	0.046256575	upregulated
Solyc04g076220.3	998.0275122	1.417910759	8.84E-08	1.10E-05	upregulated
Solyc04g076820.1	3549.826078	1.015632906	1.89E-06	0.00016959	upregulated
Solyc04g077840.2	133.6878214	1.883489011	9.19E-08	1.14E-05	upregulated
Solyc04g077850.3	480.9998485	1.455529815	0.000768043	0.021023087	upregulated
Solyc04g077860.4	1549.609441	2.589105473	8.00E-10	1.54E-07	upregulated
Solyc04g078060.1	52.297034	1.411138845	0.001140186	0.028910581	upregulated
Solyc04g078090.3	446.3523377	0.919862429	0.00150615	0.03575442	upregulated
Solyc04g078390.3	2493.698822	1.157141802	0.000174865	0.006909149	upregulated
Solyc04g078490.1	1749.877523	0.760603748	4.91E-05	0.002455511	upregulated
Solyc04g078840.3	783.513117	0.816323639	0.002097736	0.045003276	upregulated
Solyc04g080370.3	1461.780003	0.984255115	3.82E-05	0.002015657	upregulated
Solyc04g080500.3	23.55709962	2.944575224	0.00047115	0.014663104	upregulated
Solyc04g080530.3	23.64904824	5.850282138	8.94E-07	8.74E-05	upregulated
Solyc04g080640.1	750.7099987	1.001913324	0.00024922	0.009088342	upregulated
Solyc04g080720.4	163.7885441	1.064726068	0.000196461	0.007552263	upregulated
Solyc04g081230.3	2102.673989	1.298436536	1.17E-08	1.87E-06	upregulated
Solyc04g081870.4	4431.887341	1.162345745	0.000502459	0.01542441	upregulated
Solyc04g082050.3	527.358646	2.893383948	2.04E-25	3.57E-22	upregulated
Solyc04g082910.1	923.8613958	1.070586435	0.000310264	0.010687635	upregulated
Solyc04g082915.1	36.05769159	1.468931477	0.002366292	0.048961556	upregulated
Solyc05g005150.1	935.830056	0.829879366	0.000331708	0.01123111	upregulated

Solyc05g005640.4	1470.010999	0.744142351	0.000195823	0.007552263	upregulated
Solyc05g005750.3	1908.27573	0.832944365	0.000174794	0.006909149	upregulated
Solyc05g006990.3	1403.270214	1.274170577	1.50E-14	6.44E-12	upregulated
Solyc05g007020.4	6688.797897	0.62593202	0.000276571	0.009895133	upregulated
Solyc05g007480.1	1372.204522	0.868865081	0.001993173	0.043664862	upregulated
Solyc05g007960.4	1069.342497	0.744379799	2.29E-05	0.001349276	upregulated
Solyc05g008090.3	1411.485703	1.006426032	0.000244863	0.008972652	upregulated
Solyc05g008230.3	4020.349262	1.215326192	6.66E-05	0.003144671	upregulated
Solyc05g008250.2	18.52038937	4.377020737	2.91E-06	0.000237772	upregulated
Solyc05g009720.3	560.9888574	1.998124164	4.67E-12	1.25E-09	upregulated
Solyc05g010010.1	249.62054	0.85576333	0.000581679	0.017139964	upregulated
Solyc05g010060.4	66.33712062	1.583438	0.000606066	0.017585193	upregulated
Solyc05g010330.4	20.3037799	8.050627954	4.93E-09	8.45E-07	upregulated
Solyc05g010400.3	1195.09205	0.668603658	0.000136006	0.005755664	upregulated
Solyc05g010810.1	3312.303737	0.874621676	1.73E-05	0.00109464	upregulated
Solyc05g012010.3	618.7448358	0.957979863	2.33E-05	0.001361586	upregulated
Solyc05g012110.4	2708.990069	1.754930555	8.73E-08	1.10E-05	upregulated
Solyc05g012650.4	1981.62675	0.960437391	2.14E-05	0.001291204	upregulated
Solyc05g015420.4	1512.563255	0.886360378	0.001128216	0.028781574	upregulated
Solyc05g015815.1	95.08798232	1.799464598	0.000240362	0.008850559	upregulated
Solyc05g015880.3	264.0154487	1.60937047	7.20E-06	0.000527985	upregulated
Solyc05g015950.3	1580.956094	0.782174472	0.000173257	0.006893582	upregulated
Solyc05g023995.1	448.9637625	0.758268842	0.000285738	0.010127441	upregulated
Solyc05g046180.1	10.80633143	3.94059646	0.000634193	0.018238253	upregulated
Solyc05g046270.3	119.36023	1.274782855	0.001468644	0.035048438	upregulated
Solyc05g047460.3	2152.068667	0.577229553	0.000383537	0.012573705	upregulated
Solyc05g050110.3	5281.021962	0.721528471	0.001274025	0.031325305	upregulated
Solyc05g051350.2	8.734236291	6.833026666	1.92E-05	0.001174574	upregulated
Solyc05g051720.1	13.17781994	7.423656719	8.36E-06	0.000597468	upregulated
Solyc05g051730.1	19.79326335	8.011002885	8.27E-08	1.06E-05	upregulated
Solyc05g051900.3	1012.092566	1.655019901	0.001439392	0.034531734	upregulated
Solyc05g052340.4	15.08687513	5.133678192	2.86E-06	0.000234519	upregulated
Solyc05g052360.2	37.80753371	7.112247063	1.02E-09	1.92E-07	upregulated
Solyc05g052370.3	121.8021506	4.317607982	6.76E-23	7.68E-20	upregulated
Solyc05g052715.1	1823.845845	0.901481826	6.12E-05	0.002940986	upregulated
Solyc05g052870.4	11.27510096	7.203236121	2.78E-06	0.000229992	upregulated
Solyc05g052880.4	83.1578766	5.225933942	5.59E-22	6.04E-19	upregulated
Solyc05g052890.3	90.30678016	5.550272581	0.000350458	0.011708905	upregulated
Solyc05g052980.4	3864.026459	0.965761634	2.65E-08	3.77E-06	upregulated
Solyc05g053620.3	4.593529244	5.906930875	0.002079235	0.044775494	upregulated
Solyc05g053760.4	1229.363639	1.43480442	0.000205067	0.007769949	upregulated

Solyc05g054350.3	5672.844705	1.727027322	1.48E-07	1.76E-05	upregulated
Solyc05g054570.3	1003.631992	0.839228205	0.000167228	0.006749425	upregulated
Solyc05g054880.3	131.3815473	0.910644267	0.001384475	0.033568726	upregulated
Solyc05g054890.4	77.4738096	3.968880168	4.45E-15	2.06E-12	upregulated
Solyc05g054900.3	8.497029145	5.798091523	0.000216721	0.008151792	upregulated
Solyc05g055460.1	99.90143754	1.236203485	0.000242814	0.008926365	upregulated
Solyc05g056030.3	175.7659773	1.402416414	6.89E-07	7.02E-05	upregulated
Solyc05g056140.4	2548.585095	1.494496561	3.63E-14	1.47E-11	upregulated
Solyc06g005620.3	5.059412896	6.044595358	0.001162416	0.029343243	upregulated
Solyc06g005820.3	68.43975173	5.550107393	2.06E-16	1.04E-13	upregulated
Solyc06g006010.3	19.67096205	2.965154126	4.38E-05	0.002259223	upregulated
Solyc06g007180.3	65.05455177	2.88825268	0.000204262	0.007760264	upregulated
Solyc06g007430.3	1095.434269	1.180676552	4.33E-05	0.002247193	upregulated
Solyc06g007440.4	4916.856049	1.248683992	5.68E-06	0.000434264	upregulated
Solyc06g008030.3	5185.578249	0.832996817	0.000165235	0.006691581	upregulated
Solyc06g008050.4	182.5727981	1.733097759	0.000188533	0.007309361	upregulated
Solyc06g008590.3	313.1438519	1.096240033	2.48E-05	0.001428215	upregulated
Solyc06g008620.1	295.7051607	2.595284853	5.12E-11	1.19E-08	upregulated
Solyc06g034290.3	723.2174316	2.824638597	2.72E-30	6.17E-27	upregulated
Solyc06g036100.3	527.3528449	0.715170992	0.001795089	0.040620147	upregulated
Solyc06g036170.1	772.4934695	0.862586267	0.002004239	0.043740936	upregulated
Solyc06g048410.4	27105.82916	0.814017041	2.95E-05	0.001628921	upregulated
Solyc06g048860.3	10.11492265	5.185958554	0.000260284	0.009409003	upregulated
Solyc06g050250.1	893.6960647	1.054670562	6.46E-07	6.68E-05	upregulated
Solyc06g050440.3	430.9981717	2.789162955	2.66E-17	1.51E-14	upregulated
Solyc06g050530.3	85.78696008	7.299216506	4.36E-18	2.83E-15	upregulated
Solyc06g050710.4	1206.199206	0.910523946	0.000570061	0.016821562	upregulated
Solyc06g050800.4	106.6025369	1.569876937	0.001857837	0.041707708	upregulated
Solyc06g050837.1	112.3243034	1.177760396	0.000342863	0.011488939	upregulated
Solyc06g051520.3	1444.135435	0.754950781	1.43E-05	0.000949153	upregulated
Solyc06g051960.3	10226.3456	0.793170092	0.001842316	0.041482248	upregulated
Solyc06g052020.2	59.24136214	1.793656432	0.000428254	0.013642958	upregulated
Solyc06g053450.4	5660.500606	0.625406544	0.000217359	0.008162269	upregulated
Solyc06g053670.1	772.4584884	0.806025997	0.000355898	0.011838443	upregulated
Solyc06g053790.3	2808.967768	0.731595922	1.11E-05	0.000767755	upregulated
Solyc06g053910.4	3203.794736	1.061817028	1.28E-05	0.000868317	upregulated
Solyc06g054010.3	1580.755165	0.706087847	0.000107589	0.004744664	upregulated
Solyc06g054060.1	11.10394917	4.646466296	0.000399264	0.012939914	upregulated
Solyc06g054270.3	1227.900367	2.021601924	4.99E-09	8.46E-07	upregulated
Solyc06g054470.1	119.9110002	1.265690542	0.001355613	0.033009831	upregulated
Solyc06g054540.3	816.0159486	1.655866193	0.000161858	0.006590055	upregulated

Solyc06g054570.1	770.7852377	1.886526366	4.53E-10	9.36E-08	upregulated
Solyc06g054580.4	605.877667	1.470186963	9.32E-12	2.38E-09	upregulated
Solyc06g060140.4	871.0902549	1.378179913	8.14E-09	1.32E-06	upregulated
Solyc06g060590.3	364.4897762	2.200303972	2.82E-10	5.98E-08	upregulated
Solyc06g060830.3	1822.662847	2.120657622	1.30E-05	0.000878326	upregulated
Solyc06g061230.3	894.271919	1.26370358	4.39E-05	0.002259223	upregulated
Solyc06g064550.3	17243.08983	1.642979074	2.49E-08	3.59E-06	upregulated
Solyc06g065100.3	298.6777872	1.351271518	1.81E-05	0.00112733	upregulated
Solyc06g067870.3	96.68000713	1.746391962	0.001600139	0.037247496	upregulated
Solyc06g067910.3	304.3533965	1.755917082	0.001035937	0.02686695	upregulated
Solyc06g068140.3	3571.826828	0.909030539	0.000117462	0.005090357	upregulated
Solyc06g068490.3	951.3644708	0.992411909	4.40E-05	0.002261593	upregulated
Solyc06g068500.3	300.2551582	2.472510853	6.00E-06	0.000453246	upregulated
Solyc06g068570.4	78.35684292	2.64982927	3.17E-12	8.99E-10	upregulated
Solyc06g068680.3	452.880123	0.745103122	0.000518863	0.015696468	upregulated
Solyc06g069240.2	187.4741104	1.743124074	0.002286153	0.047870138	upregulated
Solyc06g069880.1	1581.29039	1.188579403	4.78E-10	9.79E-08	upregulated
Solyc06g070980.3	9096.994886	0.901790136	1.44E-05	0.000953757	upregulated
Solyc06g071220.1	94.03778361	1.954846348	0.000246697	0.009025306	upregulated
Solyc06g072520.2	18.05808562	3.067451717	0.000703929	0.01970421	upregulated
Solyc06g073540.4	8124.313903	1.17888779	5.19E-05	0.002568189	upregulated
Solyc06g074420.1	15.17169595	3.881761197	1.19E-05	0.00081487	upregulated
Solyc06g075170.1	392.3573942	1.837674495	4.50E-10	9.36E-08	upregulated
Solyc06g075360.3	279.366101	1.155191214	3.95E-06	0.000311624	upregulated
Solyc06g076320.1	8.871911412	3.537971492	0.001538776	0.036378202	upregulated
Solyc06g076400.3	3043.489046	0.665209714	0.000136106	0.005755664	upregulated
Solyc06g076470.3	3661.700507	0.705075475	0.001916697	0.042608072	upregulated
Solyc06g076800.3	51.87175053	5.947725122	1.06E-13	3.89E-11	upregulated
Solyc06g082240.2	105.8268823	5.284600259	5.29E-29	1.00E-25	upregulated
Solyc06g082980.3	5431.241145	0.820783399	0.000548118	0.016320688	upregulated
Solyc06g083040.3	8088.303917	0.677362724	0.000599197	0.017511455	upregulated
Solyc06g084380.4	373.4040334	2.128565284	1.62E-12	4.91E-10	upregulated
Solyc07g005890.3	1550.955214	0.815835268	4.83E-05	0.002433705	upregulated
Solyc07g006110.4	853.0865709	1.491930833	4.03E-08	5.48E-06	upregulated
Solyc07g006310.1	178.5669778	1.52264005	0.000147916	0.006119262	upregulated
Solyc07g006500.3	241.2524445	3.095749817	2.85E-24	3.98E-21	upregulated
Solyc07g006570.4	418.721372	1.460913995	0.000384862	0.012598972	upregulated
Solyc07g006630.4	11887.62917	0.845021533	2.27E-05	0.001342956	upregulated
Solyc07g008030.3	414.9725276	0.722038047	0.002003083	0.043740936	upregulated
Solyc07g008240.3	739.4541856	3.469441523	4.65E-12	1.25E-09	upregulated
Solyc07g009230.3	20.20384278	6.13432338	1.92E-05	0.001174574	upregulated

Solyc07g016180.3	2878.325112	0.894609566	0.000413582	0.013285335	upregulated
Solyc07g017980.1	76.67998273	6.939280411	9.39E-05	0.00426487	upregulated
Solyc07g022830.3	750.3999097	1.597907754	1.90E-07	2.20E-05	upregulated
Solyc07g027020.4	1357.365514	0.634276152	0.001668435	0.038482422	upregulated
Solyc07g040680.3	114.1651792	1.669399522	0.000626009	0.018071526	upregulated
Solyc07g041940.3	10.80211353	3.529533077	0.001725249	0.039313875	upregulated
Solyc07g042560.4	134.0796883	1.205594348	0.000894926	0.023891692	upregulated
Solyc07g042630.4	4831.681284	1.030058122	0.00027769	0.009919558	upregulated
Solyc07g045540.4	6175.649152	0.820586178	0.000244121	0.008959918	upregulated
Solyc07g047940.4	3145.473454	1.333164291	0.000221911	0.008292114	upregulated
Solyc07g047950.1	2078.644006	0.738682845	2.42E-05	0.001405293	upregulated
Solyc07g049290.3	4788.983793	0.730734672	0.002001413	0.043740936	upregulated
Solyc07g052950.3	872.5418703	0.774168486	0.000666224	0.018935529	upregulated
Solyc07g053280.4	21145.97458	0.570681503	0.001565093	0.036770789	upregulated
Solyc07g054270.3	1033.83945	1.919823754	6.94E-09	1.15E-06	upregulated
Solyc07g054430.3	385.5290672	1.544681888	0.001243708	0.030880661	upregulated
Solyc07g054630.4	29.64208249	1.8679253	0.002061463	0.044561722	upregulated
Solyc07g054720.2	15.37390107	4.157564406	9.43E-05	0.004276323	upregulated
Solyc07g054730.1	3393.047329	1.743908512	0.000179676	0.007086905	upregulated
Solyc07g054840.4	6.162621207	6.327213974	0.000520208	0.015716235	upregulated
Solyc07g055060.3	29740.52154	1.300372343	2.17E-05	0.001297174	upregulated
Solyc07g055120.4	477.4118561	0.898960008	0.000335195	0.011271448	upregulated
Solyc07g055470.3	1034.113682	1.487479044	0.000136541	0.005755664	upregulated
Solyc07g056640.1	1046.713573	3.100117055	9.43E-21	8.57E-18	upregulated
Solyc07g056670.3	155.2580619	1.659323202	0.000114886	0.005000178	upregulated
Solyc07g061890.1	138.9695985	1.605471606	1.70E-05	0.001078836	upregulated
Solyc07g061935.1	1077.39726	0.835936433	0.002072461	0.044714381	upregulated
Solyc07g061940.4	13488.00336	0.835448835	0.000287099	0.010153776	upregulated
Solyc07g062700.3	10602.71852	1.236437868	0.000122104	0.005263911	upregulated
Solyc07g063460.3	1244.632174	0.983118695	0.001725062	0.039313875	upregulated
Solyc07g063910.4	1628.511373	1.231646347	4.85E-08	6.52E-06	upregulated
Solyc07g064960.2	101.6115144	1.611235472	1.32E-05	0.000883917	upregulated
Solyc07g065380.4	2690.531501	0.924773008	0.001950866	0.042994365	upregulated
Solyc07g066330.3	81.81637357	5.499104762	1.80E-12	5.38E-10	upregulated
Solyc07g066360.1	150.0842502	5.397680835	1.26E-36	5.75E-33	upregulated
Solyc07g150103.1	140.6222373	1.871180551	7.07E-07	7.14E-05	upregulated
Solyc08g005580.3	690.5896304	2.309719264	4.36E-14	1.74E-11	upregulated
Solyc08g006730.1	22.46710718	5.105266583	1.16E-05	0.000794845	upregulated
Solyc08g007430.2	122.3983329	3.15855501	3.30E-16	1.63E-13	upregulated
Solyc08g007540.3	106.5916427	1.26816155	0.000292723	0.010310125	upregulated
Solyc08g008305.1	124.9318693	2.366156563	1.09E-09	2.04E-07	upregulated

Solyc08g016804.1	81.76825782	1.719513518	0.00045477	0.014211715	upregulated
Solyc08g021820.3	144.6389751	1.837553431	2.73E-05	0.001536048	upregulated
Solyc08g061240.3	56.39776906	1.225990414	0.002060106	0.044561722	upregulated
Solyc08g065320.3	1459.573606	1.144095028	0.00014814	0.006119262	upregulated
Solyc08g065940.4	4248.49045	1.30360877	1.02E-11	2.57E-09	upregulated
Solyc08g066670.3	47.88490413	2.18331876	0.000665222	0.018935529	upregulated
Solyc08g067540.1	343.046065	0.929891338	0.000744753	0.020558991	upregulated
Solyc08g068780.3	312.5911683	0.994706751	0.001201459	0.030094765	upregulated
Solyc08g074630.2	312.4050995	1.176279197	0.000101208	0.004517364	upregulated
Solyc08g075490.4	25356.10852	1.414483049	0.001005202	0.026340469	upregulated
Solyc08g075520.4	2247.379654	0.879324141	0.001554059	0.03662518	upregulated
Solyc08g076320.3	2224.349076	0.750978538	0.000288438	0.010175516	upregulated
Solyc08g076830.1	349.0251025	0.819118652	0.000380453	0.012490613	upregulated
Solyc08g076870.1	261.9996013	0.872246589	0.000598434	0.017511455	upregulated
Solyc08g077230.3	1658.723779	0.69268139	0.001562514	0.036748201	upregulated
Solyc08g077900.3	24.50530868	3.78068108	2.44E-05	0.001408783	upregulated
Solyc08g078870.3	4093.616467	1.385605075	0.000730192	0.020230761	upregulated
Solyc08g080570.4	1327.123136	0.878832063	0.00083322	0.02253562	upregulated
Solyc08g080590.3	323.1682278	1.215461557	2.25E-05	0.001334766	upregulated
Solyc08g080640.2	829.4497076	1.965428133	9.40E-07	9.05E-05	upregulated
Solyc08g080650.3	16553.28484	1.727435485	2.58E-06	0.000217933	upregulated
Solyc08g081370.1	285.2510761	1.151328177	8.76E-05	0.004030929	upregulated
Solyc08g081380.3	804.1301737	1.287380813	0.000919891	0.024471914	upregulated
Solyc08g081530.3	1528.811129	0.636040796	0.000582422	0.017139964	upregulated
Solyc08g081945.1	3091.127646	0.775899391	0.001361579	0.033119614	upregulated
Solyc08g082180.3	2181.579851	0.79980441	0.000145405	0.006039228	upregulated
Solyc08g082870.3	350.538989	0.872453769	0.000182929	0.007185558	upregulated
Solyc09g005970.1	26.68752131	6.036585584	1.69E-08	2.59E-06	upregulated
Solyc09g008250.4	140.4604098	1.831259047	1.71E-09	3.16E-07	upregulated
Solyc09g008430.4	279.097295	1.651581709	2.61E-06	0.000219768	upregulated
Solyc09g009080.4	6888.502584	0.812685414	0.000200406	0.00763929	upregulated
Solyc09g009480.1	166.6364579	0.883025601	0.001435229	0.034522613	upregulated
Solyc09g011470.3	363.8620058	2.218616377	8.09E-06	0.000579937	upregulated
Solyc09g014770.3	5757.0037	1.19197438	3.43E-06	0.000277673	upregulated
Solyc09g018060.4	696.358079	0.791636886	0.000160855	0.006560959	upregulated
Solyc09g061700.3	152.9784952	1.432091725	0.002085324	0.044779271	upregulated
Solyc09g064860.3	2798.838531	0.657907874	0.001208257	0.030231708	upregulated
Solyc09g064910.1	134.7300537	3.042870984	2.28E-18	1.52E-15	upregulated
Solyc09g065420.3	14.05734142	7.518852071	2.49E-07	2.79E-05	upregulated
Solyc09g065430.4	77.01281662	5.046455745	9.58E-13	3.07E-10	upregulated
Solyc09g065440.4	29.7548928	7.631665712	6.87E-09	1.15E-06	upregulated

Solyc09g065475.1	171.250616	1.386499876	0.000911327	0.024300984	upregulated
Solyc09g065480.2	526.8450396	1.326640081	4.91E-05	0.002455511	upregulated
Solyc09g065760.4	216.7047765	1.076191661	6.64E-05	0.003142085	upregulated
Solyc09g072750.2	407.8253968	1.441379418	0.000819451	0.022189649	upregulated
Solyc09g072753.1	1075.343211	1.87890151	5.07E-08	6.77E-06	upregulated
Solyc09g072770.1	120.9048032	2.156049369	0.001020932	0.026629808	upregulated
Solyc09g074410.4	673.6671683	0.76024674	0.000502616	0.01542441	upregulated
Solyc09g074590.1	21.11204166	3.148722604	7.41E-05	0.003455514	upregulated
Solyc09g074760.1	14.93839195	4.092723283	8.08E-06	0.000579937	upregulated
Solyc09g075210.3	22960.28773	1.283611928	0.000391463	0.012741617	upregulated
Solyc09g075570.1	590.6579687	0.886826922	0.000198463	0.007578041	upregulated
Solyc09g076050.4	13280.31974	0.6348227	2.66E-05	0.001500839	upregulated
Solyc09g082270.4	42.89037451	2.744611022	1.82E-05	0.00112733	upregulated
Solyc09g082300.3	28.45927907	4.894965078	5.37E-06	0.000413472	upregulated
Solyc09g082580.4	1597.432251	1.298117286	4.65E-05	0.002359408	upregulated
Solyc09g082810.3	2784.81771	3.708613937	2.31E-05	0.001350551	upregulated
Solyc09g084470.3	95.36571366	2.5424294	9.81E-05	0.00440071	upregulated
Solyc09g089530.3	63.46649882	5.168209283	6.27E-06	0.000470448	upregulated
Solyc09g090100.3	3704.113125	0.564521128	0.002058378	0.044561722	upregulated
Solyc09g090140.4	27524.85433	0.556042489	0.001045855	0.027093251	upregulated
Solyc09g090430.3	3062.597426	0.707800911	0.000359837	0.011934493	upregulated
Solyc09g090900.4	14.37298997	3.051583521	0.000235764	0.008709476	upregulated
Solyc09g091250.4	2421.899483	0.614720635	0.001094229	0.028153775	upregulated
Solyc09g092270.3	6614.3684	0.816700399	2.90E-05	0.001616952	upregulated
Solyc09g092720.3	147.7859464	2.716792075	6.43E-05	0.003055346	upregulated
Solyc09g097770.3	71253.07177	1.453989588	5.54E-07	5.80E-05	upregulated
Solyc09g097780.2	11397.36417	1.440573065	0.001383419	0.033568726	upregulated
Solyc09g097850.1	452.935435	2.541525808	4.58E-16	2.21E-13	upregulated
Solyc10g006220.4	625.2921401	0.675031241	0.000855588	0.023058247	upregulated
Solyc10g006760.3	2290.981192	0.563306855	0.000444102	0.013993824	upregulated
Solyc10g007600.3	27612.03239	0.906950938	4.23E-07	4.51E-05	upregulated
Solyc10g008680.3	57.2348741	2.911897988	0.000115956	0.005037085	upregulated
Solyc10g008810.3	6.295017443	5.35801744	0.001184186	0.029759304	upregulated
Solyc10g009080.4	1142.782415	1.280108591	7.78E-07	7.75E-05	upregulated
Solyc10g009320.3	292.0545146	0.838947455	0.001239958	0.030821244	upregulated
Solyc10g017960.2	17.08247721	2.405739134	0.001305766	0.031967335	upregulated
Solyc10g045240.2	979.9920077	1.296373861	0.00010561	0.004674556	upregulated
Solyc10g050460.1	42.21163174	2.142717	0.000132907	0.005654513	upregulated
Solyc10g050510.1	493.157306	6.068985678	1.17E-31	3.33E-28	upregulated
Solyc10g050890.2	1705.574918	1.914100538	6.80E-07	6.96E-05	upregulated
Solyc10g054900.2	21.8462901	7.179228563	6.20E-07	6.46E-05	upregulated

Solyc10g055720.2	3848.640043	0.643969174	2.63E-05	0.001499346	upregulated
Solyc10g055800.2	9704.670323	1.928873834	2.34E-11	5.60E-09	upregulated
Solyc10g055810.2	21607.23559	1.405429822	0.002058441	0.044561722	upregulated
Solyc10g074440.2	115.0472487	1.860468489	0.000428423	0.013642958	upregulated
Solyc10g074980.2	12631.76563	0.771559163	4.68E-05	0.002368921	upregulated
Solyc10g075090.3	115.936351	1.015614127	0.002265134	0.047517614	upregulated
Solyc10g075103.1	295.2739402	0.898975783	0.000927541	0.024646547	upregulated
Solyc10g076790.2	349.1673503	1.060067674	0.00098367	0.025955866	upregulated
Solyc10g079640.2	1566.200692	0.569325385	0.00114012	0.028910581	upregulated
Solyc10g080610.1	10290.01403	1.038234321	7.33E-07	7.33E-05	upregulated
Solyc10g080980.2	79.69447833	2.71163525	2.69E-08	3.79E-06	upregulated
Solyc10g081680.1	318.1156908	0.982566209	0.001580016	0.03692579	upregulated
Solyc10g081840.3	122.776732	1.639041915	9.62E-05	0.00433788	upregulated
Solyc10g083260.1	66.37678212	2.795652498	2.61E-10	5.60E-08	upregulated
Solyc10g083380.2	1136.808092	0.997112729	0.001750167	0.039801846	upregulated
Solyc10g083860.3	1004.571798	0.860557943	2.20E-05	0.00131281	upregulated
Solyc10g083940.1	1142.62237	0.841878187	0.001062995	0.027474604	upregulated
Solyc10g083950.1	368.2635908	1.067958703	2.02E-06	0.000178464	upregulated
Solyc10g083960.2	1487.372914	1.13628628	9.11E-05	0.004162151	upregulated
Solyc10g084320.3	1697.186525	1.444489633	4.03E-07	4.32E-05	upregulated
Solyc10g084950.3	1197.263646	1.039294142	0.001346598	0.03286074	upregulated
Solyc10g085200.2	1166.928447	0.835195295	7.20E-07	7.24E-05	upregulated
Solyc10g085500.2	345.5219755	1.518582127	2.63E-08	3.75E-06	upregulated
Solyc10g085850.1	215.3361198	1.93457971	0.00064499	0.018474729	upregulated
Solyc10g086400.2	3358.767384	0.722882641	0.001292084	0.031700719	upregulated
Solyc10g086570.3	9838.767444	1.378576683	2.35E-06	0.000203088	upregulated
Solyc11g005190.3	724.494825	0.987987109	2.17E-06	0.000190744	upregulated
Solyc11g005270.1	46.18402106	2.704741333	2.29E-08	3.31E-06	upregulated
Solyc11g005280.1	347.0287812	2.771031844	2.57E-21	2.43E-18	upregulated
Solyc11g005290.1	37.60187676	1.481629735	0.001954891	0.042994365	upregulated
Solyc11g006710.2	390.5833301	2.532814233	3.00E-11	7.09E-09	upregulated
Solyc11g006910.3	50.45225318	2.599715821	0.000452797	0.014169554	upregulated
Solyc11g007180.3	4.918722301	6.003129207	0.001500186	0.035651388	upregulated
Solyc11g007190.2	119.1935442	1.193388501	0.000150248	0.00619507	upregulated
Solyc11g007200.3	9622.356063	1.015792589	1.33E-06	0.000123668	upregulated
Solyc11g007690.3	10007.78764	1.741675662	2.56E-17	1.49E-14	upregulated
Solyc11g008440.3	530.4541979	1.070241538	6.85E-05	0.003220268	upregulated
Solyc11g008640.1	8.945586022	5.004226572	0.000816751	0.022142906	upregulated
Solyc11g010930.2	469.6375855	0.757387694	0.000210956	0.007948116	upregulated
Solyc11g011110.3	26.45971877	4.965384174	4.95E-09	8.45E-07	upregulated
Solyc11g011630.3	56.94895125	1.791735723	0.000679396	0.019150371	upregulated

Solyc11g012360.2	23771.7137	1.920865303	5.18E-14	2.03E-11	upregulated
Solyc11g012420.2	49.76603712	1.953410042	0.000168777	0.006762694	upregulated
Solyc11g013150.1	589.2313636	1.183788858	0.000474695	0.014733043	upregulated
Solyc11g020290.3	2552.374391	1.140845528	0.001128764	0.028781574	upregulated
Solyc11g020670.1	427.3667251	1.123266699	0.000681336	0.019181264	upregulated
Solyc11g021060.2	4946.435642	1.278794259	1.94E-05	0.001183392	upregulated
Solyc11g044910.2	2269.813869	1.968613854	5.17E-07	5.46E-05	upregulated
Solyc11g045330.2	726.8623698	1.012072689	0.001570113	0.036775779	upregulated
Solyc11g064980.1	14.69929358	7.585024494	1.58E-07	1.87E-05	upregulated
Solyc11g065530.1	348.7072232	1.041081751	0.000505959	0.015470903	upregulated
Solyc11g066700.2	6.949891455	6.506902059	0.001133485	0.028869556	upregulated
Solyc11g067180.2	53.74656977	1.959960532	0.000677072	0.019108573	upregulated
Solyc11g067190.3	127.6177367	1.536759078	2.65E-07	2.95E-05	upregulated
Solyc11g069330.1	4690.012235	0.868459859	0.002048667	0.044482958	upregulated
Solyc11g069450.1	1450.805302	2.906552802	2.43E-39	1.84E-35	upregulated
Solyc11g071600.2	58.3513765	3.084548157	1.84E-09	3.37E-07	upregulated
Solyc11g073010.1	145.8879796	1.220124115	2.48E-05	0.00142739	upregulated
Solyc11g073020.3	962.6172803	1.097980247	0.000167709	0.006749425	upregulated
Solyc12g005310.2	134.2496219	1.673919576	6.38E-05	0.003051261	upregulated
Solyc12g006050.2	2589.875127	1.218539361	3.55E-05	0.001908256	upregulated
Solyc12g006505.1	73.6070647	1.692762634	1.46E-05	0.000960258	upregulated
Solyc12g006520.2	3583.735716	0.565090557	0.001096235	0.02817349	upregulated
Solyc12g006600.3	25.11921033	4.723091622	8.96E-07	8.74E-05	upregulated
Solyc12g007060.1	251.7175919	1.815319628	3.70E-08	5.13E-06	upregulated
Solyc12g007285.1	943.3247596	0.690134391	0.000137307	0.005766119	upregulated
Solyc12g008560.1	1947.55124	1.275647455	0.00076525	0.020997235	upregulated
Solyc12g008660.1	272.140519	2.469433524	4.14E-09	7.28E-07	upregulated
Solyc12g008840.2	1023.722072	1.347596272	1.45E-07	1.74E-05	upregulated
Solyc12g009875.1	138.8626611	1.730619334	0.000439742	0.013914331	upregulated
Solyc12g009880.1	414.8246245	1.079719786	0.000629488	0.01812877	upregulated
Solyc12g009920.1	339.8282613	1.533754101	7.31E-06	0.00053371	upregulated
Solyc12g010900.1	860.7495951	1.986493004	8.04E-08	1.03E-05	upregulated
Solyc12g011350.3	13.56319704	3.717320321	0.000187196	0.007294848	upregulated
Solyc12g011440.2	1451.41591	0.808514274	9.40E-06	0.000662959	upregulated
Solyc12g013830.2	121.47857	3.693485051	3.60E-12	1.01E-09	upregulated
Solyc12g013900.3	24427.64571	1.174026222	1.82E-05	0.00112733	upregulated
Solyc12g019230.2	46.18281475	6.101046159	6.04E-12	1.58E-09	upregulated
Solyc12g019740.2	2467.68668	1.949901594	1.70E-05	0.001078836	upregulated
Solyc12g035130.2	19222.3725	0.881986537	0.001581443	0.03692579	upregulated
Solyc12g042070.3	3888.523307	0.597040871	0.001941377	0.042946595	upregulated
Solyc12g042470.2	2666.904481	0.999010716	0.000140455	0.005876614	upregulated

Solyc12g088050.2	607.226413	0.751066669	0.001035328	0.02686695	upregulated
Solyc12g088840.1	1669.378517	1.106115969	0.00059303	0.017384572	upregulated
Solyc12g089220.3	1068.707525	1.666901067	1.05E-08	1.68E-06	upregulated
Solyc12g089350.3	33.1008992	5.592739285	6.13E-11	1.39E-08	upregulated
Solyc12g094570.1	309.4987229	2.075251349	5.72E-05	0.00276923	upregulated
Solyc12g094580.3	240.1238019	1.94701075	0.000266408	0.00957676	upregulated
Solyc12g094610.3	63.66142499	2.245927944	5.34E-05	0.002623402	upregulated
Solyc12g094620.3	59937.83007	1.439494225	4.85E-05	0.002437091	upregulated
Solyc12g096210.2	78.99532062	1.549398367	0.000662743	0.018891918	upregulated
Solyc12g096430.1	36.8216674	1.601198868	0.001271527	0.031297752	upregulated
Solyc12g096490.1	73.44759467	1.532315457	8.28E-05	0.00384818	upregulated
Solyc12g096500.2	11708.17799	1.02046682	2.57E-09	4.63E-07	upregulated
Solyc12g096760.2	2896.806065	0.678498716	0.00022149	0.008289988	upregulated
Solyc12g098900.2	57.13916658	4.589711885	4.44E-12	1.22E-09	upregulated
Solyc12g098910.2	932.8652394	1.395750017	9.28E-10	1.77E-07	upregulated
Solyc12g099430.2	467.9107465	0.90843807	0.00055768	0.016518828	upregulated
Solyc12g099580.2	44.74916281	2.503545873	2.01E-07	2.31E-05	upregulated
Solyc12g099600.2	1217.484266	1.436158806	4.79E-17	2.59E-14	upregulated
Solyc12g099780.2	573.0170332	4.776726919	9.53E-06	0.000669985	upregulated
Solyc12g099790.3	372.5151116	3.065124062	1.32E-12	4.11E-10	upregulated
Solyc12g099970.2	2085.035198	1.571662677	0.000198465	0.007578041	upregulated

Supplementary Material 7.3. Table of mobile sRNAs locates in tomato scions produced by the eggplant rootstock in heterograft conditions: Tomato/Eggplant heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Locus	RPM_TomEgg_2	RPM_TomEgg_3	RPM_TomEgg_4	DicerCounts	DicerConsensus
B_0:254571-254986	0.478110888	0.614582066	1.468729285	3	N
B_0:25321641-25322357	0.478110888	1.229164132	0.489576428	2	21
B_0:31852174-31852595	0.478110888	1.229164132	0.979152857	3	22
B_0:46451500-46452457	0.956221777	0.614582066	0.489576428	2	22
B_1:3881165-3881601	0.478110888	0.614582066	0.489576428	2	21
B_1:4827687-4829024	0.478110888	0.614582066	0.979152857	3	N
B_1:6784680-6785240	0.956221777	0.614582066	0.489576428	3	24
B_1:12853858-12854297	0.478110888	0.614582066	0.489576428	2	23
B_1:17939951-17940759	0.478110888	1.229164132	0.979152857	3	N

B_1:34281642-34282215	1.912443553	1.843746197	0.489576428	2	24
B_1:45507477-45507892	0.956221777	0.614582066	0.979152857	3	N
B_1:102405089-102407395	0.478110888	0.614582066	0.489576428	2	N
B_1:106125388-106126602	1.912443553	1.843746197	3.427034998	2	21
B_1:113122218-113122649	0.478110888	0.614582066	0.489576428	3	N
B_10:47009391-47009806	0.478110888	0.614582066	0.489576428	3	N
B_10:68133628-68134053	0.478110888	0.614582066	0.489576428	2	22
B_10:70561213-70561889	0.956221777	0.614582066	0.979152857	3	N
B_10:78147835-78148280	0.478110888	0.614582066	0.489576428	0	N
B_10:80317580-80318565	0.956221777	1.843746197	0.979152857	2	N
B_10:81357382-81358103	0.478110888	0.614582066	0.489576428	2	N
B_10:82074802-82075297	0.478110888	0.614582066	0.489576428	2	N
B_11:1934787-1935209	0.956221777	0.614582066	0.489576428	2	N
B_11:76565289-76565778	0.478110888	0.614582066	0.489576428	3	22
B_11:93653436-93656188	0.478110888	1.229164132	1.468729285	2	22
B_11:94403786-94405614	0.478110888	0.614582066	0.489576428	2	22
B_11:94406405-94407890	0.956221777	1.229164132	0.979152857	0	N
B_11:94702642-94703064	0.478110888	1.229164132	0.489576428	3	N
B_11:97743687-97744699	1.912443553	1.229164132	1.958305713	3	21
B_11:100573310-100573724	0.956221777	0.614582066	0.979152857	3	N
B_11:102272494-102272970	0.478110888	0.614582066	0.489576428	0	N
B_11:103261245-103262506	0.478110888	1.229164132	0.489576428	3	N
B_12:1249990-1250403	0.478110888	0.614582066	0.489576428	3	N
B_12:2967070-2967676	0.478110888	0.614582066	0.489576428	2	21
B_12:16850410-16851387	1.434332665	2.458328263	1.958305713	2	21
B_12:66323227-66324006	0.478110888	0.614582066	1.468729285	3	21
B_12:66325124-66327477	1.434332665	1.229164132	1.958305713	2	21

B_12:69351277-69351908	0.478110888	0.614582066	0.489576428	2	N
B_12:70088595-70091848	4.302997994	7.989566855	5.385340711	3	21
B_2:6859327-6859740	1.912443553	0.614582066	0.979152857	3	N
B_2:23436318-23436732	0.478110888	0.614582066	0.489576428	3	N
B_2:40393059-40393967	0.478110888	1.229164132	0.489576428	2	N
B_2:49308909-49311296	1.912443553	3.072910329	0.979152857	2	22
B_2:62019645-62020060	0.478110888	0.614582066	0.489576428	3	N
B_2:62445270-62445685	0.478110888	0.614582066	0.489576428	3	N
B_2:67565271-67565720	0.478110888	0.614582066	0.489576428	2	24
B_2:68917746-68918212	0.478110888	0.614582066	0.489576428	3	N
B_3:26267619-26268027	0.478110888	0.614582066	0.489576428	3	N
B_3:56542447-56545563	0.956221777	0.614582066	0.489576428	0	N
B_3:65571141-65572380	0.478110888	0.614582066	0.489576428	3	24
B_3:70162855-70166518	0.478110888	0.614582066	0.489576428	0	N
B_3:86993994-86994703	0.478110888	0.614582066	0.489576428	3	N
B_3:94992646-94995791	1.434332665	0.614582066	0.489576428	2	N
B_3:96319236-96319845	0.478110888	1.229164132	0.489576428	2	N
B_3:98470941-98471356	0.478110888	1.229164132	0.979152857	3	N
B_4:4790934-4791497	0.478110888	0.614582066	0.489576428	2	N
B_4:7586580-7587357	0.478110888	0.614582066	0.489576428	3	N
B_4:8175982-8176567	0.478110888	0.614582066	0.489576428	0	N
B_4:15892738-15893152	0.478110888	0.614582066	0.489576428	3	N
B_4:20530697-20531111	0.478110888	0.614582066	0.489576428	3	N
B_4:21784022-21784440	2.390554441	0.614582066	3.427034998	3	N
B_4:45887397-45887812	0.956221777	0.614582066	0.979152857	3	N
B_4:51351874-51356406	0.478110888	0.614582066	0.489576428	2	24
B_4:60727408-60730194	0.478110888	0.614582066	0.979152857	2	N

B_4:78126121-78126537	0.478110888	0.614582066	0.489576428	3	N
B_5:1268080-1268507	0.478110888	1.229164132	0.489576428	3	N
B_5:3074070-3075024	1.434332665	0.614582066	0.489576428	0	N
B_5:3851624-3852222	0.478110888	1.229164132	0.979152857	3	N
B_5:5283447-5286446	0.956221777	1.229164132	0.979152857	2	N
B_5:5603140-5603565	0.478110888	0.614582066	0.489576428	3	N
B_5:24102617-24103047	0.956221777	1.229164132	0.979152857	3	21
B_5:63081648-63084566	0.478110888	1.229164132	0.489576428	2	24
B_5:77310254-77313428	4.781108883	1.229164132	2.93745857	3	21
B_6:2486014-2486429	0.956221777	0.614582066	0.489576428	3	N
B_6:12425962-12426378	0.478110888	0.614582066	0.489576428	2	N
B_6:20262598-20263014	0.478110888	0.614582066	0.489576428	3	N
B_6:45860832-45861246	0.478110888	0.614582066	0.489576428	3	N
B_6:70116372-70116788	0.478110888	0.614582066	1.468729285	0	N
B_6:74854714-74855205	0.478110888	1.229164132	0.489576428	3	N
B_6:75988524-75990135	0.956221777	0.614582066	1.958305713	2	21
B_6:76669436-76669989	0.478110888	0.614582066	0.489576428	0	N
B_6:78165196-78165624	0.478110888	0.614582066	0.489576428	2	24
B_6:78340994-78343805	0.478110888	0.614582066	0.979152857	0	N
B_6:80052438-80052920	0.478110888	0.614582066	0.489576428	3	24
B_6:80997055-80997560	0.478110888	0.614582066	0.489576428	3	24
B_6:84422151-84422568	0.478110888	0.614582066	0.489576428	2	N
B_6:92767434-92768353	0.956221777	0.614582066	0.489576428	2	N
B_6:94627940-94628976	0.478110888	0.614582066	0.979152857	0	N
B_7:1867825-1868269	0.478110888	1.229164132	0.979152857	2	N
B_7:21083159-21085521	2.390554441	0.614582066	0.489576428	3	21
B_7:65162150-65162568	0.956221777	1.229164132	0.489576428	3	N

B_7:93571100-93572708	0.956221777	0.614582066	0.489576428	0	N
B_7:97721001-97721416	0.956221777	0.614582066	0.979152857	3	N
B_7:100231181-100233631	0.478110888	1.229164132	0.489576428	0	N
B_7:100461221-100461636	1.434332665	1.229164132	0.979152857	3	N
B_7:102804157-102804845	0.956221777	1.229164132	1.468729285	3	N
B_7:103824829-103825324	0.478110888	0.614582066	0.489576428	2	N
B_7:104058963-104059842	0.478110888	0.614582066	0.979152857	3	21
B_8:37261281-37261696	0.478110888	0.614582066	0.979152857	3	N
B_8:68686133-68686548	0.478110888	0.614582066	0.979152857	3	N
B_8:80874300-80875559	0.478110888	0.614582066	0.489576428	0	N
B_8:87163141-87163899	0.478110888	0.614582066	0.489576428	2	N
B_8:88756555-88758083	0.478110888	0.614582066	0.489576428	3	24
B_8:90518594-90519108	0.478110888	0.614582066	0.489576428	2	24
B_9:541481-542008	0.478110888	0.614582066	0.489576428	2	N
B_9:4233277-4233749	0.478110888	1.229164132	0.489576428	2	24
B_9:18957545-18957959	0.478110888	0.614582066	0.489576428	3	N
B_9:74434582-74442742	0.956221777	1.843746197	1.958305713	0	N
B_9:74443485-74448626	0.478110888	0.614582066	1.958305713	2	22
B_9:74448699-74450758	0.478110888	0.614582066	0.489576428	0	N
B_9:75970794-75973523	0.956221777	0.614582066	0.489576428	2	22
B_9:80874097-80874699	0.478110888	0.614582066	0.489576428	3	N
B_9:82373360-82373854	0.478110888	0.614582066	0.489576428	2	N
B_9:83109574-83110146	0.478110888	0.614582066	0.979152857	2	24
B_9:87890266-87890735	0.956221777	1.229164132	0.489576428	2	N
B_9:88175552-88176070	0.478110888	0.614582066	0.489576428	0	N
B_9:89148311-89148715	0.478110888	0.614582066	0.979152857	3	N
B_9:90789897-90791145	0.956221777	0.614582066	0.489576428	3	22

Supplementary Material 7.4. Table of mobile sRNA sequences. Tomato/Eggplant heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Mobile sRNA	Consensus Sequence
B_0:31852174-31852595	UGCACAGCCUCUUCCCUGGCUC
B_1:4827687-4829024	ACAGCUCUUCCUUCACUUU
B_1:6784680-6785240	AUGUGCGUACAGAUCUGUUACUCC
B_1:17939951-17940759	GGUAGCUCGUCAGGCU
B_1:34281642-34282215	UUGACUGACAUCUGAUUUCUCAAGG
B_1:45507477-45507892	CGGGGUGUAGCUCAGU
B_1:106125388-106126602	AUCAGAUGAAAGGCUGUCCGG
B_10:47009391-47009806	GGUCUAUGUAGCACUU
B_10:81357382-81358103	UAUUGAGGAUUGGGCUACUUCAUC
B_10:82074802-82075297	UUCGGAUUCGAGCCCUACCUCUA
B_11:1934787-1935209	AUCAUGUGGAAUUAGUCAAGGUGCA
B_11:76565289-76565778	UUCCCAGUCCAGGCAUUCCAAC
B_11:94702642-94703064	AAUUUCUGACUCUGUCACA
B_11:97743687-97744699	CGAUAAGUGGAUCUGGACCGAC
B_11:100573310-100573724	GGGGCUACCGAGGGUUC
B_12:1249990-1250403	UCUUCGACUGGGAAC
B_12:16850410-16851387	UAAAUGGACUCUUAGAAUGCU
B_12:69351277-69351908	AAGAUCAUGGACUCACAGCUCACU
B_2:6859327-6859740	AUCCUACUCCCGCAACC
B_2:23436318-23436732	CGUGUGCAAGGCUUU
B_2:62019645-62020060	GCUCGAGUGGCGGAAC
B_2:62445270-62445685	AACUGAAGAACCAUCA
B_2:68917746-68918212	AGGUCUGAAUUCGAGUUCU
B_3:26267619-26268027	CUCUUUGACUCUCUUUCU
B_3:86993994-86994703	UUUGGUGUUCUUCUGAUGAC
B_3:94992646-94995791	GAGGUACGGGGAAACUCUAAACA
B_3:98470941-98471356	UUGAAGACCCUGGAAGU
B_4:7586580-7587357	GUGCUCUGAAUGUUUUU
B_4:15892738-15893152	CCACUCCUGACACCA
B_4:20530697-20531111	ACCUAGGGCGGACUU
B_4:21784022-21784440	GAAAAACCUUACCCACCUU
B_4:78126121-78126537	AACUUUGAAGACUGAAG
B_5:1268080-1268507	AUUCUGACUUGACACA
B_5:3851624-3852222	CGAUAGUAGGCUCCA
B_6:2486014-2486429	UCAAAUCCUACUCCCGCG
B_6:20262598-20263014	CCUACGGGCCAAGGUAC
B_6:45860832-45861246	GCCCUUGUAGCUCAG

B_6:70116372-70116788	GGUGGACUUGAAUCUCCUUAAAGA
B_6:74854714-74855205	UUUUCUCAGAAAGUCACUCG
B_6:80052438-80052920	GAUGUGUCUGCUUGAGCUACCUGC
B_6:80997055-80997560	AAUCUCACAAGUGGUAUCUCAGAA
B_7:65162150-65162568	GAUUCAUGAAGCUCUCUCG
B_7:100461221-100461636	CAGACACCAGCUCAC
B_7:102804157-102804845	CUUGUAGAGUCCCGACU
B_7:103824829-103825324	AUCACGCACUGCAGAUGCGUGAUC
B_8:68686133-68686548	CGGAUGACUUGUGGAUA
B_8:87163141-87163899	UAAAUUCUGAAUCCGCCUCCC
B_8:88756555-88758083	ACGUGUGACUCUAGAAAGGCAAGG
B_9:18957545-18957959	GGAGACGUGGGUGAG
B_9:80874097-80874699	UGAAGUGACGAAAUUCGAUU
B_9:89148311-89148715	AAAAAAAAAGGGCAGGGAU

Supplementary Material 7.5. Table of mobile mRNAs locates in tomato scions produced by the eggplant rootstock in heterograft conditions: Tomato/Eggplant heterografted samples in comparison to Tomato/Tomato self-grafted samples.

mRNA	FPKM_TomEgg_2	FPKM_TomEgg_3	FPKM_TomEgg_4
SMEL4.1_00g001690.1.01	0.011487877	0.01093814	0.01200077
SMEL4.1_00g002920.1.01	0.011487877	0.01093814	0.02400154
SMEL4.1_00g004610.1.01	0.00991111	0.009436827	0.010353605
SMEL4.1_00g011240.1.01	0.004172186	0.007945062	0.039226128
SMEL4.1_01g011050.1.01	0.009864221	0.004696091	0.010304623
SMEL4.1_01g015470.1.01	0.003662533	0.001162423	0.002550702
SMEL4.1_01g028150.1.01	0.008510407	0.008103153	0.044451831
SMEL4.1_01g036120.1.01	0.011225032	0.021375746	0.01172619
SMEL4.1_01g039220.1.01	0.0077964	0.014846627	0.016288963
SMEL4.1_02g007210.1.01	0.00681853	0.012984477	0.004748635
SMEL4.1_02g010740.1.01	0.015161242	0.011548576	0.003167627
SMEL4.1_02g012150.1.01	0.001814073	0.001727263	0.001895064
SMEL4.1_02g019230.1.01	0.001245829	0.002372422	0.007808702
SMEL4.1_02g031240.1.01	0.006868601	0.013079827	0.00358763
SMEL4.1_03g014200.1.01	0.003881419	0.001847839	0.00405471
SMEL4.1_03g019590.1.01	0.002163195	0.008238713	0.002259774
SMEL4.1_03g025970.1.01	0.00717128	0.010242162	0.071168796
SMEL4.1_03g029510.1.01	0.003339419	0.003179616	0.003488512
SMEL4.1_03g031800.1.01	0.047932178	0.091276894	0.050072178
SMEL4.1_04g001340.1.01	0.026540013	0.025269976	0.180212038
SMEL4.1_05g000360.1.01	0.052454082	0.049943961	0.012176882

SMEL4.1_05g021800.1.01	0.002963823	0.002821994	0.003096147
SMEL4.1_06g002070.1.01	0.018699998	0.008902567	0.004883721
SMEL4.1_06g008880.1.01	0.015789423	0.004295383	0.007069013
SMEL4.1_06g014230.1.01	0.003860607	0.003675863	0.001344323
SMEL4.1_06g018830.1.01	0.012305716	0.005858421	0.006427561
SMEL4.1_06g020840.1.01	0.018356042	0.002496805	0.001369684
SMEL4.1_07g007730.1.01	0.00050651	0.000482272	0.000529124
SMEL4.1_08g006150.1.01	0.009045769	0.008612896	0.023624075
SMEL4.1_08g006500.1.01	0.010309269	0.019631866	0.021539083
SMEL4.1_08g006630.1.01	0.007809175	0.022306432	0.02447348
SMEL4.1_08g010190.1.01	0.057320955	0.054577937	0.479041041
SMEL4.1_08g014760.1.01	0.009256603	0.00440682	0.019339753
SMEL4.1_09g006090.1.01	0.002522365	0.004803321	0.002634979
SMEL4.1_10g000220.1.01	0.001394216	0.000663749	0.013108163
SMEL4.1_10g011740.1.01	0.007586309	0.010834915	0.001981253
SMEL4.1_10g013500.1.01	0.000913644	0.001739845	0.000954435
SMEL4.1_10g023700.1.01	0.023335755	0.022219054	0.004875523
SMEL4.1_10g024800.1.01	0.014346673	0.004553377	0.0149872
SMEL4.1_10g025480.1.01	0.002568982	0.002446046	0.002683677
SMEL4.1_11g007560.1.01	0.004089335	0.005191527	0.007119849
SMEL4.1_11g017430.1.01	0.002064661	0.005897579	0.004313682
SMEL4.1_11g027240.1.01	0.003584484	0.003412954	0.003744519
SMEL4.1_12g010100.1.01	0.00038307	0.000364739	0.000400173
SMEL4.1_12g011730.1.01	0.016786714	0.005327803	0.005845393
SMEL4.1_12g017650.1.01	0.080001909	0.266607332	0.376081681

Supplementary Material 7.6. Table of differentially expressed sRNAs in tomato scions between self-grafted and heterografted conditions: Tomato/Eggplant heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Locus	DicerCall Consensus	logFC	pvalue	padjusted	expression
SL40ch01:84310797-84311212	N	-3.0038212	0.08567685	0	downregulated
SL40ch06:3209906-3210328	N	-3.0040679	0.08400594	0	downregulated
SL40ch06:32169173-32169592	N	-3.0074296	0.08437856	0	downregulated
SL40ch04:50155757-50156177	N	-3.0074416	0.08429091	0	downregulated
SL40ch06:40927914-40928332	N	-3.0074416	0.08429091	0	downregulated
SL40ch09:46045632-46046057	N	-3.0108219	0.08461552	0	downregulated

SL40ch10:44950436-44950845	N	-3.011019	0.08305921	0	downregulated
SL40ch09:3465332-3465817	N	-3.0139931	0.08693764	0	downregulated
SL40ch12:6821098-6821508	N	-3.0139931	0.08693764	0	downregulated
SL40ch10:6277150-6277881	N	-3.0171087	0.10022121	0	downregulated
SL40ch08:3392967-3393384	N	-3.0216716	0.08568211	0	downregulated
SL40ch02:46851618-46852211	N	-3.0217903	0.08414647	0	downregulated
SL40ch12:5008031-5008448	N	-3.0255242	0.08002323	0	downregulated
SL40ch05:9503057-9503470	N	-3.0255302	0.07994157	0	downregulated
SL40ch05:41156137-41156540	N	-3.0255302	0.07994157	0	downregulated
SL40ch07:67604549-67604965	N	-3.0255302	0.07994157	0	downregulated
SL40ch07:30344-31002	N	-3.025639	0.07848575	0	downregulated
SL40ch08:373907-374331	N	-3.0290833	0.07750002	0	downregulated
SL40ch01:56056081-56056500	N	-3.0290885	0.07742032	0	downregulated
SL40ch05:61195377-61195800	N	-3.0290885	0.07742032	0	downregulated
SL40ch07:26370021-26370443	N	-3.0290885	0.07742032	0	downregulated
SL40ch09:56627244-56627660	N	-3.0465916	0.07825721	0	downregulated
SL40ch04:57735599-57736005	N	-3.0498956	0.07335541	0	downregulated
SL40ch12:62598453-62598869	N	-3.0531934	0.07172378	0	downregulated
SL40ch02:19841207-19841619	N	-3.0532413	0.0730419	0	downregulated
SL40ch02:32606813-32607229	N	-3.0566414	0.07393493	0	downregulated
SL40ch02:52924894-52925385	N	-3.0643455	0.08998118	0	downregulated
SL40ch05:356229-356669	N	-3.0709343	0.07574395	0	downregulated
SL40ch05:62752365-62752783	N	-3.0709343	0.07574395	0	downregulated
SL40ch11:23297904-23298309	N	-3.070942	0.07581866	0	downregulated
SL40ch12:4871703-4872162	N	-3.070942	0.07581866	0	downregulated
SL40ch08:63240410-63240833	N	-3.0717068	0.22570351	0	downregulated
SL40ch11:30918931-30919341	N	-3.0717068	0.22570351	0	downregulated

SL40ch08:59972878-59973296	N	-3.0737005	0.07042855	0	downregulated
SL40ch10:51065875-51066298	N	-3.0738623	0.0716936	0	downregulated
SL40ch10:64701312-64701734	N	-3.0738623	0.0716936	0	downregulated
SL40ch11:52174674-52175101	N	-3.0738623	0.0716936	0	downregulated
SL40ch03:2075260-2075674	N	-3.0738712	0.07176453	0	downregulated
SL40ch09:63895256-63895673	N	-3.0770028	0.07003774	0	downregulated
SL40ch10:17697714-17698137	N	-3.0770028	0.07003774	0	downregulated
SL40ch05:54171014-54171432	N	-3.0771798	0.07129248	0	downregulated
SL40ch05:928818-929241	N	-3.0808297	0.07318398	0	downregulated
SL40ch03:54750628-54751046	N	-3.0820744	0.18929402	0	downregulated
SL40ch04:64396158-64396560	N	-3.0820744	0.18929402	0	downregulated
SL40ch05:7736865-7737283	N	-3.0820744	0.18929402	0	downregulated
SL40ch08:874593-875002	N	-3.0820744	0.18929402	0	downregulated
SL40ch09:17996233-17996651	N	-3.0820744	0.18929402	0	downregulated
SL40ch12:4942868-4943277	N	-3.0820744	0.18929402	0	downregulated
SL40ch10:62774103-62774519	N	-3.0860763	0.08717971	0	downregulated
SL40ch03:50185258-50185680	N	-3.0895456	0.18181968	0	downregulated
SL40ch03:54399707-54400127	N	-3.0895456	0.18181968	0	downregulated
SL40ch05:60654634-60655053	N	-3.0895456	0.18181968	0	downregulated
SL40ch08:58058078-58058486	N	-3.0895456	0.18181968	0	downregulated
SL40ch11:4153179-4153599	N	-3.0895456	0.18181968	0	downregulated
SL40ch03:53798889-53799303	N	-3.0951099	0.07344172	0	downregulated
SL40ch04:5294562-5294976	N	-3.0951239	0.07351242	0	downregulated
SL40ch01:70416665-70417080	N	-3.096375	0.18013782	0	downregulated
SL40ch02:48097176-48097590	N	-3.096375	0.18013782	0	downregulated
SL40ch03:51115730-51116142	N	-3.096375	0.18013782	0	downregulated
SL40ch03:62640530-62640942	N	-3.096375	0.18013782	0	downregulated

SL40ch05:61685878-61686301	N	-3.096375	0.18013782	0	downregulated
SL40ch07:55666632-55667051	N	-3.096375	0.18013782	0	downregulated
SL40ch08:34198332-34198747	N	-3.096375	0.18013782	0	downregulated
SL40ch09:5200533-5200949	N	-3.096375	0.18013782	0	downregulated
SL40ch09:7272626-7273036	N	-3.096375	0.18013782	0	downregulated
SL40ch09:60503308-60503725	N	-3.096375	0.18013782	0	downregulated
SL40ch11:51400345-51400765	N	-3.096375	0.18013782	0	downregulated
SL40ch12:65358769-65359217	N	-3.096375	0.18013782	0	downregulated
SL40ch05:22450595-22450997	N	-3.1027075	0.18419156	0	downregulated
SL40ch06:33720947-33721364	N	-3.1027075	0.18419156	0	downregulated
SL40ch09:57437933-57438352	N	-3.1027075	0.18419156	0	downregulated
SL40ch11:52162011-52162428	N	-3.1027075	0.18419156	0	downregulated
SL40ch12:44051447-44051869	N	-3.1027075	0.18419156	0	downregulated
SL40ch10:60152276-60152691	N	-3.1073642	0.21627126	0	downregulated
SL40ch11:48466303-48466711	N	-3.1195768	0.07285209	0	downregulated
SL40ch08:4481256-4481667	N	-3.119596	0.07291996	0	downregulated
SL40ch01:77158331-77158744	N	-3.1247589	0.17865012	0	downregulated
SL40ch05:6850514-6850923	N	-3.1247589	0.17865012	0	downregulated
SL40ch09:5637854-5638274	N	-3.1247589	0.17865012	0	downregulated
SL40ch06:46911912-46912344	N	-3.1255228	0.08274341	0	downregulated
SL40ch05:62019490-62019921	N	-3.1290724	0.08268969	0	downregulated
SL40ch08:57740663-57741210	N	-3.1292221	0.08057707	0	downregulated
SL40ch01:3720795-3721266	N	-3.1326327	0.14966344	0	downregulated
SL40ch01:6488575-6488978	N	-3.1326327	0.14966344	0	downregulated
SL40ch01:74302107-74302528	N	-3.1326327	0.14966344	0	downregulated
SL40ch01:81088878-81089292	N	-3.1326327	0.14966344	0	downregulated
SL40ch02:28219453-28219854	N	-3.1326327	0.14966344	0	downregulated

SL40ch02:50817370-50817775	N	-3.1326327	0.14966344	0	downregulated
SL40ch03:30597107-30597529	N	-3.1326327	0.14966344	0	downregulated
SL40ch04:63593464-63593885	N	-3.1326327	0.14966344	0	downregulated
SL40ch05:55924082-55924496	N	-3.1326327	0.14966344	0	downregulated
SL40ch06:46731901-46732319	N	-3.1326327	0.14966344	0	downregulated
SL40ch08:25016756-25017164	N	-3.1326327	0.14966344	0	downregulated
SL40ch08:52786487-52786898	N	-3.1326327	0.14966344	0	downregulated
SL40ch08:56388988-56389403	N	-3.1326327	0.14966344	0	downregulated
SL40ch08:62611644-62612059	N	-3.1326327	0.14966344	0	downregulated
SL40ch11:45781231-45781637	N	-3.1326327	0.14966344	0	downregulated
SL40ch11:52635840-52636240	N	-3.1326327	0.14966344	0	downregulated
SL40ch12:15512948-15513370	N	-3.1326327	0.14966344	0	downregulated
SL40ch06:39415461-39415887	N	-3.1361872	0.07814665	0	downregulated
SL40ch01:78254800-78255221	N	-3.139207	0.14447938	0	downregulated
SL40ch02:51012812-51013229	N	-3.139207	0.14447938	0	downregulated
SL40ch04:41475413-41475833	N	-3.139207	0.14447938	0	downregulated
SL40ch05:58793865-58794266	N	-3.139207	0.14447938	0	downregulated
SL40ch05:63762293-63762693	N	-3.139207	0.14447938	0	downregulated
SL40ch06:37915149-37915563	N	-3.139207	0.14447938	0	downregulated
SL40ch06:38403150-38403567	N	-3.139207	0.14447938	0	downregulated
SL40ch06:45591736-45592157	N	-3.139207	0.14447938	0	downregulated
SL40ch07:62179976-62180394	N	-3.139207	0.14447938	0	downregulated
SL40ch07:64629371-64629773	N	-3.139207	0.14447938	0	downregulated
SL40ch07:67662247-67662648	N	-3.139207	0.14447938	0	downregulated
SL40ch08:55919139-55919544	N	-3.139207	0.14447938	0	downregulated
SL40ch08:58343796-58344214	N	-3.139207	0.14447938	0	downregulated
SL40ch09:23871176-23871579	N	-3.139207	0.14447938	0	downregulated

SL40ch09:47638816-47639231	N	-3.139207	0.14447938	0	downregulated
SL40ch12:15412807-15413227	N	-3.139207	0.14447938	0	downregulated
SL40ch01:67633668-67634070	N	-3.1454639	0.1468716	0	downregulated
SL40ch01:81584966-81585377	N	-3.1454639	0.1468716	0	downregulated
SL40ch02:44739673-44740079	N	-3.1454639	0.1468716	0	downregulated
SL40ch02:46969793-46970201	N	-3.1454639	0.1468716	0	downregulated
SL40ch05:2623084-2623498	N	-3.1454639	0.1468716	0	downregulated
SL40ch06:1224763-1225177	N	-3.1454639	0.1468716	0	downregulated
SL40ch07:33510976-33511377	N	-3.1454639	0.1468716	0	downregulated
SL40ch07:64724319-64724740	N	-3.1454639	0.1468716	0	downregulated
SL40ch08:63398340-63398754	N	-3.1454639	0.1468716	0	downregulated
SL40ch09:63156319-63156726	N	-3.1454639	0.1468716	0	downregulated
SL40ch10:43024474-43024875	N	-3.1454639	0.1468716	0	downregulated
SL40ch10:62428961-62429374	N	-3.1454639	0.1468716	0	downregulated
SL40ch12:11542346-11542760	N	-3.1454639	0.1468716	0	downregulated
SL40ch03:5877536-5877945	N	-3.1514351	0.17231976	0	downregulated
SL40ch03:55955637-55956048	N	-3.1514351	0.17231976	0	downregulated
SL40ch10:49966109-49966526	N	-3.1514351	0.17231976	0	downregulated
SL40ch11:30918182-30918600	N	-3.1514351	0.17231976	0	downregulated
SL40ch06:704053-704758	N	-3.1519964	0	0	downregulated
SL40ch06:4797582-4798000	N	-3.1551927	0.06456785	0	downregulated
SL40ch09:59456148-59456570	N	-3.1551927	0.06456785	0	downregulated
SL40ch04:63330815-63331633	N	-3.1552045	0.06450129	0	downregulated
SL40ch11:9406971-9407450	N	-3.164143	0.06730922	0	downregulated
SL40ch01:81178287-81178696	N	-3.1716551	0.06163349	0	downregulated
SL40ch02:44950632-44951095	N	-3.1726497	0.16169569	0	downregulated
SL40ch03:46278713-46279133	N	-3.1726497	0.16169569	0	downregulated

SL40ch04:16040189-16040606	N	-3.1726497	0.16169569	0	downregulated
SL40ch05:48530227-48530639	N	-3.1726497	0.16169569	0	downregulated
SL40ch06:31030927-31031346	N	-3.1726497	0.16169569	0	downregulated
SL40ch07:49216490-49216945	N	-3.1726497	0.16169569	0	downregulated
SL40ch08:57927641-57928064	N	-3.1726497	0.16169569	0	downregulated
SL40ch12:52362008-52362424	N	-3.1726497	0.16169569	0	downregulated
SL40ch01:79580194-79580612	N	-3.1750035	0.05907491	0	downregulated
SL40ch06:32060919-32061341	N	-3.1750035	0.05907491	0	downregulated
SL40ch09:64989624-64990050	N	-3.1750098	0.05901473	0	downregulated
SL40ch01:81271752-81272168	N	-3.178238	0.13605921	0	downregulated
SL40ch02:5433772-5434190	N	-3.178238	0.13605921	0	downregulated
SL40ch02:38523486-38523904	N	-3.178238	0.13605921	0	downregulated
SL40ch06:42679409-42679824	N	-3.178238	0.13605921	0	downregulated
SL40ch09:2055613-2056033	N	-3.178238	0.13605921	0	downregulated
SL40ch11:11669062-11669479	N	-3.178238	0.13605921	0	downregulated
SL40ch12:3298788-3299211	N	-3.178238	0.13605921	0	downregulated
SL40ch01:2061598-2062002	N	-3.1844376	0.13478432	0	downregulated
SL40ch01:41049298-41049718	N	-3.1844376	0.13478432	0	downregulated
SL40ch03:49646769-49647191	N	-3.1844376	0.13478432	0	downregulated
SL40ch04:23543554-23543973	N	-3.1844376	0.13478432	0	downregulated
SL40ch04:58168136-58168541	N	-3.1844376	0.13478432	0	downregulated
SL40ch08:7774536-7774956	N	-3.1844376	0.13478432	0	downregulated
SL40ch11:16298949-16299371	N	-3.1844376	0.13478432	0	downregulated
SL40ch12:66349363-66349781	N	-3.1844376	0.13478432	0	downregulated
SL40ch02:10823909-10824331	N	-3.1919388	0.15733839	0	downregulated
SL40ch06:45086090-45086506	N	-3.1919388	0.15733839	0	downregulated
SL40ch09:30568132-30568549	N	-3.1919388	0.15733839	0	downregulated

SL40ch12:2497915-2498329	N	-3.1919388	0.15733839	0	downregulated
SL40ch12:11646331-11646753	N	-3.1919388	0.15733839	0	downregulated
SL40ch01:1468528-1468949	N	-3.2187963	0.15121154	0	downregulated
SL40ch01:22511865-22512285	N	-3.2187963	0.15121154	0	downregulated
SL40ch01:56832536-56832952	N	-3.2187963	0.15121154	0	downregulated
SL40ch02:39966036-39966456	N	-3.2187963	0.15121154	0	downregulated
SL40ch03:6619613-6620023	N	-3.2187963	0.15121154	0	downregulated
SL40ch03:46519402-46519824	N	-3.2187963	0.15121154	0	downregulated
SL40ch08:60856195-60856615	N	-3.2187963	0.15121154	0	downregulated
SL40ch10:57755445-57755860	N	-3.2187963	0.15121154	0	downregulated
SL40ch11:24169818-24170225	N	-3.2187963	0.15121154	0	downregulated
SL40ch03:53838208-53838623	N	-3.2227976	0.13053016	0	downregulated
SL40ch05:6858452-6858863	N	-3.2227976	0.13053016	0	downregulated
SL40ch07:59373297-59373707	N	-3.2227976	0.13053016	0	downregulated
SL40ch09:2648643-2649060	N	-3.2227976	0.13053016	0	downregulated
SL40ch09:3920858-3921277	N	-3.2227976	0.13053016	0	downregulated
SL40ch10:53653568-53653990	N	-3.2227976	0.13053016	0	downregulated
SL40ch11:10587186-10587604	N	-3.2227976	0.13053016	0	downregulated
SL40ch12:31937726-31938141	N	-3.2227976	0.13053016	0	downregulated
SL40ch12:64452202-64452623	N	-3.2227976	0.13053016	0	downregulated
SL40ch01:83793028-83793448	N	-3.231296	0.14850801	0	downregulated
SL40ch02:30953066-30953489	N	-3.231296	0.14850801	0	downregulated
SL40ch03:46834157-46834580	N	-3.231296	0.14850801	0	downregulated
SL40ch04:32391495-32391916	N	-3.231296	0.14850801	0	downregulated
SL40ch05:61843704-61844119	N	-3.231296	0.14850801	0	downregulated
SL40ch07:27588984-27589402	N	-3.231296	0.14850801	0	downregulated
SL40ch08:11878285-11878703	N	-3.231296	0.14850801	0	downregulated

SL40ch12:50566720-50567140	N	-3.231296	0.14850801	0	downregulated
SL40ch03:54537959-54538376	N	-3.2644461	0.14673858	0	downregulated
SL40ch04:2032033-2032442	N	-3.2644461	0.14673858	0	downregulated
SL40ch08:57101820-57102243	N	-3.2644461	0.14673858	0	downregulated
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SL40ch11:47228973-47229422	N	3.77930483	0.06077043	0	upregulated
SL40ch02:30272632-30273049	N	3.7473608	0.04993316	0	upregulated
SL40ch03:1875759-1876169	N	3.74532897	0.05013198	0	upregulated
SL40ch03:56577187-56577597	N	3.71174339	0.05257263	0	upregulated
SL40ch07:29977532-29977955	24	3.71174339	0.05257263	0	upregulated
SL40ch04:43722001-43722415	N	3.70934738	0.05055284	0	upregulated
SL40ch09:17901710-17902130	21	3.70934738	0.05055284	0	upregulated
SL40ch01:69700336-69700767	N	3.70760105	0.05300037	0	upregulated
SL40ch07:61768451-61768972	23	3.70760105	0.05300037	0	upregulated

SL40ch09:4356021-4356440	N	3.70760105	0.05300037	0	upregulated
SL40ch10:45713531-45713945	N	3.70760105	0.05300037	0	upregulated
SL40ch09:4900772-4901189	N	3.70704137	0.06721938	0	upregulated
SL40ch03:47917552-47917973	N	3.67796974	0.0729639	0	upregulated
SL40ch03:56666626-56667039	N	3.6756319	0.05760853	0	upregulated
SL40ch04:46660344-46660993	N	3.6756319	0.05760853	0	upregulated
SL40ch08:58298295-58298712	N	3.6756319	0.05760853	0	upregulated
SL40ch02:42479860-42480281	N	3.67349222	0.05437902	0	upregulated
SL40ch05:1762837-1763258	22	3.67349222	0.05437902	0	upregulated
SL40ch08:60261820-60262235	N	3.67349222	0.05437902	0	upregulated
SL40ch12:57720920-57721333	24	3.67349222	0.05437902	0	upregulated
SL40ch12:59843509-59843931	N	3.67349222	0.05437902	0	upregulated
SL40ch01:9329286-9329709	24	3.67138781	0.05460504	0	upregulated
SL40ch01:51564360-51564767	N	3.67138781	0.05460504	0	upregulated
SL40ch01:88587523-88587937	N	3.67138781	0.05460504	0	upregulated
SL40ch05:18042097-18042504	N	3.67138781	0.05460504	0	upregulated
SL40ch01:88698769-88699185	24	3.63804513	0.06632384	0	upregulated
SL40ch03:13953502-13954070	N	3.63634258	0.06223571	0	upregulated
SL40ch06:21048948-21049365	N	3.6325788	0.31749585	0	upregulated
SL40ch07:22244458-22244873	N	3.63198474	0.06275509	0	upregulated
SL40ch09:13968496-13968912	24	3.62922944	0.06741491	0	upregulated
SL40ch03:65139146-65139554	N	3.59276871	0.08315831	0	upregulated
SL40ch12:33393128-33393544	N	3.58773761	0.08598523	0	upregulated
SL40ch06:37576582-37576997	N	3.55384263	0.09033771	0	upregulated
SL40ch12:6704559-6704973	N	3.54904485	0.09107099	0	upregulated
SL40ch05:64516801-64517223	22	3.54824074	0.07741035	0	upregulated
SL40ch06:34279993-34280413	21	3.54824074	0.07741035	0	upregulated

SL40ch06:40835566-40835987	N	3.54824074	0.07741035	0	upregulated
SL40ch12:21312890-21313308	24	3.54824074	0.07741035	0	upregulated
SL40ch08:51710447-51710854	N	3.51143433	0.0957372	0	upregulated
SL40ch09:65816012-65816427	N	3.51143433	0.0957372	0	upregulated
SL40ch11:2651260-2651682	N	3.51143433	0.0957372	0	upregulated
SL40ch04:38422498-38422918	N	3.50659468	0.07920851	0	upregulated
SL40ch08:61373994-61374475	N	3.50659468	0.07920851	0	upregulated
SL40ch12:38785844-38786260	N	3.50659468	0.07920851	0	upregulated
SL40ch04:1830348-1830766	23	3.50421242	0.07954327	0	upregulated
SL40ch04:63818268-63818683	N	3.50421242	0.07954327	0	upregulated
SL40ch05:8631991-8632407	N	3.50421242	0.07954327	0	upregulated
SL40ch05:63612280-63612700	N	3.50421242	0.07954327	0	upregulated
SL40ch08:1687434-1687842	N	3.50421242	0.07954327	0	upregulated
SL40ch10:46709601-46710021	24	3.50421242	0.07954327	0	upregulated
SL40ch02:21272099-21272513	N	3.46496822	0.08539928	0	upregulated
SL40ch02:48675700-48676109	N	3.46496822	0.08539928	0	upregulated
SL40ch04:9557983-9558400	N	3.46496822	0.08539928	0	upregulated
SL40ch05:20654757-20655174	24	3.46496822	0.08539928	0	upregulated
SL40ch04:530306-530720	22	3.46241506	0.08277923	0	upregulated
SL40ch06:11555772-11556183	N	3.46241506	0.08277923	0	upregulated
SL40ch07:3487316-3487731	N	3.46241506	0.08277923	0	upregulated
SL40ch09:53035796-53036210	N	3.46241506	0.08277923	0	upregulated
SL40ch10:12210899-12211313	N	3.46241506	0.08277923	0	upregulated
SL40ch11:49555643-49556060	N	3.46241506	0.08277923	0	upregulated
SL40ch05:56063348-56063770	N	3.46007225	0.08613356	0	upregulated
SL40ch05:58236646-58237066	24	3.46007225	0.08613356	0	upregulated
SL40ch10:45413449-45413871	N	3.46007225	0.08613356	0	upregulated

SL40ch03:50888427-50888843	N	3.45802427	0.10626283	0	upregulated
SL40ch06:40089946-40090366	N	3.45802427	0.10626283	0	upregulated
SL40ch05:28103068-28103488	21	3.42186794	0.09672163	0	upregulated
SL40ch07:58196260-58196676	24	3.42186794	0.09672163	0	upregulated
SL40ch01:78234238-78234659	N	3.41967246	0.09258069	0	upregulated
SL40ch06:3184261-3184678	N	3.41967246	0.09258069	0	upregulated
SL40ch09:70297-70717	N	3.41967246	0.09258069	0	upregulated
SL40ch12:12264929-12265348	N	3.41967246	0.09258069	0	upregulated
SL40ch03:57402261-57402940	N	3.41715362	0.09298396	0	upregulated
SL40ch04:51940313-51940727	N	3.41715362	0.09298396	0	upregulated
SL40ch05:522855-523276	N	3.41715362	0.09298396	0	upregulated
SL40ch01:82616528-82616943	N	3.4142393	0.09797034	0	upregulated
SL40ch01:84761144-84761554	N	3.4142393	0.09797034	0	upregulated
SL40ch05:6485000-6485423	24	3.4142393	0.09797034	0	upregulated
SL40ch10:27709635-27710046	N	3.4142393	0.09797034	0	upregulated
SL40ch10:59987154-59987562	23	3.4142393	0.09797034	0	upregulated
SL40ch11:50438633-50439049	N	3.4142393	0.09797034	0	upregulated
SL40ch12:64245284-64245686	N	3.4142393	0.09797034	0	upregulated
SL40ch12:65629514-65629962	N	3.4142393	0.09797034	0	upregulated
SL40ch03:57965614-57966035	N	3.40999114	0.12082061	0	upregulated
SL40ch01:63729498-63729917	N	3.40501909	0.38900583	0	upregulated
SL40ch04:49560362-49560784	24	3.37200984	0.12242039	0	upregulated
SL40ch12:66119860-66120267	N	3.37200984	0.12242039	0	upregulated
SL40ch05:26966196-26966619	24	3.36953198	0.12139228	0	upregulated
SL40ch09:58215623-58216025	N	3.36953198	0.12139228	0	upregulated
SL40ch10:26108009-26108429	N	3.36660337	0.12346941	0	upregulated
SL40ch11:6694374-6694794	21	3.36660337	0.12346941	0	upregulated

SL40ch01:86125207-86125625	N	3.3630113	0.13008483	0	upregulated
SL40ch02:29976603-29977019	23	3.3630113	0.13008483	0	upregulated
SL40ch02:44324412-44324823	N	3.3630113	0.13008483	0	upregulated
SL40ch10:63054066-63054476	N	3.3630113	0.13008483	0	upregulated
SL40ch01:78709287-78709760	N	3.32402267	0.13570032	0	upregulated
SL40ch02:14193148-14193564	N	3.32402267	0.13570032	0	upregulated
SL40ch06:7321281-7321696	N	3.32402267	0.13570032	0	upregulated
SL40ch08:6712568-6712990	N	3.32402267	0.13570032	0	upregulated
SL40ch10:64642280-64642702	23	3.32402267	0.13570032	0	upregulated
SL40ch12:6715182-6715596	N	3.32402267	0.13570032	0	upregulated
SL40ch03:5092720-5093130	N	3.32120381	0.13626017	0	upregulated
SL40ch12:9414215-9414634	N	3.32120381	0.13626017	0	upregulated
SL40ch03:4994740-4995159	N	3.27348433	0.14085755	0	upregulated
SL40ch04:30556933-30557341	N	3.27348433	0.14085755	0	upregulated
SL40ch06:31619845-31620260	N	3.27348433	0.14085755	0	upregulated
SL40ch07:42031296-42031719	24	3.27348433	0.14085755	0	upregulated
SL40ch10:32367171-32367834	N	3.27348433	0.14085755	0	upregulated
SL40ch11:37100257-37100680	N	3.27348433	0.14085755	0	upregulated
SL40ch02:41115155-41115571	N	3.26769664	0.1420602	0	upregulated
SL40ch03:44804086-44804493	N	3.26769664	0.1420602	0	upregulated
SL40ch10:20099487-20099907	N	3.26769664	0.1420602	0	upregulated
SL40ch03:38341725-38342140	N	3.26769444	0.12295052	0	upregulated
SL40ch03:56383025-56383436	N	3.26769444	0.12295052	0	upregulated
SL40ch04:44690473-44690894	24	3.26769444	0.12295052	0	upregulated
SL40ch07:65865726-65866149	N	3.26769444	0.12295052	0	upregulated
SL40ch09:50140395-50140818	24	3.26769444	0.12295052	0	upregulated
SL40ch10:62344177-62344594	N	3.26769444	0.12295052	0	upregulated

SL40ch12:860789-861209	21	3.26769444	0.12295052	0	upregulated
SL40ch02:33156749-33157217	N	3.22244784	0.15201012	0	upregulated
SL40ch05:13094750-13095162	N	3.22244784	0.15201012	0	upregulated
SL40ch05:37486676-37487090	N	3.22244784	0.15201012	0	upregulated
SL40ch05:52938120-52938537	N	3.22244784	0.15201012	0	upregulated
SL40ch06:46292097-46292519	N	3.22244784	0.15201012	0	upregulated
SL40ch10:43671396-43671808	N	3.22244784	0.15201012	0	upregulated
SL40ch01:1035255-1035664	24	3.21806665	0.12926647	0	upregulated
SL40ch01:56060297-56060710	N	3.21806665	0.12926647	0	upregulated
SL40ch02:49909388-49909804	N	3.21806665	0.12926647	0	upregulated
SL40ch03:11473734-11474148	N	3.21806665	0.12926647	0	upregulated
SL40ch04:10352701-10353125	N	3.21806665	0.12926647	0	upregulated
SL40ch04:49883622-49884041	N	3.21806665	0.12926647	0	upregulated
SL40ch04:56569237-56569656	24	3.21806665	0.12926647	0	upregulated
SL40ch05:8167362-8167780	N	3.21806665	0.12926647	0	upregulated
SL40ch05:8195702-8196125	N	3.21806665	0.12926647	0	upregulated
SL40ch06:37040652-37041071	N	3.21806665	0.12926647	0	upregulated
SL40ch06:43340514-43340924	N	3.21806665	0.12926647	0	upregulated
SL40ch07:65157578-65157992	24	3.21806665	0.12926647	0	upregulated
SL40ch09:3022324-3022739	N	3.21806665	0.12926647	0	upregulated
SL40ch10:55357944-55358361	24	3.21806665	0.12926647	0	upregulated
SL40ch11:29275254-29275669	N	3.21806665	0.12926647	0	upregulated
SL40ch01:9536314-9536737	N	3.2151748	0.12984258	0	upregulated
SL40ch01:18580689-18581108	21	3.2151748	0.12984258	0	upregulated
SL40ch02:42839122-42839534	N	3.2151748	0.12984258	0	upregulated
SL40ch03:49780989-49781411	23	3.2151748	0.12984258	0	upregulated
SL40ch05:61414729-61415151	23	3.2151748	0.12984258	0	upregulated

SL40ch06:35046977-35047397	N	3.2151748	0.12984258	0	upregulated
SL40ch06:39948092-39948503	N	3.2151748	0.12984258	0	upregulated
SL40ch07:342419-342834	N	3.2151748	0.12984258	0	upregulated
SL40ch08:47662801-47663219	N	3.2151748	0.12984258	0	upregulated
SL40ch08:62390953-62391367	N	3.2151748	0.12984258	0	upregulated
SL40ch11:12519477-12519894	N	3.2151748	0.12984258	0	upregulated
SL40ch12:49889762-49890181	24	3.2151748	0.12984258	0	upregulated
SL40ch02:14005488-14005905	N	3.21345921	0.15398483	0	upregulated
SL40ch02:35229814-35230266	N	3.21345921	0.15398483	0	upregulated
SL40ch08:61655043-61655466	24	3.21345921	0.15398483	0	upregulated
SL40ch02:34626821-34627241	N	3.19825338	0.0637881	0	upregulated
SL40ch03:29187374-29187784	23	3.17619067	0.06247115	0	upregulated
SL40ch01:89163649-89164067	N	3.17616066	0.06260991	0	upregulated
SL40ch01:59287886-59288292	N	3.17464276	0.06289627	0	upregulated
SL40ch01:84834684-84835100	N	3.17444737	0.06379325	0	upregulated
SL40ch03:43059489-43059911	23	3.17441716	0.06393379	0	upregulated
SL40ch11:52973531-52973951	21	3.16980505	0.07215827	0	upregulated
SL40ch01:20049395-20049797	N	3.16944544	0.16972635	0	upregulated
SL40ch01:42590553-42590976	22	3.16944544	0.16972635	0	upregulated
SL40ch01:79327576-79327987	N	3.16944544	0.16972635	0	upregulated
SL40ch07:2155778-2156191	N	3.16944544	0.16972635	0	upregulated
SL40ch01:74984811-74985229	24	3.16725419	0.14366435	0	upregulated
SL40ch02:20154366-20154782	N	3.16725419	0.14366435	0	upregulated
SL40ch02:41199621-41200045	N	3.16725419	0.14366435	0	upregulated
SL40ch03:213243-213662	N	3.16725419	0.14366435	0	upregulated
SL40ch03:62164327-62164743	N	3.16725419	0.14366435	0	upregulated
SL40ch04:31280203-31280604	N	3.16725419	0.14366435	0	upregulated

SL40ch05:56235964-56236384	N	3.16725419	0.14366435	0	upregulated
SL40ch06:45101691-45102107	24	3.16725419	0.14366435	0	upregulated
SL40ch07:42239144-42239562	N	3.16725419	0.14366435	0	upregulated
SL40ch09:46179194-46179617	N	3.16725419	0.14366435	0	upregulated
SL40ch10:58859953-58860375	24	3.16725419	0.14366435	0	upregulated
SL40ch11:994113-994530	N	3.16725419	0.14366435	0	upregulated
SL40ch12:31100466-31100883	24	3.16725419	0.14366435	0	upregulated
SL40ch11:52114310-52114737	N	3.16584884	0.08704221	0	upregulated
SL40ch01:70637280-70637701	N	3.16441294	0.14056124	0	upregulated
SL40ch02:47986528-47986951	23	3.16441294	0.14056124	0	upregulated
SL40ch02:50058328-50058749	N	3.16441294	0.14056124	0	upregulated
SL40ch03:53985843-53986261	N	3.16441294	0.14056124	0	upregulated
SL40ch06:1473396-1473815	N	3.16441294	0.14056124	0	upregulated
SL40ch06:43089190-43089607	23	3.16441294	0.14056124	0	upregulated
SL40ch10:2969628-2970037	N	3.16441294	0.14056124	0	upregulated
SL40ch01:61155673-61156087	N	3.16122979	0.14495174	0	upregulated
SL40ch10:40762657-40763070	23	3.16122979	0.14495174	0	upregulated
SL40ch11:31336185-31336594	N	3.16122979	0.14495174	0	upregulated
SL40ch11:47227170-47227582	N	3.16122979	0.14495174	0	upregulated
SL40ch01:69916335-69916745	22	3.15692769	0.17265191	0	upregulated
SL40ch04:4491756-4492173	N	3.15692769	0.17265191	0	upregulated
SL40ch10:20211085-20211501	N	3.15692769	0.17265191	0	upregulated
SL40ch10:59144000-59144416	N	3.15692769	0.17265191	0	upregulated
SL40ch05:26943491-26943913	N	3.14715106	0.07696778	0	upregulated
SL40ch02:34916425-34916847	N	3.14028321	0.06617059	0	upregulated
SL40ch11:42566854-42567279	24	3.1393788	0.06854639	0	upregulated
SL40ch10:59220552-59220979	N	3.138035	0.08977131	0	upregulated

SL40ch12:63403762-63404210	N	3.12546144	0.42709749	0	upregulated
SL40ch06:46382068-46382486	21	3.1155678	0.0706889	0	upregulated
SL40ch08:55068667-55069080	N	3.11554184	0.07054207	0	upregulated
SL40ch01:84934648-84935070	N	3.11335473	0.06726244	0	upregulated
SL40ch08:10800761-10801184	22	3.11318464	0.06636421	0	upregulated
SL40ch07:59691906-59692321	24	3.1118317	0.06758186	0	upregulated
SL40ch06:24276408-24276828	N	3.11180618	0.0674405	0	upregulated
SL40ch10:60527822-60528375	N	3.11180618	0.0674405	0	upregulated
SL40ch01:303505-303915	N	3.11091804	0.18400189	0	upregulated
SL40ch01:71765517-71765934	N	3.11091804	0.18400189	0	upregulated
SL40ch01:81298753-81299164	N	3.11091804	0.18400189	0	upregulated
SL40ch02:45004704-45005120	N	3.11091804	0.18400189	0	upregulated
SL40ch03:49344909-49345323	N	3.11091804	0.18400189	0	upregulated
SL40ch05:1717677-1718093	N	3.11091804	0.18400189	0	upregulated
SL40ch05:4695221-4695633	N	3.11091804	0.18400189	0	upregulated
SL40ch05:59201245-59201657	N	3.11091804	0.18400189	0	upregulated
SL40ch09:57709351-57709760	N	3.11091804	0.18400189	0	upregulated
SL40ch12:65549813-65550221	24	3.11091804	0.18400189	0	upregulated
SL40ch01:74198534-74198954	N	3.10833051	0.1790509	0	upregulated
SL40ch02:15746351-15746771	N	3.10833051	0.1790509	0	upregulated
SL40ch03:58240713-58241130	N	3.10833051	0.1790509	0	upregulated
SL40ch05:18791391-18791797	N	3.10833051	0.1790509	0	upregulated
SL40ch05:29269999-29270413	N	3.10833051	0.1790509	0	upregulated
SL40ch07:7786647-7787062	N	3.10833051	0.1790509	0	upregulated
SL40ch10:28871027-28871443	N	3.10833051	0.1790509	0	upregulated
SL40ch12:3276624-3277038	N	3.10833051	0.1790509	0	upregulated
SL40ch01:66575304-66575726	N	3.10510054	0.17984307	0	upregulated

SL40ch01:87866792-87867205	N	3.10510054	0.17984307	0	upregulated
SL40ch05:59691706-59692116	N	3.10510054	0.17984307	0	upregulated
SL40ch05:64406419-64406823	N	3.10510054	0.17984307	0	upregulated
SL40ch06:24701207-24701616	N	3.10510054	0.17984307	0	upregulated
SL40ch07:62729241-62729658	N	3.10510054	0.17984307	0	upregulated
SL40ch08:48842577-48842992	N	3.10510054	0.17984307	0	upregulated
SL40ch12:53305862-53306279	24	3.10510054	0.17984307	0	upregulated
SL40ch05:10032061-10032478	N	3.10116021	0.1864054	0	upregulated
SL40ch01:16546456-16546863	N	3.09412349	0.22171446	0	upregulated
SL40ch02:21114832-21115233	N	3.09412349	0.22171446	0	upregulated
SL40ch07:56118951-56119394	N	3.09412349	0.22171446	0	upregulated
SL40ch12:60127813-60128233	N	3.08851595	0.0746272	0	upregulated
SL40ch06:34768013-34768432	23	3.08668001	0.07061986	0	upregulated
SL40ch06:38654281-38654681	N	3.08661137	0.06950505	0	upregulated
SL40ch12:2162868-2163282	N	3.08504253	0.06960841	0	upregulated
SL40ch05:57854659-57855415	24	3.08503407	0.0694586	0	upregulated
SL40ch11:7148719-7149142	N	3.08497935	0.06850348	0	upregulated
SL40ch05:22161651-22162064	N	3.06090494	0.07965114	0	upregulated
SL40ch10:56501109-56501532	N	3.06084612	0.08092266	0	upregulated
SL40ch06:34883082-34883498	24	3.05955768	0.07482231	0	upregulated
SL40ch12:9965857-9966275	N	3.05955768	0.07482231	0	upregulated
SL40ch01:1904807-1905224	N	3.05802111	0.07406308	0	upregulated
SL40ch07:65140036-65140453	N	3.05641586	0.07442685	0	upregulated
SL40ch12:1609820-1610240	N	3.05641586	0.07442685	0	upregulated
SL40ch01:69679703-69680125	N	3.05601559	0.22772355	0	upregulated
SL40ch01:87651115-87651520	N	3.05601559	0.22772355	0	upregulated
SL40ch04:62579074-62579481	N	3.05601559	0.22772355	0	upregulated

SL40ch05:36413706-36414109	N	3.05601559	0.22772355	0	upregulated
SL40ch08:31982340-31982755	N	3.05601559	0.22772355	0	upregulated
SL40ch12:59234978-59235395	N	3.05601559	0.22772355	0	upregulated
SL40ch05:6943183-6943604	N	3.054682	0.07648958	0	upregulated
SL40ch08:50024596-50025005	N	3.054682	0.07648958	0	upregulated
SL40ch01:82275755-82276173	N	3.05013786	0.09610458	0	upregulated
SL40ch02:49043655-49044059	N	3.0297392	0.08243632	0	upregulated
SL40ch04:7098478-7098899	22	3.0297392	0.08243632	0	upregulated
SL40ch09:61945755-61946169	24	3.02842965	0.08069094	0	upregulated
SL40ch05:58343966-58344379	N	3.02665455	0.08170581	0	upregulated
SL40ch08:55350047-55350581	24	3.02645034	0.08288427	0	upregulated
SL40ch08:47989926-47990347	N	3.02641874	0.08306909	0	upregulated
SL40ch01:89175248-89175825	N	3.02433627	0.08583016	0	upregulated
SL40ch07:19368859-19369510	N	3.02433627	0.08583016	0	upregulated
SL40ch09:193436-193857	N	3.01767587	0.10924371	0	upregulated

Supplementary Material 7.7. Table of differentially expressed genes between self-grafted and heterografted conditions: Tomato/RS-1 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Gene ID	baseMean	logFC	pvalue	padj	expression
Solyc01g005300.4	406.78223	-2.1783666	1.68E-14	1.62E-10	downregulated
Solyc01g005560.3	12337.2558	-0.465984	0.00029339	0.01033904	downregulated
Solyc01g005780.1	248.596279	-1.1975498	0.00016173	0.00671123	downregulated
Solyc01g006010.3	491.454924	-0.7069578	0.00066672	0.0184989	downregulated
Solyc01g006100.4	320.694788	-1.0211141	6.72E-06	0.0007102	downregulated
Solyc01g006140.4	157.423867	-1.4176384	5.23E-05	0.00306844	downregulated
Solyc01g006180.4	169.450396	-1.1324199	5.24E-05	0.00306844	downregulated
Solyc01g006370.3	4130.60648	-0.5050248	3.40E-05	0.002356	downregulated
Solyc01g006830.3	9024.18728	-0.4520691	1.26E-05	0.00111476	downregulated
Solyc01g009180.4	1489.14773	-0.4689169	0.00195386	0.03759772	downregulated
Solyc01g009230.4	2057.6563	-0.4592915	0.00072538	0.01946187	downregulated
Solyc01g009380.3	615.596881	-0.6316924	0.00022969	0.00867573	downregulated
Solyc01g010460.4	465.436591	-0.6902145	0.00070603	0.01925807	downregulated

Solyc01g014270.3	1069.11149	-0.5181457	0.00221439	0.04051483	downregulated
Solyc01g044360.4	5720.86167	-0.5862425	7.44E-05	0.00384462	downregulated
Solyc01g057520.4	609.98824	-0.7318728	0.00102772	0.02447664	downregulated
Solyc01g058160.3	134.028638	-1.2837719	0.00010382	0.00489037	downregulated
Solyc01g067530.3	2305.58731	-0.5832238	6.11E-05	0.00337761	downregulated
Solyc01g067750.3	3858.96406	-0.4633756	0.000735	0.01960567	downregulated
Solyc01g067790.3	486.280246	-0.739721	1.58E-05	0.00135236	downregulated
Solyc01g067930.4	769.611312	-0.5698192	0.00140415	0.03007962	downregulated
Solyc01g068240.3	1530.88818	-0.607996	0.00024638	0.00914551	downregulated
Solyc01g079450.3	6427.6943	-0.5570182	6.22E-07	0.0001308	downregulated
Solyc01g079470.4	17076.6723	-0.9904681	0.00018084	0.00734739	downregulated
Solyc01g079500.4	1339.08768	-1.1233562	3.61E-05	0.00245214	downregulated
Solyc01g079520.3	715.824028	-1.0058918	4.43E-06	0.00053519	downregulated
Solyc01g079750.3	259.78482	-0.7357001	0.00276789	0.0467584	downregulated
Solyc01g080300.4	578.234109	-0.6805556	6.04E-05	0.00336449	downregulated
Solyc01g080310.4	698.363828	-0.5264869	0.00218569	0.04034378	downregulated
Solyc01g080840.3	13099.0346	-0.4717135	6.61E-05	0.00354948	downregulated
Solyc01g081320.4	1029.24835	-0.7935754	0.00265766	0.0455239	downregulated
Solyc01g081390.4	2121.0129	-0.7339375	8.11E-06	0.00081648	downregulated
Solyc01g081490.3	7336.42336	-0.5696578	0.00218098	0.04034378	downregulated
Solyc01g086710.4	627.430966	-0.8112068	6.14E-05	0.00337895	downregulated
Solyc01g086750.4	4367.94002	-0.5318053	5.43E-05	0.00314646	downregulated
Solyc01g087670.3	646.034144	-0.5530095	0.00119747	0.027117	downregulated
Solyc01g088080.3	2948.54788	-0.5072665	2.06E-05	0.00164685	downregulated
Solyc01g088170.4	2953.73697	-0.5483649	4.21E-05	0.00266708	downregulated
Solyc01g089870.3	3040.54562	-0.7679702	0.00015851	0.00666377	downregulated
Solyc01g090690.4	880.069462	-0.5842003	0.00118522	0.02693033	downregulated
Solyc01g090940.3	1955.72421	-0.4005672	0.0025217	0.04397405	downregulated
Solyc01g091080.3	606.594059	-0.6091409	0.0010162	0.02437131	downregulated
Solyc01g091460.3	5441.56193	-0.6516154	1.45E-06	0.00023785	downregulated
Solyc01g091640.3	3271.93767	-0.3512347	0.00276083	0.0467285	downregulated
Solyc01g091650.3	2070.06978	-0.4278711	0.00039731	0.01302295	downregulated
Solyc01g091690.3	493.572561	-0.7509676	0.00072067	0.01938394	downregulated
Solyc01g094280.3	946.451066	-0.7517517	0.00186269	0.03656922	downregulated
Solyc01g094290.3	8161.80741	-0.4977625	1.90E-05	0.00155986	downregulated
Solyc01g094720.3	6217.405	-0.448239	0.00244452	0.04325208	downregulated
Solyc01g094830.4	1257.60898	-0.4429772	0.00196962	0.03782571	downregulated
Solyc01g095680.2	1841.96749	-1.0547722	2.49E-07	6.43E-05	downregulated
Solyc01g095740.4	1987.3468	-0.9008395	8.25E-07	0.00016427	downregulated
Solyc01g095900.4	12497.4604	-0.5166358	1.73E-05	0.00145432	downregulated
Solyc01g096010.4	1378.35574	-0.7287732	4.27E-05	0.00267811	downregulated

Solyc01g096060.4	1683.5653	-0.5849589	1.69E-05	0.0014243	downregulated
Solyc01g096400.4	537.799851	-0.7234729	0.00104348	0.02476066	downregulated
Solyc01g096830.3	2418.82816	-0.4238675	0.00111545	0.02586543	downregulated
Solyc01g096900.3	985.83967	-0.7372131	0.00010023	0.00476233	downregulated
Solyc01g096920.3	619.533315	-0.7318708	0.00041294	0.01335417	downregulated
Solyc01g096950.4	317.894116	-0.9524253	1.60E-06	0.00025769	downregulated
Solyc01g097000.3	947.928956	-0.806083	2.67E-05	0.00200477	downregulated
Solyc01g097640.3	548.324084	-0.7759337	8.09E-05	0.00412749	downregulated
Solyc01g098150.3	1215.43061	-1.0417047	0.0005533	0.01628666	downregulated
Solyc01g099460.3	265.502527	-1.1403729	3.72E-05	0.00249186	downregulated
Solyc01g100030.5.1	1107.6437	-0.8395648	0.00118097	0.0268691	downregulated
Solyc01g100570.4	3049.55576	-0.6809132	0.00033528	0.01131578	downregulated
Solyc01g101030.4	651.252023	-0.9582758	0.00016262	0.00672009	downregulated
Solyc01g102370.4	666.094415	-0.8893916	0.00010852	0.005057	downregulated
Solyc01g102550.4	95.2602319	-1.1362751	0.00305724	0.04990796	downregulated
Solyc01g102570.4	913.236278	-0.9060609	2.98E-09	2.40E-06	downregulated
Solyc01g102800.3	1549.09692	-0.5160382	0.00291628	0.04824459	downregulated
Solyc01g103000.3	417.276855	-1.3251053	3.69E-06	0.00047268	downregulated
Solyc01g103010.4	4300.18875	-0.4404662	0.00055033	0.01622392	downregulated
Solyc01g103160.3	1274.28659	-0.7206307	6.85E-06	0.00071686	downregulated
Solyc01g103720.4	1793.65902	-0.5918958	0.00031116	0.01076467	downregulated
Solyc01g104070.3	1231.09628	-0.6044698	0.00059907	0.0170764	downregulated
Solyc01g104490.3	221.816305	-0.8681045	0.00125111	0.02795964	downregulated
Solyc01g105020.3	11696.5473	-0.3717871	0.00292932	0.04841895	downregulated
Solyc01g105990.3	3690.50596	-0.3635856	0.00272177	0.04629408	downregulated
Solyc01g106220.4	5609.38342	-0.7658904	9.69E-14	4.69E-10	downregulated
Solyc01g106963.1	28.2951936	-2.9456331	0.00052163	0.01561669	downregulated
Solyc01g107180.3	3601.39738	-0.3082397	0.00220908	0.04051483	downregulated
Solyc01g107320.3	962.60726	-0.5111319	0.00093772	0.02310125	downregulated
Solyc01g107870.3	47782.9087	-0.3995273	0.00109942	0.02567825	downregulated
Solyc01g108300.3	2263.99341	-0.5596621	0.00054828	0.01618807	downregulated
Solyc01g108330.2	439.772347	-0.8863096	0.001927	0.03726632	downregulated
Solyc01g108600.3	20995.5375	-0.6840084	3.54E-12	1.14E-08	downregulated
Solyc01g108670.4	344.985114	-0.8374731	6.07E-05	0.00336449	downregulated
Solyc01g109500.4	1805.19978	-0.8960553	0.00011074	0.00513555	downregulated
Solyc01g109630.4	713.55627	-0.4533991	0.00140607	0.03007962	downregulated
Solyc01g109790.3	881.470073	-0.523344	0.00129718	0.02857215	downregulated
Solyc01g110120.3	13644.9808	-0.3646951	0.0030656	0.04998797	downregulated
Solyc01g110130.3	3285.12108	-1.2061415	5.62E-06	0.00063135	downregulated
Solyc01g110490.4	1653.066	-0.6619275	8.41E-09	4.40E-06	downregulated
Solyc01g111020.3	6782.04468	-0.8432469	3.83E-10	4.35E-07	downregulated

Solyc01g111420.3	425.517945	-1.0042238	0.00101951	0.02437131	downregulated
Solyc01g111870.3	254.953352	-0.9188904	0.00012814	0.005723	downregulated
Solyc01g111910.3	727.073919	-0.7091991	1.08E-05	0.0009865	downregulated
Solyc01g111990.3	7808.30118	-0.3784169	0.00210356	0.0395561	downregulated
Solyc02g014310.4	4573.58907	-0.7131172	1.32E-08	6.72E-06	downregulated
Solyc02g021560.4	4164.01585	-0.4849411	0.00027563	0.00994469	downregulated
Solyc02g021650.3	3168.45944	-0.3549578	0.00137972	0.02971312	downregulated
Solyc02g022870.4	1308.21909	-0.6595617	6.42E-07	0.0001334	downregulated
Solyc02g032960.2	1831.41052	-0.8781935	5.78E-08	2.23E-05	downregulated
Solyc02g062700.3	503.876462	-0.8787593	0.00057174	0.01665667	downregulated
Solyc02g063090.3	742.929484	-0.6928078	0.00195752	0.03763072	downregulated
Solyc02g064950.3	5648.38439	-0.4985393	0.00163527	0.03357764	downregulated
Solyc02g065300.1	6940.43596	-0.5321254	2.61E-05	0.00197759	downregulated
Solyc02g065500.4	1273.3871	-0.4338314	0.00139775	0.03000127	downregulated
Solyc02g066930.3	355.473489	-0.828331	6.24E-06	0.00068958	downregulated
Solyc02g067010.3	283.463474	-0.6712854	0.00170419	0.03443808	downregulated
Solyc02g067180.3	28086.0527	-0.3950907	0.00264965	0.045427	downregulated
Solyc02g067210.3	3276.52121	-0.3663761	0.00105984	0.02508724	downregulated
Solyc02g068050.4	3578.35462	-0.4739668	0.00129719	0.02857215	downregulated
Solyc02g068140.3	1238.99016	-0.7477036	0.00010393	0.00489037	downregulated
Solyc02g068750.1	1161.37772	-0.4530157	0.00166998	0.03393776	downregulated
Solyc02g069560.3	73.0792044	-1.3317235	0.00093247	0.02302697	downregulated
Solyc02g069570.3	1397.14358	-0.4493437	0.00235018	0.0420834	downregulated
Solyc02g070000.4	2039.57786	-0.5336562	8.85E-06	0.0008737	downregulated
Solyc02g070240.3	395.262217	-0.7126347	6.72E-05	0.0035888	downregulated
Solyc02g070390.3	451.786177	-1.5202293	9.63E-07	0.00017865	downregulated
Solyc02g070780.4	2061.87009	-1.1412825	1.97E-05	0.00161033	downregulated
Solyc02g070810.4	716.607921	-0.8178549	2.71E-05	0.00202461	downregulated
Solyc02g071180.3	3874.42026	-0.5310283	5.94E-05	0.0033406	downregulated
Solyc02g071260.3	4220.9316	-0.461602	2.34E-05	0.00180759	downregulated
Solyc02g071280.3	1037.05701	-0.7077075	1.51E-05	0.00130184	downregulated
Solyc02g071580.4	1836.38643	-0.6477714	3.69E-06	0.00047268	downregulated
Solyc02g071870.4	245.506892	-0.7117032	0.00285342	0.04757822	downregulated
Solyc02g076690.3	3450.47357	-0.7824637	5.64E-05	0.00322887	downregulated
Solyc02g076720.3	4471.66577	-1.0304687	4.97E-11	8.01E-08	downregulated
Solyc02g078360.4	821.285975	-0.539996	0.00029604	0.01035773	downregulated
Solyc02g078390.3	999.62234	-0.5615907	0.00057531	0.01673065	downregulated
Solyc02g078450.3	1734.93379	-0.7651523	0.00010061	0.0047689	downregulated
Solyc02g079770.3	5577.18994	-0.727833	2.34E-05	0.00180759	downregulated
Solyc02g080070.3	2916.10118	-0.4770658	0.00048345	0.0149831	downregulated
Solyc02g080420.4	2998.77187	-0.564058	2.27E-07	6.09E-05	downregulated

Solyc02g080570.3	14973.3724	-0.4775108	2.29E-06	0.00033083	downregulated
Solyc02g080990.2	3659.2573	-0.5108715	0.00030947	0.01072568	downregulated
Solyc02g081060.4	307.963258	-1.1402045	5.68E-05	0.00322887	downregulated
Solyc02g081200.1	2335.60493	-0.6753176	4.22E-05	0.00266708	downregulated
Solyc02g081910.2	995.923143	-0.9731164	1.33E-05	0.00117567	downregulated
Solyc02g082180.3	1618.29502	-1.0341698	0.00033419	0.0112988	downregulated
Solyc02g082220.3	2881.95601	-0.4191568	0.00107737	0.02537794	downregulated
Solyc02g082830.3	1595.79608	-0.5035669	0.00132345	0.0289856	downregulated
Solyc02g084020.3	626.186608	-0.6191459	0.00049815	0.01525062	downregulated
Solyc02g084490.1	1785.13009	-0.548351	0.00108761	0.02552594	downregulated
Solyc02g085340.1	1579.73933	-0.4421586	0.00099121	0.0240556	downregulated
Solyc02g086452.1	752.288328	-1.5637848	5.13E-09	3.31E-06	downregulated
Solyc02g086454.1	1321.72825	-1.2877001	7.57E-08	2.52E-05	downregulated
Solyc02g086456.1	364.975597	-1.4227817	2.25E-06	0.00032979	downregulated
Solyc02g086458.1	7284.38721	-0.9979096	0.00011041	0.0051329	downregulated
Solyc02g086470.3	139.529664	-1.4644149	0.00201549	0.03848204	downregulated
Solyc02g087560.1	1432.56986	-0.9283932	1.51E-06	0.00024548	downregulated
Solyc02g087980.3	377.563196	-0.7983715	0.00092373	0.02290267	downregulated
Solyc02g088780.4	200.052033	-1.1076797	0.00200045	0.03834169	downregulated
Solyc02g089260.4	6699.83595	-0.5377621	0.00125915	0.02802156	downregulated
Solyc02g090230.4	1014.24623	-0.5757847	0.00021544	0.00831597	downregulated
Solyc02g090430.3	2419.18499	-0.5480648	0.0023496	0.0420834	downregulated
Solyc02g090570.4	3025.4418	-0.457455	0.0020374	0.0387426	downregulated
Solyc02g090760.4	6665.66423	-0.5631932	0.00053643	0.01593963	downregulated
Solyc02g091197.1	89.8956649	-1.4763834	0.00042201	0.01351215	downregulated
Solyc02g092800.3	2823.62302	-0.6617905	4.31E-05	0.00268209	downregulated
Solyc02g092980.3	874.403638	-0.7002155	0.00012306	0.00560899	downregulated
Solyc02g093190.3	1136.07842	-0.5350547	0.00183415	0.0362314	downregulated
Solyc02g093300.3	1132.04504	-1.2474321	2.17E-06	0.00032658	downregulated
Solyc02g094100.4	290.464894	-1.0909383	1.16E-06	0.00020142	downregulated
Solyc02g150147.1	2217.05984	-0.5432769	0.00123612	0.02782921	downregulated
Solyc03g005260.3	11689.6348	-0.5056477	0.00277343	0.0467584	downregulated
Solyc03g005730.4	18412.8998	-0.3055943	0.00302269	0.04966505	downregulated
Solyc03g006410.3	2963.00247	-0.8500567	6.71E-06	0.0007102	downregulated
Solyc03g006870.3	11958.6976	-0.4990605	0.00027705	0.00997742	downregulated
Solyc03g007100.3	1383.26017	-0.4713502	0.00125875	0.02802156	downregulated
Solyc03g007260.3	916.491921	-0.6637661	0.00137758	0.02970022	downregulated
Solyc03g007330.3	5457.74115	-0.6069148	2.07E-07	5.79E-05	downregulated
Solyc03g007770.3	3280.15397	-1.0445161	9.91E-06	0.00093958	downregulated
Solyc03g019650.3	1900.22867	-0.6861159	6.82E-05	0.00359367	downregulated
Solyc03g019890.3	2154.8135	-0.5153616	1.94E-06	0.00030002	downregulated

Solyc03g019940.4	5865.55963	-0.4618361	0.00128144	0.02838688	downregulated
Solyc03g019950.3	2783.67462	-0.3986096	0.00264464	0.04538125	downregulated
Solyc03g025540.3	1144.96717	-0.5125026	4.73E-05	0.00289369	downregulated
Solyc03g025610.3	999.520081	-0.8927039	1.43E-05	0.0012455	downregulated
Solyc03g026010.3	369.810641	-0.8249556	5.29E-05	0.00309141	downregulated
Solyc03g026100.1	397.941421	-0.71038	0.00194995	0.03755976	downregulated
Solyc03g026240.4	1742.04976	-0.4095633	0.00090154	0.02255472	downregulated
Solyc03g031600.3	1721.00129	-0.5034658	0.00093351	0.02302697	downregulated
Solyc03g031990.4	904.646608	-1.5349776	2.38E-09	2.05E-06	downregulated
Solyc03g032090.1	580.351501	-1.1132881	0.00027116	0.00985717	downregulated
Solyc03g044590.2	266.184038	-0.8767528	0.00124439	0.02789343	downregulated
Solyc03g046340.3	3154.71951	-0.3910837	0.00166454	0.03388469	downregulated
Solyc03g051900.4	758.622369	-0.7868118	1.86E-07	5.52E-05	downregulated
Solyc03g058190.3	12744.9208	-0.5706459	0.00060122	0.01709148	downregulated
Solyc03g058350.4	3387.25031	-0.5027645	3.83E-05	0.00252369	downregulated
Solyc03g058390.2	1063.82233	-0.5539138	0.00234993	0.0420834	downregulated
Solyc03g059180.4	18314.4538	-0.4531169	6.55E-05	0.00354948	downregulated
Solyc03g062650.3	975.042875	-0.7391436	3.85E-06	0.00048922	downregulated
Solyc03g063560.3	82440.4263	-0.473553	6.39E-06	0.0006904	downregulated
Solyc03g078000.3	9510.12775	-0.3885707	0.00070019	0.01917975	downregulated
Solyc03g080010.3	2673.24802	-0.491343	0.00071416	0.01934327	downregulated
Solyc03g081220.1	1429.38308	-0.5501288	0.00148833	0.03125169	downregulated
Solyc03g081240.3	111.074492	-1.6568247	0.00012053	0.0055237	downregulated
Solyc03g081300.4	1755.6833	-0.6100026	0.00141691	0.0301781	downregulated
Solyc03g082620.4	4639.9545	-0.8466113	3.27E-05	0.00232794	downregulated
Solyc03g082940.3	2723.58197	-0.4530746	0.00277567	0.0467584	downregulated
Solyc03g083090.4	3509.30145	-0.6213161	3.64E-05	0.00245214	downregulated
Solyc03g083250.3	3225.11928	-0.5084938	0.00012771	0.00571724	downregulated
Solyc03g093150.3	235.068454	-0.8018053	0.0012567	0.02802156	downregulated
Solyc03g093240.4	2426.14421	-0.568955	0.002375	0.04244937	downregulated
Solyc03g093480.3	1568.46981	-0.8083645	8.08E-09	4.40E-06	downregulated
Solyc03g096000.3	3532.55663	-0.4034612	0.00029566	0.01035773	downregulated
Solyc03g096830.4	596.536862	-0.9532259	1.91E-07	5.54E-05	downregulated
Solyc03g097000.3	752.419729	-0.6241105	2.45E-05	0.00188063	downregulated
Solyc03g097050.3	568.570278	-0.6348348	0.00154109	0.03211547	downregulated
Solyc03g097160.4	361.904576	-1.0629695	0.00032984	0.01119096	downregulated
Solyc03g097370.4	28807.6608	-0.4271707	0.00100117	0.02417177	downregulated
Solyc03g097570.3	58.8414886	-1.8095868	0.00254634	0.04424401	downregulated
Solyc03g098175.1	25.7598797	-7.0897382	6.87E-05	0.00360257	downregulated
Solyc03g111260.3	2012.15823	-0.8326346	7.23E-08	2.45E-05	downregulated
Solyc03g111850.3	2616.80227	-0.3181353	0.00218551	0.04034378	downregulated

Solyc03g112060.3	10302.0073	-0.5147967	5.04E-05	0.00302381	downregulated
Solyc03g112150.1	22092.3371	-0.4899818	0.00019603	0.00776858	downregulated
Solyc03g112420.3	78.6871713	-1.2643675	0.00267405	0.04572357	downregulated
Solyc03g113060.3	2288.2952	-0.6536186	3.80E-05	0.00252369	downregulated
Solyc03g113630.3	1598.78396	-0.8793641	0.00024786	0.00916527	downregulated
Solyc03g113920.4	8162.23027	-0.6639097	1.88E-05	0.0015528	downregulated
Solyc03g114690.4	445.710795	-1.0589008	0.00043651	0.01388433	downregulated
Solyc03g115510.3	1296.56039	-0.4460716	0.00305601	0.04990796	downregulated
Solyc03g116460.4	490.553899	-1.2177501	9.56E-07	0.00017865	downregulated
Solyc03g116560.1	226.638613	-0.9770817	0.00019726	0.00777476	downregulated
Solyc03g117120.4	1038.27457	-0.6386105	0.00079245	0.02068186	downregulated
Solyc03g118170.3	3949.16679	-0.7926081	6.08E-08	2.26E-05	downregulated
Solyc03g118910.1	2347.95601	-0.5286039	5.68E-05	0.00322887	downregulated
Solyc03g118920.3	4973.61812	-0.6283256	2.54E-06	0.00035921	downregulated
Solyc03g119080.4	7315.48086	-0.3773384	0.001291	0.02853325	downregulated
Solyc03g119450.3	5096.98744	-0.7151588	5.99E-11	8.27E-08	downregulated
Solyc03g119950.1	332.482041	-1.3036994	3.68E-05	0.00246907	downregulated
Solyc03g119970.3	4130.96846	-0.8264597	5.21E-08	2.06E-05	downregulated
Solyc03g120080.4	363.101586	-1.2102115	0.00149187	0.03129203	downregulated
Solyc03g120490.3	1365.6264	-0.4325596	0.00073935	0.01964055	downregulated
Solyc03g121030.2	298.753806	-0.8030304	8.14E-05	0.00413833	downregulated
Solyc03g121070.3	2468.06898	-0.5853989	7.21E-06	0.00074153	downregulated
Solyc03g121910.1	13981.872	-0.3835201	0.00113918	0.02622689	downregulated
Solyc03g122340.3	1235.27073	-0.7613934	9.44E-05	0.00456518	downregulated
Solyc03g122370.4	955.836066	-0.5519945	6.80E-05	0.00359367	downregulated
Solyc03g123530.4	803.011349	-0.7792462	0.00019903	0.00780749	downregulated
Solyc03g123610.4	3572.97379	-0.4513105	3.80E-05	0.00252369	downregulated
Solyc03g123700.4	3346.29642	-0.6925939	5.40E-06	0.00061422	downregulated
Solyc03g123860.4	362.239625	-0.7609251	6.81E-05	0.00359367	downregulated
Solyc04g005180.4	254.276433	-1.1072211	0.00136495	0.02952661	downregulated
Solyc04g005190.2	1211.10152	-0.6814213	0.00021222	0.00822465	downregulated
Solyc04g005555.1	411.888213	-0.9263496	0.00059627	0.01706893	downregulated
Solyc04g007060.4	1174.89433	-0.4185526	0.0006844	0.01885427	downregulated
Solyc04g007150.3	667.033488	-0.7635874	0.00065491	0.01825054	downregulated
Solyc04g007510.4	408.616838	-0.6478041	0.00123811	0.02784172	downregulated
Solyc04g008040.4	7736.88227	-0.4315631	0.00014747	0.006349	downregulated
Solyc04g008620.3	2991.79069	-0.5059173	0.00127113	0.02820793	downregulated
Solyc04g009300.4	1479.60793	-0.4474955	0.00224465	0.04091359	downregulated
Solyc04g010050.4	287.313133	-0.8678585	0.00029732	0.01037893	downregulated
Solyc04g010070.4	3115.63525	-0.3510681	0.00146369	0.03086847	downregulated
Solyc04g010260.3	2260.97692	-0.552084	0.00188063	0.03669332	downregulated

Solyc04g011580.4	1201.13878	-0.4954805	0.00053137	0.01585824	downregulated
Solyc04g012060.3	1590.16428	-0.8145263	0.00203683	0.0387426	downregulated
Solyc04g015440.4	3014.76612	-0.6619409	2.18E-09	2.01E-06	downregulated
Solyc04g015750.3	266660.665	-0.4920544	8.16E-07	0.00016427	downregulated
Solyc04g015830.3	6246.37604	-0.3821803	0.0002673	0.00975328	downregulated
Solyc04g015940.3	403.865744	-1.0582477	3.15E-06	0.00043216	downregulated
Solyc04g015950.3	776.172291	-1.0128362	0.00108152	0.02544461	downregulated
Solyc04g016240.3	1905.79967	-0.3863182	0.00135076	0.02928508	downregulated
Solyc04g016260.3	5998.27929	-0.6395053	2.99E-06	0.00041652	downregulated
Solyc04g045530.4	315.184511	-0.9903002	0.00030058	0.01045481	downregulated
Solyc04g049130.4	2038.65516	-0.4283235	0.00089354	0.0224693	downregulated
Solyc04g049140.4	1114.59681	-0.4514537	0.0005719	0.01665667	downregulated
Solyc04g049380.4	5638.69555	-0.6058603	0.00264234	0.04538125	downregulated
Solyc04g050520.3	1353.69346	-0.8986374	5.06E-07	0.00011646	downregulated
Solyc04g050540.4	1915.78935	-0.7939472	0.00026101	0.00957665	downregulated
Solyc04g051670.3	589.494457	-0.7362845	0.00095823	0.02348686	downregulated
Solyc04g054200.3	1617.39923	-0.4019849	0.00226375	0.0409553	downregulated
Solyc04g054410.3	540.625704	-0.5992654	0.00053822	0.01593963	downregulated
Solyc04g057930.4	2309.76832	-0.4641696	0.00091042	0.02271817	downregulated
Solyc04g058190.3	128.4144	-1.2084634	0.0001336	0.0058586	downregulated
Solyc04g063360.3	2552.68331	-0.6463964	8.36E-05	0.00420104	downregulated
Solyc04g064790.3	1581.84882	-0.4471036	0.00014853	0.00636894	downregulated
Solyc04g071660.3	586.007495	-0.7131744	9.06E-05	0.00445827	downregulated
Solyc04g071990.3	2392.4482	-0.6842753	1.30E-06	0.00022019	downregulated
Solyc04g072260.3	945.732947	-0.8696076	4.18E-06	0.00051848	downregulated
Solyc04g074920.2	434.508413	-0.8588482	0.00182974	0.03618139	downregulated
Solyc04g076090.3	9989.05312	-0.5671989	6.15E-05	0.00337895	downregulated
Solyc04g076320.4	2361.99762	-0.4646744	0.00172826	0.03474301	downregulated
Solyc04g076480.3	971.636334	-0.671809	0.00040887	0.01331335	downregulated
Solyc04g076880.3	5228.17649	-0.6280673	5.13E-05	0.00303104	downregulated
Solyc04g077050.3	1831.6945	-0.5644253	0.00111516	0.02586543	downregulated
Solyc04g077320.2	289.828969	-0.8958191	0.00016206	0.00671123	downregulated
Solyc04g077680.3	1023.98816	-0.5356291	5.10E-05	0.00302573	downregulated
Solyc04g079040.4	2160.91037	-0.4158181	0.00066331	0.01843079	downregulated
Solyc04g079640.3	1440.05633	-0.6340918	0.00213635	0.03982903	downregulated
Solyc04g080200.4	697.255467	-0.9773399	0.0013473	0.0292757	downregulated
Solyc04g080340.3	1841.86655	-0.4221748	0.00087728	0.02223277	downregulated
Solyc04g080730.3	3849.31867	-0.3814242	0.00079723	0.0207784	downregulated
Solyc04g081070.3	3853.30275	-0.4855834	2.17E-05	0.00170567	downregulated
Solyc04g081360.3	431.713627	-1.179923	2.17E-07	5.91E-05	downregulated
Solyc04g081550.3	784.649952	-0.7438505	0.00012617	0.00567455	downregulated

Solyc04g081580.4	853.329879	-0.8087996	0.00089696	0.0224693	downregulated
Solyc04g081675.1	746.44937	-0.7466595	3.34E-05	0.002356	downregulated
Solyc04g081820.3	2998.85701	-0.4212941	0.00015602	0.0066022	downregulated
Solyc04g081970.3	50880.8922	-0.5259919	0.00304657	0.04988793	downregulated
Solyc04g082010.1	9545.11819	-0.9935948	0.00024237	0.00903138	downregulated
Solyc04g082040.3	1136.64307	-0.6728056	0.00021837	0.00836267	downregulated
Solyc04g082250.3	48015.9683	-0.3628117	0.00061692	0.01741702	downregulated
Solyc04g082330.3	965.626518	-0.6753408	0.00091994	0.02286734	downregulated
Solyc04g082700.3	3603.58043	-0.6010454	8.92E-07	0.00017077	downregulated
Solyc04g150161.1	2568.74496	-0.8110963	6.43E-06	0.0006904	downregulated
Solyc05g005280.4	793.643486	-0.7838563	5.84E-05	0.00330102	downregulated
Solyc05g006530.4	1369.01468	-0.5879414	4.01E-05	0.00257907	downregulated
Solyc05g006920.4	2173.95725	-0.5650455	0.00037059	0.01233527	downregulated
Solyc05g006990.3	1148.81265	-0.7631712	0.0008169	0.02120531	downregulated
Solyc05g007070.2	3570.97565	-0.5935375	0.00018282	0.00741225	downregulated
Solyc05g007450.3	163.631172	-1.237475	0.00158858	0.03278714	downregulated
Solyc05g007490.3	1911.90219	-0.4843116	0.00053308	0.01588494	downregulated
Solyc05g008120.4	51.3759814	-1.8817013	0.00047841	0.0148507	downregulated
Solyc05g008200.4	6479.80385	-0.3990194	0.00221375	0.04051483	downregulated
Solyc05g008290.4	4544.73878	-0.7168857	7.30E-07	0.00015022	downregulated
Solyc05g009170.3	36.1135945	-1.9475595	0.00140486	0.03007962	downregulated
Solyc05g009470.4	16669.517	-0.6312921	5.61E-05	0.003228	downregulated
Solyc05g009630.4	817.762228	-0.6905068	1.06E-06	0.00018554	downregulated
Solyc05g010160.3	732.708629	-0.6251217	0.00049526	0.01520281	downregulated
Solyc05g010240.4	824.579792	-1.702345	4.05E-19	7.84E-15	downregulated
Solyc05g010340.3	324.404025	-0.9066586	0.00033419	0.0112988	downregulated
Solyc05g010660.4	633.301356	-0.664814	0.0013076	0.02873605	downregulated
Solyc05g010670.3	11670.701	-0.7024984	0.00031801	0.01093271	downregulated
Solyc05g010700.1	377.460621	-0.6789653	0.00059105	0.01700952	downregulated
Solyc05g010780.1	143.382542	-1.4454484	3.92E-05	0.00254657	downregulated
Solyc05g012100.3	1155.26296	-0.9464666	9.32E-05	0.00452767	downregulated
Solyc05g012200.3	706.133319	-0.9822393	1.19E-05	0.00106957	downregulated
Solyc05g012390.4	1102.99526	-0.7627674	3.29E-05	0.00233122	downregulated
Solyc05g013200.1	205.891	-1.0665866	0.0016373	0.03357764	downregulated
Solyc05g013280.4	2068.1685	-0.3976761	0.00258211	0.04460339	downregulated
Solyc05g013450.4	1272.35646	-0.5036481	0.00276181	0.0467285	downregulated
Solyc05g013740.3	671.852431	-0.4612317	0.0008963	0.0224693	downregulated
Solyc05g013990.3	2937.1786	-0.6514893	3.03E-06	0.00041816	downregulated
Solyc05g014130.3	434.518293	-1.0153319	0.00027879	0.01000287	downregulated
Solyc05g014540.3	377.613901	-0.9436537	0.00286708	0.04765032	downregulated
Solyc05g014690.3	127.006724	-1.8924718	6.95E-09	4.07E-06	downregulated

Solyc05g014790.3	1271.09517	-0.4887032	0.00068656	0.0188566	downregulated
Solyc05g017990.4	2624.39504	-0.4813005	0.00092985	0.0230112	downregulated
Solyc05g026490.3	4465.73375	-0.9994865	5.56E-09	3.47E-06	downregulated
Solyc05g047550.4	2060.49521	-0.5357539	0.00189178	0.03680594	downregulated
Solyc05g047680.4	479.423467	-1.2144664	0.00229303	0.04128949	downregulated
Solyc05g050630.4	2540.77648	-0.9911154	4.37E-06	0.00053154	downregulated
Solyc05g051680.4	1014.96983	-0.5457348	0.00011447	0.00529583	downregulated
Solyc05g052880.4	25.9886648	-2.836343	0.0028066	0.04699299	downregulated
Solyc05g053650.3	3105.00833	-0.4005952	0.00053799	0.01593963	downregulated
Solyc05g054240.3	1018.94262	-0.4504915	0.00086573	0.02208536	downregulated
Solyc05g054630.4	985.973726	-0.4679366	0.00187887	0.03669332	downregulated
Solyc05g054640.4	4585.38758	-0.5317411	9.99E-07	0.00018031	downregulated
Solyc05g054960.4	928.953663	-0.6400572	0.00031595	0.01089169	downregulated
Solyc05g055100.2	497.1871	-0.7686512	2.18E-06	0.00032658	downregulated
Solyc05g056310.3	3097.23391	-0.4827872	0.00108484	0.02549168	downregulated
Solyc05g056350.3	5956.53193	-0.4610751	5.72E-05	0.00324399	downregulated
Solyc06g005060.3	25578.647	-0.3727431	0.00075066	0.01983212	downregulated
Solyc06g005970.2	555.4641	-0.6036288	0.00071853	0.01935331	downregulated
Solyc06g006080.3	12600.7669	-1.106945	5.62E-12	1.36E-08	downregulated
Solyc06g006100.3	1321.34961	-0.5599745	0.00021769	0.00835312	downregulated
Solyc06g008700.3	554.610524	-0.7810291	0.00251271	0.04385679	downregulated
Solyc06g009190.4	1818.87109	-0.6086614	0.00272775	0.04634091	downregulated
Solyc06g017970.4	2334.75507	-0.5500561	0.00017947	0.00731285	downregulated
Solyc06g018110.3	119.329364	-1.2823495	0.00047675	0.01482308	downregulated
Solyc06g019200.4	3018.43299	-0.4120881	0.0005115	0.01546096	downregulated
Solyc06g034290.3	923.787385	-0.7770852	0.00099236	0.0240556	downregulated
Solyc06g036580.4	1332.38698	-0.5326037	0.00026146	0.00957665	downregulated
Solyc06g050620.3	3866.23567	-0.4062616	0.00244274	0.04325208	downregulated
Solyc06g051080.4	8985.30045	-0.5661375	5.31E-07	0.00011812	downregulated
Solyc06g052030.3	2316.48182	-0.3746471	0.00258316	0.04460339	downregulated
Solyc06g054560.3	2801.30289	-0.3588571	0.00133517	0.02912198	downregulated
Solyc06g060620.4	1953.29655	-0.4568828	0.00135038	0.02928508	downregulated
Solyc06g062610.2	42.7742078	-2.1352963	0.00242767	0.04308979	downregulated
Solyc06g062840.4	2125.59392	-0.5747336	0.00074648	0.01977561	downregulated
Solyc06g063270.4	145.855273	-1.1354766	0.00045431	0.01426276	downregulated
Solyc06g065520.3	3240.15639	-0.4419068	9.82E-05	0.00470829	downregulated
Solyc06g065540.3	3787.0468	-0.5579332	1.98E-05	0.00161279	downregulated
Solyc06g065650.3	1177.2096	-0.7863148	8.74E-06	0.00087099	downregulated
Solyc06g065680.3	826.133597	-0.786674	0.00206538	0.03908263	downregulated
Solyc06g065800.3	167.021443	-0.8112514	0.00153507	0.03202442	downregulated
Solyc06g068620.3	1055.33923	-0.5192508	0.00211116	0.03960006	downregulated

Solyc06g069450.4	939.31033	-0.4840544	0.00280179	0.04698588	downregulated
Solyc06g071100.4	41785.8258	-0.4286529	6.74E-05	0.00359047	downregulated
Solyc06g073330.4	3461.68572	-0.5791267	4.95E-05	0.00299245	downregulated
Solyc06g075340.4	3482.33529	-0.766169	1.12E-05	0.00101792	downregulated
Solyc06g076360.4	5734.41346	-0.5311249	3.08E-05	0.00221655	downregulated
Solyc06g076850.3	11731.0085	-0.5633844	4.48E-06	0.00053767	downregulated
Solyc06g076860.4	431.456423	-1.2361527	0.00017538	0.00718578	downregulated
Solyc06g082050.2	42.6822494	-1.8689314	0.00305812	0.04990796	downregulated
Solyc06g082100.4	4720.99258	-0.4719609	3.21E-05	0.00230068	downregulated
Solyc06g082910.3	4518.97359	-0.7223658	2.97E-08	1.27E-05	downregulated
Solyc06g083730.3	642.397612	-0.6060836	0.00298058	0.04909829	downregulated
Solyc06g084210.3	4180.99592	-0.4325157	0.00176246	0.03524741	downregulated
Solyc06g084250.4	752.356455	-0.5961557	0.00095049	0.02337557	downregulated
Solyc07g005020.3	1728.36832	-1.2976728	7.02E-06	0.00072972	downregulated
Solyc07g005810.3	9922.6897	-0.5343207	0.00027423	0.00993151	downregulated
Solyc07g005930.4	1050.88524	-1.7285085	4.24E-11	7.46E-08	downregulated
Solyc07g005950.4	1999.79963	-0.7705832	5.89E-08	2.23E-05	downregulated
Solyc07g006030.4	33496.6661	-0.6579361	1.76E-08	8.29E-06	downregulated
Solyc07g006050.3	218.467861	-1.0899164	5.65E-05	0.00322887	downregulated
Solyc07g007210.3	2832.36838	-0.3690081	0.00075867	0.02001616	downregulated
Solyc07g007390.3	3376.51024	-0.5151254	5.52E-06	0.00062395	downregulated
Solyc07g007600.3	68109.7386	-0.6052465	1.84E-06	0.00028763	downregulated
Solyc07g007650.3	1893.86425	-0.5084937	0.0010954	0.02561545	downregulated
Solyc07g007690.4	1486.07374	-0.4012568	0.00050546	0.01532156	downregulated
Solyc07g008160.3	2140.85581	-0.4686588	0.00269275	0.04599101	downregulated
Solyc07g008540.3	5681.09669	-0.7392597	4.23E-05	0.00266708	downregulated
Solyc07g008880.3	10664.5434	-0.4248758	0.00064234	0.01797727	downregulated
Solyc07g014590.4	1120.76883	-0.7625514	6.62E-05	0.00354948	downregulated
Solyc07g015980.4	469.821059	-0.5357124	0.0021296	0.03975314	downregulated
Solyc07g017760.1	2089.22315	-0.7507039	0.00015637	0.00660275	downregulated
Solyc07g018360.3	40094.5298	-0.6392695	0.00012172	0.00556473	downregulated
Solyc07g021120.3	556.029329	-0.6760094	0.00095984	0.02349657	downregulated
Solyc07g024000.3	1351.83648	-0.7542494	4.67E-09	3.23E-06	downregulated
Solyc07g025210.2	397.201547	-0.7405188	0.00252966	0.04403338	downregulated
Solyc07g032100.3	3551.28646	-0.3570571	0.00150191	0.03146842	downregulated
Solyc07g039200.4	1421.49218	-0.5102713	0.00169799	0.03434881	downregulated
Solyc07g039500.4	2220.89283	-0.4679381	0.00044206	0.01399189	downregulated
Solyc07g039550.4	1035.79483	-0.4553324	0.00269444	0.04599101	downregulated
Solyc07g041870.3	1365.8584	-0.7042558	0.00272932	0.04634091	downregulated
Solyc07g041900.3	1817.02958	-0.741111	0.0014249	0.0303147	downregulated
Solyc07g041930.3	869.089239	-0.4989699	0.00224972	0.04093594	downregulated

Solyc07g042030.2	423.534556	-0.7400907	0.00079152	0.02068186	downregulated
Solyc07g042260.4	2110.44315	-0.4036489	0.00032152	0.01099755	downregulated
Solyc07g042380.4	1461.63807	-0.5996856	0.0002982	0.01039086	downregulated
Solyc07g044760.3	2466.38205	-0.541204	9.35E-07	0.00017737	downregulated
Solyc07g044930.3	753.834643	-0.5725121	0.00121182	0.02734819	downregulated
Solyc07g045170.3	686.843689	-0.5850752	0.00020405	0.00795577	downregulated
Solyc07g045210.1	3609.77351	-0.440869	0.00066313	0.01843079	downregulated
Solyc07g045470.3	579.423249	-0.6380868	0.00147489	0.03107073	downregulated
Solyc07g045540.4	8577.33812	-0.4044058	0.00099387	0.0240556	downregulated
Solyc07g047670.3	5389.55198	-0.4398165	0.00129074	0.02853325	downregulated
Solyc07g047860.4	1013.62728	-0.5799071	0.00040822	0.01331335	downregulated
Solyc07g048100.3	80.7704471	-1.3887457	0.00041993	0.01346765	downregulated
Solyc07g052350.3	13443.4901	-0.8035306	3.02E-11	5.84E-08	downregulated
Solyc07g052590.1	392.076035	-1.0269792	0.00087603	0.02223277	downregulated
Solyc07g052730.3	177.128919	-0.9779271	0.00059753	0.01706893	downregulated
Solyc07g053470.4	757.044705	-0.7722039	4.92E-05	0.00299245	downregulated
Solyc07g053650.4	7514.63431	-0.3845258	0.0004949	0.01520281	downregulated
Solyc07g053980.3	2822.36084	-0.5321866	2.82E-05	0.00205293	downregulated
Solyc07g054210.3	52698.5174	-0.4296893	0.00179353	0.03569563	downregulated
Solyc07g054220.1	299.067849	-0.8568581	0.00029618	0.01035773	downregulated
Solyc07g054460.4	421.646764	-1.3603343	1.02E-06	0.00018031	downregulated
Solyc07g054480.3	498.69537	-1.3867718	1.69E-09	1.65E-06	downregulated
Solyc07g054820.4	14749.56	-0.4664436	7.65E-05	0.00394594	downregulated
Solyc07g055050.3	6165.05677	-0.9500789	0.00028998	0.01025405	downregulated
Solyc07g055720.4	158.796248	-2.489359	3.66E-08	1.54E-05	downregulated
Solyc07g056020.3	39327.2876	-0.4099578	0.0004127	0.01335417	downregulated
Solyc07g056050.1	4379.82588	-0.3098694	0.00230988	0.04151556	downregulated
Solyc07g056570.1	3365.70247	-0.7046643	0.00034953	0.01169483	downregulated
Solyc07g062100.4	105.641369	-1.3864804	0.00277479	0.0467584	downregulated
Solyc07g062440.1	529.041842	-0.7567847	0.00044744	0.01411577	downregulated
Solyc07g063650.4	1359.89055	-0.4432174	0.00070229	0.01920414	downregulated
Solyc07g064160.3	162828.061	-0.7573582	1.59E-07	4.86E-05	downregulated
Solyc07g064330.3	2218.87853	-0.5357494	0.00049269	0.01519386	downregulated
Solyc07g065320.4	3912.84711	-0.4498363	0.00095127	0.02337557	downregulated
Solyc07g065600.3	154.423047	-1.0864354	0.00085722	0.02198635	downregulated
Solyc07g065630.4	8584.90441	-0.5458621	0.00227173	0.04101512	downregulated
Solyc07g066410.4	536.047969	-0.7802442	0.0009937	0.0240556	downregulated
Solyc07g066470.3	18333.3168	-0.5119141	0.00219016	0.04037701	downregulated
Solyc07g150114.1	102.549848	-1.862342	0.00205614	0.03902094	downregulated
Solyc08g005960.2	6766.5694	-0.9778662	9.15E-05	0.00448562	downregulated
Solyc08g006770.3	659.890943	-0.7893805	0.00082937	0.02141415	downregulated

Solyc08g006880.3	7231.24709	-0.433457	0.00031827	0.01093271	downregulated
Solyc08g006890.3	74289.0916	-0.357557	0.00087857	0.02223277	downregulated
Solyc08g006990.3	1372.73325	-0.5549674	0.00194462	0.03749453	downregulated
Solyc08g007060.4	292.936533	-1.2044708	2.95E-05	0.00213134	downregulated
Solyc08g007790.3	967.23881	-0.6439571	0.00046962	0.01462481	downregulated
Solyc08g007950.3	4369.26313	-0.4116911	8.57E-05	0.00427565	downregulated
Solyc08g008170.4	1030.42799	-0.5619549	0.00022844	0.00864557	downregulated
Solyc08g013850.1	425.494076	-0.9236145	3.92E-06	0.00049218	downregulated
Solyc08g013900.3	1055.56692	-0.9258103	4.10E-09	3.05E-06	downregulated
Solyc08g013940.3	251.297359	-1.0367436	0.00015812	0.00666195	downregulated
Solyc08g016060.1	185.627365	-0.8901569	0.00098592	0.02398318	downregulated
Solyc08g042050.3	16114.3883	-0.5769392	0.0005856	0.01687756	downregulated
Solyc08g045780.4	2605.72506	-0.4512033	0.00012684	0.00569134	downregulated
Solyc08g045850.3	2873.0013	-0.4177367	0.00043954	0.01393472	downregulated
Solyc08g048390.3	1635.25574	-0.5212752	2.44E-05	0.00188063	downregulated
Solyc08g062910.4	10400.1301	-0.5861298	5.04E-05	0.00302381	downregulated
Solyc08g062920.3	11589.0946	-0.6151889	0.00041686	0.01343611	downregulated
Solyc08g062960.4	132.574984	-1.3640597	0.00012617	0.00567455	downregulated
Solyc08g063090.2	2506.27417	-1.1591956	3.80E-07	9.41E-05	downregulated
Solyc08g066010.2	364.127379	-0.7614664	0.00056883	0.01664247	downregulated
Solyc08g066120.4	1596.33525	-0.8513475	1.38E-05	0.00121553	downregulated
Solyc08g067050.3	689.426787	-0.7608565	0.00189499	0.03683131	downregulated
Solyc08g067150.4	619.001922	-0.9480534	3.87E-07	9.47E-05	downregulated
Solyc08g067790.4	4016.7013	-0.5092365	3.38E-05	0.002356	downregulated
Solyc08g067840.3	2774.18271	-0.680049	0.00056245	0.01653083	downregulated
Solyc08g067870.2	1745.39658	-1.0095498	1.01E-06	0.00018031	downregulated
Solyc08g068310.3	1292.35089	-0.4643523	0.00049339	0.01519386	downregulated
Solyc08g068920.4	240.710984	-0.8329115	0.00144101	0.0306077	downregulated
Solyc08g069010.4	5610.78879	-0.4874618	5.87E-05	0.00330936	downregulated
Solyc08g074370.4	1737.16764	-0.4042179	0.00259842	0.04474704	downregulated
Solyc08g074520.2	555.754843	-0.7738778	0.00197974	0.03798232	downregulated
Solyc08g074560.3	6428.37241	-0.2810816	0.00249401	0.04368804	downregulated
Solyc08g075500.4	940.11725	-1.3668974	2.29E-06	0.00033083	downregulated
Solyc08g075710.3	1189.54243	-0.5070512	0.00019684	0.00777476	downregulated
Solyc08g076030.3	3679.32976	-0.3939167	0.00028179	0.01008731	downregulated
Solyc08g076200.4	2077.71122	-0.4935834	0.00139195	0.02994315	downregulated
Solyc08g076220.3	227734.846	-0.410766	0.00050273	0.01526417	downregulated
Solyc08g076290.3	81503.3379	-0.4143227	0.00018493	0.00748175	downregulated
Solyc08g076910.3	538.185839	-0.7895652	2.46E-06	0.00035095	downregulated
Solyc08g077120.2	1017.59807	-1.5190851	1.02E-05	0.00095923	downregulated
Solyc08g077130.2	80.3074029	-2.2836769	0.00017285	0.00710777	downregulated

Solyc08g077990.3	286.256756	-0.8810055	0.00037997	0.01258257	downregulated
Solyc08g078150.1	606.963674	-0.5717826	0.001661	0.03384842	downregulated
Solyc08g078320.3	1558.66228	-0.4688267	0.00089583	0.0224693	downregulated
Solyc08g078440.3	346.32214	-0.9141662	2.95E-05	0.00213134	downregulated
Solyc08g078900.1	3189.84391	-0.8316555	0.00028892	0.01025205	downregulated
Solyc08g079180.3	31285.794	-0.6960567	3.55E-05	0.00243256	downregulated
Solyc08g079280.3	13359.5542	-0.4986046	0.00012881	0.00572727	downregulated
Solyc08g079880.2	2641.2703	-0.6516375	0.00087877	0.02223277	downregulated
Solyc08g079890.2	3398.93777	-0.6296817	0.00139574	0.02999134	downregulated
Solyc08g080180.1	566.693565	-0.5886016	0.0025071	0.04385679	downregulated
Solyc08g080200.4	3587.84252	-0.3938678	0.00229561	0.0412975	downregulated
Solyc08g080250.4	984.24576	-0.6768805	3.27E-05	0.00232794	downregulated
Solyc08g080550.1	2373.15936	-0.6135059	0.00287681	0.04771417	downregulated
Solyc08g081250.4	31936.7787	-0.5172711	0.00021769	0.00835312	downregulated
Solyc08g081900.4	1785.23921	-0.4057933	0.00067018	0.01856831	downregulated
Solyc08g082250.3	11233.1109	-0.4386396	7.19E-05	0.00373816	downregulated
Solyc08g082530.4	4534.21202	-0.5313729	0.00040892	0.01331335	downregulated
Solyc08g082640.2	4419.03038	-0.7060434	1.31E-06	0.00022044	downregulated
Solyc08g082650.2	262.650467	-1.1854787	0.00058463	0.01687488	downregulated
Solyc08g083030.4	572.416775	-0.6382357	0.00076484	0.02014297	downregulated
Solyc08g083140.4	1908.53387	-0.6851395	0.00226388	0.0409553	downregulated
Solyc09g005010.4	1035.46103	-0.6800764	0.00046886	0.01462451	downregulated
Solyc09g007250.4	9836.71678	-0.4966484	0.00212926	0.03975314	downregulated
Solyc09g007320.4	1723.64086	-0.9489386	0.0001047	0.00490279	downregulated
Solyc09g007430.1	221.054724	-1.5366474	4.51E-06	0.00053807	downregulated
Solyc09g009190.4	8887.09688	-0.5764187	1.03E-05	0.00096008	downregulated
Solyc09g010870.4	4325.85011	-0.463884	5.55E-05	0.00320413	downregulated
Solyc09g014210.3	69.7270201	-1.4286816	0.00073644	0.01961707	downregulated
Solyc09g015840.4	953.524011	-0.5820944	0.00051777	0.01554838	downregulated
Solyc09g015930.3	3050.03005	-0.4183425	0.00082702	0.02138213	downregulated
Solyc09g018450.3	5490.66044	-0.3609565	0.00037587	0.01246804	downregulated
Solyc09g018720.3	38.3729923	-2.1916212	0.00283729	0.04742467	downregulated
Solyc09g031650.3	2741.88997	-0.5818465	0.00084186	0.02167873	downregulated
Solyc09g031780.3	5959.1158	-0.7378402	3.33E-06	0.000444	downregulated
Solyc09g042740.4	990.921578	-0.5503453	0.00031278	0.01080166	downregulated
Solyc09g055260.4	1836.16123	-0.4215744	0.00116048	0.02652071	downregulated
Solyc09g055350.3	2025.64193	-0.5203033	0.00020996	0.00815352	downregulated
Solyc09g056390.1	1331.69429	-0.7789986	0.00219331	0.04039144	downregulated
Solyc09g064800.3	4592.2829	-0.4715436	4.66E-05	0.00286192	downregulated
Solyc09g064890.4	433.802627	-0.8197553	0.00085871	0.02199538	downregulated
Solyc09g065620.3	807.344672	-1.0345887	0.00109374	0.02560761	downregulated

Solyc09g065840.3	833.989456	-1.1662108	6.29E-09	3.80E-06	downregulated
Solyc09g065900.3	9671.98577	-0.3337454	0.00052166	0.01561669	downregulated
Solyc09g066290.3	148.819797	-1.5213023	0.00046578	0.01455207	downregulated
Solyc09g074610.3	2695.28797	-0.4631919	0.00302776	0.04970616	downregulated
Solyc09g074940.3	8228.11225	-0.7259502	0.00062294	0.01752541	downregulated
Solyc09g074990.4	450.07546	-0.7674186	1.03E-05	0.00095923	downregulated
Solyc09g075060.3	1527.26545	-0.6562753	6.05E-05	0.00336449	downregulated
Solyc09g075390.4	7591.62279	-0.5069227	1.47E-05	0.00127732	downregulated
Solyc09g075640.4	664.462003	-0.5934982	8.20E-05	0.00415267	downregulated
Solyc09g075860.3	2096.59835	-0.4752291	0.00034212	0.01148653	downregulated
Solyc09g082060.3	10421.7983	-0.5793621	3.68E-06	0.00047268	downregulated
Solyc09g082500.4	3302.50124	-0.8857232	4.15E-08	1.71E-05	downregulated
Solyc09g083110.3	346.193704	-0.943177	0.00023726	0.00889219	downregulated
Solyc09g083350.3	2164.39794	-0.79156	1.21E-09	1.30E-06	downregulated
Solyc09g090340.3	305.29911	-0.9468267	0.00048603	0.01501483	downregulated
Solyc09g090420.4	1748.86958	-0.4683781	6.45E-05	0.00352174	downregulated
Solyc09g091050.4	638.770179	-0.6865966	0.00185644	0.036512	downregulated
Solyc09g091280.4	2201.49545	-0.7821113	1.71E-09	1.65E-06	downregulated
Solyc09g091660.3	4034.14712	-0.7348035	6.86E-05	0.00360257	downregulated
Solyc09g092240.3	731.04855	-1.0491306	2.69E-08	1.21E-05	downregulated
Solyc09g092390.2	10588.5629	-0.5750176	0.00259466	0.04473489	downregulated
Solyc09g098240.4	3418.86355	-0.4658256	0.00027841	0.01000287	downregulated
Solyc09g098260.3	1484.26385	-0.4927859	0.00058086	0.01679104	downregulated
Solyc10g005030.4	5797.18278	-0.339512	0.00219512	0.04039144	downregulated
Solyc10g005125.1	615.729087	-0.9206849	0.00012883	0.00572727	downregulated
Solyc10g005790.3	385.133548	-0.9929624	3.63E-05	0.00245214	downregulated
Solyc10g005920.4	2024.09909	-0.4067052	0.00019505	0.00774571	downregulated
Solyc10g007180.2	2592.18286	-0.5204432	0.00074773	0.0197816	downregulated
Solyc10g007300.2	119.338114	-1.4417615	0.00120025	0.02714814	downregulated
Solyc10g007400.4	374.780486	-0.864009	0.00110729	0.02579983	downregulated
Solyc10g008510.3	236.051206	-1.2748909	4.57E-06	0.00053999	downregulated
Solyc10g008660.2	2675.30031	-0.5847233	0.00216944	0.04030245	downregulated
Solyc10g011690.3	571.101129	-0.7752993	0.00118644	0.02693033	downregulated
Solyc10g012030.4	2073.98891	-0.6369414	3.92E-05	0.00254657	downregulated
Solyc10g018300.3	117199.408	-0.4417482	9.92E-05	0.00472654	downregulated
Solyc10g039190.2	892.444419	-0.6256235	0.00100435	0.02421838	downregulated
Solyc10g045630.2	1008.65102	-0.6157268	0.00017311	0.00710777	downregulated
Solyc10g047050.2	2956.51481	-0.4908415	0.00025637	0.0094438	downregulated
Solyc10g047120.2	337.657335	-1.1241927	0.00104771	0.02483055	downregulated
Solyc10g051200.2	3812.42055	-0.5481097	2.66E-06	0.00037318	downregulated
Solyc10g051377.1	6666.84932	-0.51755	7.85E-07	0.00015977	downregulated

Solyc10g054860.2	389.040142	-1.2018675	5.81E-07	0.00012494	downregulated
Solyc10g062220.2	134.227055	-0.8755765	0.00279486	0.04698588	downregulated
Solyc10g078370.2	197.553638	-0.8738499	0.00250945	0.04385679	downregulated
Solyc10g078530.2	5463.24724	-0.2862075	0.00256708	0.04448449	downregulated
Solyc10g078860.2	238.784807	-1.1201063	0.00010441	0.00490075	downregulated
Solyc10g079010.3	2976.74844	-0.3586295	0.00191628	0.03709595	downregulated
Solyc10g079840.2	349.870406	-0.8792554	0.00012553	0.00567455	downregulated
Solyc10g079850.2	1354.11914	-0.5015947	0.00102673	0.02447664	downregulated
Solyc10g080040.3	1998.62965	-0.8444375	0.00210019	0.03954773	downregulated
Solyc10g080420.3	3503.3341	-0.4521388	0.00032379	0.01102429	downregulated
Solyc10g081050.1	819.628159	-0.4909414	0.00259541	0.04473489	downregulated
Solyc10g081470.2	4549.08688	-0.6199092	1.98E-08	9.12E-06	downregulated
Solyc10g083110.3	655.601356	-0.6796025	0.00193443	0.03737254	downregulated
Solyc10g083280.4	176.729315	-1.0302419	0.00016086	0.00671123	downregulated
Solyc10g083300.2	2317.74546	-0.5785872	0.00028219	0.01008731	downregulated
Solyc10g084620.3	429.569864	-0.6961721	0.0017941	0.03569563	downregulated
Solyc10g085550.3	10304.4046	-0.786514	0.00014774	0.006349	downregulated
Solyc10g086430.3	105.907497	-1.1278715	0.00209815	0.03954773	downregulated
Solyc11g005690.3	236.660412	-0.7546678	0.00210553	0.0395561	downregulated
Solyc11g006060.2	11540.5412	-0.5969471	3.85E-05	0.00252369	downregulated
Solyc11g006200.2	272.351037	-1.5556884	5.55E-11	8.26E-08	downregulated
Solyc11g006340.2	1577.55956	-0.4087405	0.00020374	0.00795577	downregulated
Solyc11g006390.2	2264.44463	-0.5462928	6.01E-05	0.00335829	downregulated
Solyc11g006660.3	1860.61863	-0.3591408	0.00218115	0.04034378	downregulated
Solyc11g006680.3	3170.362	-0.5567425	4.95E-05	0.00299245	downregulated
Solyc11g007850.2	500.859572	-0.9389493	0.00059731	0.01706893	downregulated
Solyc11g008050.1	343.238934	-0.9740487	6.39E-06	0.0006904	downregulated
Solyc11g008110.1	339.913864	-0.8456109	0.00111715	0.02587381	downregulated
Solyc11g008670.2	983.422596	-0.5292678	0.00011978	0.00550201	downregulated
Solyc11g008870.2	10018.614	-0.4049568	0.00207852	0.03929279	downregulated
Solyc11g010480.2	13619.91	-0.7746435	0.00061787	0.01741824	downregulated
Solyc11g011370.2	161.788236	-1.0988487	0.000341	0.01146872	downregulated
Solyc11g011420.3	1224.69633	-0.4189487	0.00257467	0.0445413	downregulated
Solyc11g011460.2	555.238445	-0.5657871	0.0018822	0.03669332	downregulated
Solyc11g012140.2	4031.73293	-0.4152017	4.60E-05	0.00284095	downregulated
Solyc11g012700.2	7062.30384	-0.5955286	0.00187074	0.03661768	downregulated
Solyc11g012850.2	17864.4469	-0.4555522	0.00076884	0.02020197	downregulated
Solyc11g013030.2	2022.07504	-0.6292688	5.36E-05	0.00311943	downregulated
Solyc11g017370.3	553.42608	-0.6413975	0.00144183	0.0306077	downregulated
Solyc11g019960.2	358.509208	-0.712035	0.0015348	0.03202442	downregulated
Solyc11g020300.2	4100.48282	-0.5646918	3.38E-05	0.002356	downregulated

Solyc11g020780.2	1882.43168	-0.6776538	0.00018558	0.00749241	downregulated
Solyc11g027840.2	264.816557	-1.0554976	1.74E-05	0.00145863	downregulated
Solyc11g030600.3	2214.12107	-0.9568042	2.01E-07	5.71E-05	downregulated
Solyc11g039830.2	4557.1611	-0.5069056	0.00086006	0.02200014	downregulated
Solyc11g040060.3	110.018543	-1.062344	0.00173143	0.0347707	downregulated
Solyc11g040120.3	5039.11431	-0.8345889	0.00088651	0.0223814	downregulated
Solyc11g040390.2	1671.8536	-0.5844096	0.00041975	0.01346765	downregulated
Solyc11g044540.2	3033.02597	-0.5040559	0.00127076	0.02820793	downregulated
Solyc11g044933.1	427.264811	-0.9061617	0.00077133	0.02023991	downregulated
Solyc11g045110.3	746.337664	-0.8454716	0.00155263	0.03222556	downregulated
Solyc11g065870.3	2429.9285	-0.5881685	4.00E-05	0.00257907	downregulated
Solyc11g066020.2	2415.83	-0.443691	0.00156469	0.03236319	downregulated
Solyc11g066780.3	1515.31573	-0.6992529	9.09E-08	2.98E-05	downregulated
Solyc11g066850.3	340.866659	-1.0001917	0.00013012	0.00575842	downregulated
Solyc11g067110.2	138.549698	-1.7243295	4.24E-07	9.99E-05	downregulated
Solyc11g067140.2	774.789759	-1.3091418	2.55E-13	9.85E-10	downregulated
Solyc11g071460.2	1574.59963	-1.0867409	2.86E-11	5.84E-08	downregulated
Solyc11g071620.3	1916.80969	-0.5768653	0.00027109	0.00985717	downregulated
Solyc11g071640.3	1662.36615	-0.5960447	4.86E-05	0.00296662	downregulated
Solyc12g005250.2	102.24135	-1.0787376	0.00175804	0.03519547	downregulated
Solyc12g005400.3	5768.34577	-0.7158143	1.66E-05	0.0014161	downregulated
Solyc12g006320.3	10372.0265	-0.5744099	0.00010787	0.00503872	downregulated
Solyc12g006420.2	1149.02034	-0.5846744	0.002237	0.04081266	downregulated
Solyc12g008360.2	3285.52355	-0.3952341	0.00041115	0.01334112	downregulated
Solyc12g010910.2	2357.90863	-0.5112881	0.00129679	0.02857215	downregulated
Solyc12g014140.3	6836.19996	-0.6842789	0.00016862	0.00695306	downregulated
Solyc12g014380.3	1814.83632	-0.4403275	0.00165499	0.03383288	downregulated
Solyc12g015710.2	1069.43523	-0.8126299	5.38E-07	0.00011833	downregulated
Solyc12g017260.2	2706.67371	-0.5115852	2.82E-05	0.00205293	downregulated
Solyc12g017420.2	3699.68534	-0.3992638	8.05E-05	0.00411644	downregulated
Solyc12g017510.2	2306.11095	-0.5527291	0.00190458	0.03698054	downregulated
Solyc12g017830.3	3551.78805	-0.377041	0.00246717	0.04355207	downregulated
Solyc12g019100.2	595.367619	-0.9699872	2.77E-05	0.00204053	downregulated
Solyc12g019110.3	3233.16225	-0.6047288	0.00257496	0.0445413	downregulated
Solyc12g027800.1	276.20172	-0.7525289	0.00304145	0.04988793	downregulated
Solyc12g042060.3	57216.7272	-0.3574067	0.00033606	0.01132227	downregulated
Solyc12g042950.2	2793.06087	-1.3721388	2.43E-09	2.05E-06	downregulated
Solyc12g043110.2	6240.19704	-0.4249892	0.00238757	0.04251668	downregulated
Solyc12g043120.2	4268.35304	-0.4673602	0.00137539	0.02968604	downregulated
Solyc12g044400.3	5288.39875	-0.5003823	4.74E-06	0.00055236	downregulated
Solyc12g049440.3	114.337879	-1.3549184	0.00021597	0.00831994	downregulated

Solyc12g055970.3	1851.06913	-0.8044228	2.17E-05	0.00170567	downregulated
Solyc12g056410.2	2452.37419	-0.5193397	0.0013357	0.02912198	downregulated
Solyc12g056650.2	5038.14954	-1.0062158	6.26E-14	4.04E-10	downregulated
Solyc12g056740.2	3052.12909	-0.4262873	0.00180342	0.03580742	downregulated
Solyc12g062250.2	3770.64786	-0.5053083	0.00048557	0.01501483	downregulated
Solyc12g070270.2	3586.45354	-0.5957132	3.39E-05	0.002356	downregulated
Solyc12g095760.2	5365.11559	-0.4567073	0.00111509	0.02586543	downregulated
Solyc12g095910.2	4538.93064	-0.6827245	2.13E-07	5.88E-05	downregulated
Solyc12g095960.3	15086.2236	-0.5534572	0.00073839	0.01964055	downregulated
Solyc12g096990.2	452.07181	-0.7838094	3.57E-05	0.00243836	downregulated
Solyc12g098530.2	247.600151	-0.7015293	0.00134325	0.0292205	downregulated
Solyc12g098830.2	1247.62044	-0.4647897	0.00032187	0.01099755	downregulated
Solyc12g099600.2	1794.89666	-0.8080415	3.17E-06	0.00043236	downregulated
Solyc12g100330.2	907.689524	-0.9360976	4.04E-05	0.00259019	downregulated
Solyc00g500039.1	27.9414651	5.16644835	8.56E-07	0.00016712	upregulated
Solyc00g500259.1	254.659557	3.11969977	0.00014583	0.00632353	upregulated
Solyc00g500268.1	351.851787	3.10792308	0.00155471	0.03222556	upregulated
Solyc01g005120.3	1385.09164	0.47104643	0.00238125	0.04245752	upregulated
Solyc01g005450.3	377.403544	0.95316778	1.06E-07	3.42E-05	upregulated
Solyc01g006900.3	14959.1377	0.83799189	9.34E-06	0.00090774	upregulated
Solyc01g008620.4	195.220567	3.67610341	0.00063191	0.01773645	upregulated
Solyc01g008670.4	521.537702	1.55481072	4.66E-05	0.00286192	upregulated
Solyc01g008910.2	868.4778	0.73044385	1.74E-06	0.00027843	upregulated
Solyc01g008950.4	5653.03067	0.42194897	8.85E-05	0.00437339	upregulated
Solyc01g009430.3	2849.21534	0.78385969	0.00012428	0.00564213	upregulated
Solyc01g044556.1	509.659476	1.04512297	2.07E-05	0.00164685	upregulated
Solyc01g066640.2	183.333722	1.16858665	0.00022208	0.00845425	upregulated
Solyc01g066910.3	69.2104779	1.48870918	0.00162508	0.03343334	upregulated
Solyc01g067295.1	6352.99501	1.29255239	1.08E-07	3.42E-05	upregulated
Solyc01g068560.3	6150.10522	0.41887572	0.00124618	0.02789343	upregulated
Solyc01g079260.4	526.822318	0.86053986	0.00061002	0.01728564	upregulated
Solyc01g079590.3	1567.52491	0.5532693	1.68E-05	0.0014243	upregulated
Solyc01g080890.2	196.16093	0.90844395	0.00140934	0.030083	upregulated
Solyc01g081060.4	3263.83792	0.77179819	0.00065494	0.01825054	upregulated
Solyc01g081190.4	5220.63253	0.45095363	0.00177276	0.03541678	upregulated
Solyc01g081440.3	987.013164	0.78852168	3.26E-06	0.00044093	upregulated
Solyc01g087090.3	695.673543	0.72184868	0.00016161	0.00671123	upregulated
Solyc01g088430.4	834.588047	1.01994368	0.00185771	0.036512	upregulated
Solyc01g088660.3	705.878292	0.6112926	0.00115304	0.02647326	upregulated
Solyc01g091050.4	1732.36296	0.79404264	0.00155452	0.03222556	upregulated
Solyc01g091660.3	214.06916	1.42856558	8.84E-06	0.0008737	upregulated

Solyc01g091670.3	230.402758	1.62901547	0.00050076	0.01525062	upregulated
Solyc01g091870.3	727.87331	0.50636031	0.00043953	0.01393472	upregulated
Solyc01g093965.2	1005.6464	0.57459164	0.00180725	0.03584659	upregulated
Solyc01g094070.3	315.233238	1.51965745	3.86E-05	0.00252369	upregulated
Solyc01g094090.4	452.112065	1.2077593	3.45E-05	0.00237772	upregulated
Solyc01g094790.3	1153.06146	0.70919272	2.19E-05	0.00171012	upregulated
Solyc01g094950.3	7919.53764	0.37701838	0.00166086	0.03384842	upregulated
Solyc01g095050.3	4176.89576	0.51206197	0.00011757	0.00542662	upregulated
Solyc01g095610.4	282.731091	0.84442022	0.00061048	0.01728564	upregulated
Solyc01g096080.3	732.83835	0.81816035	2.47E-06	0.00035095	upregulated
Solyc01g096270.3	2941.28755	0.72345566	8.73E-07	0.0001688	upregulated
Solyc01g096630.3	1307.53714	0.72313696	3.92E-06	0.00049218	upregulated
Solyc01g097150.4	283.791991	0.79934442	0.00227355	0.04101512	upregulated
Solyc01g097240.3	132.018857	4.7627921	3.67E-06	0.00047268	upregulated
Solyc01g097880.4	1850.19402	0.38953186	0.00109037	0.02555956	upregulated
Solyc01g097930.3	99.2116014	1.48093269	0.00074193	0.01968211	upregulated
Solyc01g098210.3	372.837875	0.71794719	0.00210677	0.0395561	upregulated
Solyc01g098500.3	8060.69053	0.3065228	0.00270408	0.04611485	upregulated
Solyc01g098760.4	3190.68656	0.60746046	0.00054614	0.01614965	upregulated
Solyc01g099870.3	174.401908	1.48840798	0.00051487	0.01553369	upregulated
Solyc01g102720.3	478.468839	0.81509837	0.00018958	0.00759069	upregulated
Solyc01g103310.4	68.2012124	1.72689429	0.00040962	0.01331352	upregulated
Solyc01g103400.4	1451.98582	0.48710546	0.00039959	0.01307567	upregulated
Solyc01g104100.3	43.3614791	2.48158877	0.00019223	0.00764923	upregulated
Solyc01g105860.3	114.993357	1.64175766	0.00035934	0.01200207	upregulated
Solyc01g105890.3	109.558687	1.45255023	0.00016175	0.00671123	upregulated
Solyc01g106690.3	1416.30013	0.66243677	4.28E-05	0.0026784	upregulated
Solyc01g107820.2	468.341505	0.81178294	0.00227171	0.04101512	upregulated
Solyc01g108020.3	2167.88732	1.24480272	1.25E-06	0.00021637	upregulated
Solyc01g108620.3	1001.94776	0.45040208	0.00221355	0.04051483	upregulated
Solyc01g110370.4	1421.81917	0.63162007	3.83E-05	0.00252369	upregulated
Solyc01g111110.3	864.187789	0.61148578	0.00182205	0.03606616	upregulated
Solyc01g111560.3	5813.03232	0.33165372	0.00072558	0.01946187	upregulated
Solyc02g031900.3	601.321802	0.52603602	0.002378	0.04245752	upregulated
Solyc02g031920.4	398.791535	1.45528002	9.35E-05	0.00453004	upregulated
Solyc02g062640.4	1491.63469	0.41243865	0.00076556	0.02014297	upregulated
Solyc02g062690.3	854.734594	0.73667191	0.00073162	0.0195699	upregulated
Solyc02g063000.4	6940.85613	0.71119004	0.00023604	0.00888082	upregulated
Solyc02g063390.4	1569.44873	0.88795543	0.00209184	0.03946736	upregulated
Solyc02g065470.1	773.057643	0.68911214	0.00248529	0.04365406	upregulated
Solyc02g065570.1	70.6350332	1.94634695	1.42E-05	0.00124405	upregulated

Solyc02g067050.3	619.71198	1.04115004	0.00015987	0.00670651	upregulated
Solyc02g068600.3	377.910875	0.8860112	0.0005177	0.01554838	upregulated
Solyc02g068820.3	111.662046	0.96118433	0.00182193	0.03606616	upregulated
Solyc02g069180.4	992.226724	0.67113023	7.33E-05	0.00380268	upregulated
Solyc02g071710.3	1229.11102	1.47516285	8.18E-09	4.40E-06	upregulated
Solyc02g076670.3	208.427749	0.88828979	0.00111922	0.02589056	upregulated
Solyc02g077040.4	547.30179	1.83305166	0.00248525	0.04365406	upregulated
Solyc02g077080.3	2396.68654	0.64001673	0.00106482	0.02512483	upregulated
Solyc02g078240.4	2059.29931	0.51880073	0.00057189	0.01665667	upregulated
Solyc02g078320.3	196.877625	0.86106065	0.00100101	0.02417177	upregulated
Solyc02g078400.3	2569.25895	0.63661458	0.00050278	0.01526417	upregulated
Solyc02g078410.1	617.425126	0.51428081	0.00145296	0.03077663	upregulated
Solyc02g080600.1	961.532341	0.65993097	0.00115399	0.02647326	upregulated
Solyc02g081770.2	212.147029	1.430307	0.00071576	0.01934693	upregulated
Solyc02g082140.3	1784.08059	0.68345456	0.00049865	0.01525062	upregulated
Solyc02g082920.4	535.500689	2.19894684	0.00134253	0.0292205	upregulated
Solyc02g083180.4	990.164563	0.53876238	0.00051767	0.01554838	upregulated
Solyc02g083630.3	501.23146	0.73805842	0.00183879	0.03628605	upregulated
Solyc02g084240.3	515.307046	1.15045147	0.00167914	0.03400294	upregulated
Solyc02g084430.3	467.809026	0.69155959	0.00038689	0.01275766	upregulated
Solyc02g084650.3	1795.44253	0.61126383	5.23E-06	0.00060546	upregulated
Solyc02g084970.4	78.0217929	1.54571516	9.84E-05	0.00470829	upregulated
Solyc02g087930.3	4686.407	0.40220555	0.00081892	0.02122945	upregulated
Solyc02g088190.4	797.086886	0.56422662	0.00295355	0.0486945	upregulated
Solyc02g088620.3	910.702045	0.54917805	0.0011123	0.02586543	upregulated
Solyc02g088740.1	435.917998	0.81392273	0.00205809	0.03902094	upregulated
Solyc02g089065.1	14614.3987	0.44508116	0.00161271	0.03324965	upregulated
Solyc02g089160.3	1230.98953	0.80298771	4.11E-05	0.00262546	upregulated
Solyc02g089170.4	117.498646	1.73041767	3.85E-05	0.00252369	upregulated
Solyc02g089350.3	6215.85917	0.67551165	0.00022333	0.00848511	upregulated
Solyc02g089540.3	2258.77794	0.81003111	0.00032308	0.01101964	upregulated
Solyc02g089620.3	1037.27745	1.75866474	1.01E-10	1.30E-07	upregulated
Solyc02g090010.3	391.085475	0.63670699	0.00222697	0.0407064	upregulated
Solyc02g090490.3	72.0148611	1.93384947	0.00242866	0.04308979	upregulated
Solyc02g090930.3	156.324271	1.65042982	1.61E-07	4.86E-05	upregulated
Solyc02g091360.1	281.384982	0.93725105	0.00078908	0.02064949	upregulated
Solyc02g091380.1	25.5315154	3.07546467	0.00096608	0.02358611	upregulated
Solyc02g091930.3	916.860785	0.67050556	0.000191	0.00763175	upregulated
Solyc02g092270.3	3841.74437	0.31959994	0.00174967	0.03506417	upregulated
Solyc02g092410.3	122.101167	1.3152135	0.00018857	0.00758802	upregulated
Solyc02g092600.3	356.69485	0.64137933	0.00059448	0.01705745	upregulated

Solyc02g094300.4	696.438511	0.79062606	9.30E-05	0.00452767	upregulated
Solyc03g005900.4	1009.40123	0.44352996	0.00213778	0.03982903	upregulated
Solyc03g006600.1	223.646909	0.9278516	0.00038724	0.01275766	upregulated
Solyc03g006910.3	51.2772664	3.19104464	0.00184158	0.03630412	upregulated
Solyc03g007520.3	2185.38426	0.38724121	0.00225297	0.04094937	upregulated
Solyc03g019880.3	3727.10166	0.55583984	2.07E-05	0.00164685	upregulated
Solyc03g025390.3	13516.205	0.60241058	0.00255343	0.04432742	upregulated
Solyc03g025410.4	10090.3845	0.33569823	0.00112278	0.02594199	upregulated
Solyc03g025670.3	290.805807	2.69306935	5.12E-08	2.06E-05	upregulated
Solyc03g025680.3	388.714114	0.98839617	0.002448	0.04327411	upregulated
Solyc03g031800.3	585.413458	0.52349408	0.00163646	0.03357764	upregulated
Solyc03g033840.4	217.071838	1.37284466	0.00087947	0.02223277	upregulated
Solyc03g044480.3	540.834929	0.860384	8.34E-05	0.00420041	upregulated
Solyc03g044740.4	1281.02178	0.71064145	0.00022462	0.00851766	upregulated
Solyc03g045140.4	174.143785	1.97684194	5.70E-07	0.00012396	upregulated
Solyc03g071710.1	672.419739	0.54153477	0.00068741	0.0188566	upregulated
Solyc03g082720.3	943.16368	0.76248513	0.00052383	0.0156573	upregulated
Solyc03g096460.4	1056.3857	0.89868743	5.98E-05	0.00335207	upregulated
Solyc03g097650.3	212.037462	0.80344054	0.0008404	0.02166996	upregulated
Solyc03g097920.1	2096.84313	0.61022402	0.0016581	0.03384842	upregulated
Solyc03g110990.1	266.34929	1.09172756	3.45E-05	0.00237772	upregulated
Solyc03g111290.2	41.4324793	2.28778608	9.16E-05	0.00448562	upregulated
Solyc03g111620.1	154.916263	0.92499546	0.00140774	0.03008198	upregulated
Solyc03g111815.1	6715.36728	1.29213513	5.68E-06	0.00063548	upregulated
Solyc03g111970.4	1022.54659	0.72578767	1.15E-05	0.00103704	upregulated
Solyc03g112010.4	371.016153	1.00538426	8.04E-05	0.00411644	upregulated
Solyc03g112130.1	373.617847	0.99446838	9.45E-06	0.00091123	upregulated
Solyc03g112540.4	195.668399	1.09093726	0.0001777	0.00726526	upregulated
Solyc03g113250.4	1532.6531	0.9654998	0.00014664	0.00634414	upregulated
Solyc03g114120.3	600.823407	0.63479342	0.00124172	0.02789037	upregulated
Solyc03g114560.2	664.197065	0.76794683	0.00080228	0.02085397	upregulated
Solyc03g115870.3	134.730829	1.51030446	0.00057779	0.01675372	upregulated
Solyc03g115930.3	60.8626802	2.40982335	0.00167856	0.03400294	upregulated
Solyc03g116320.3	316.567367	1.00312027	0.00190861	0.03699502	upregulated
Solyc03g116340.3	936.854962	0.6657824	4.58E-06	0.00053999	upregulated
Solyc03g116490.1	198.771341	0.99880457	2.66E-05	0.0020013	upregulated
Solyc03g116590.3	3659.88946	0.96223175	0.00073163	0.0195699	upregulated
Solyc03g116630.3	1076.11947	1.01819682	0.00233735	0.04197022	upregulated
Solyc03g116740.3	1111.46196	0.82652968	0.00042492	0.01358279	upregulated
Solyc03g117590.3	2336.985	1.65942654	0.00280168	0.04698588	upregulated
Solyc03g118120.3	2799.9778	0.52985756	1.82E-06	0.00028763	upregulated

Solyc03g119110.4	2400.45515	0.40695464	0.00038633	0.01275766	upregulated
Solyc03g119520.4	746.996297	1.06508403	6.41E-06	0.0006904	upregulated
Solyc03g119600.1	276.714741	0.98953241	6.36E-06	0.0006904	upregulated
Solyc03g119700.3	8827.1545	0.41166115	0.00044498	0.01406127	upregulated
Solyc03g120170.1	136.639313	1.0455034	0.0004305	0.01371572	upregulated
Solyc03g121090.4	396.785546	1.41937969	6.86E-06	0.00071686	upregulated
Solyc03g121270.3	2487.75445	0.90095493	0.00029003	0.01025405	upregulated
Solyc03g122140.3	500.681896	1.27374058	3.96E-06	0.00049413	upregulated
Solyc03g122300.3	849.761938	0.74962669	2.79E-08	1.22E-05	upregulated
Solyc03g122350.3	231.955258	1.60565212	0.00014731	0.006349	upregulated
Solyc03g123390.4	2856.83365	0.95608096	0.00056606	0.01660162	upregulated
Solyc03g123460.4	99.8225239	1.31083528	0.00260644	0.04484521	upregulated
Solyc03g150112.1	111.329416	1.2550255	0.00026703	0.00975328	upregulated
Solyc04g005100.3	955.24863	1.09381179	2.18E-05	0.00170567	upregulated
Solyc04g005690.4	10801.3271	1.29204373	6.87E-08	2.43E-05	upregulated
Solyc04g006980.1	224.301312	1.04559206	0.00178469	0.03561202	upregulated
Solyc04g007015.1	3074.57525	0.54189657	5.07E-05	0.00302381	upregulated
Solyc04g007700.3	268.069139	0.80220378	0.00286804	0.04765032	upregulated
Solyc04g007820.3	2501.71528	1.09855895	6.62E-05	0.00354948	upregulated
Solyc04g007823.1	292.248244	1.78687819	7.98E-09	4.40E-06	upregulated
Solyc04g007825.2	1662.73338	1.58682952	0.00116154	0.02652071	upregulated
Solyc04g007950.4	2168.51769	0.51957605	0.00116042	0.02652071	upregulated
Solyc04g008210.2	1880.30855	0.71763113	0.00131708	0.02887875	upregulated
Solyc04g008400.1	237.913805	0.75237149	0.00073463	0.01960567	upregulated
Solyc04g008940.4	28.0921589	2.65921919	0.0028765	0.04771417	upregulated
Solyc04g008950.4	60.2904425	1.52270711	0.00208647	0.03940446	upregulated
Solyc04g009980.4	226.162655	0.90167134	0.00226311	0.0409553	upregulated
Solyc04g010250.3	304.057022	1.1353112	0.00071729	0.01934693	upregulated
Solyc04g010285.1	1423.33326	1.1993632	1.41E-06	0.00023317	upregulated
Solyc04g014500.3	1789.4112	0.62057328	7.35E-06	0.00075219	upregulated
Solyc04g015520.3	785.634018	0.51203756	0.00238205	0.04245752	upregulated
Solyc04g016040.1	112.33277	1.25073724	0.00014013	0.00608983	upregulated
Solyc04g016190.1	45.4332364	2.81708897	0.00221191	0.04051483	upregulated
Solyc04g017720.3	2796.20738	0.75155832	2.78E-05	0.00204053	upregulated
Solyc04g040210.4	336.092546	1.01715173	0.00020467	0.00796403	upregulated
Solyc04g053130.4	1769.59611	1.01377025	4.23E-06	0.00052131	upregulated
Solyc04g054220.3	83.3328703	1.99614591	1.54E-05	0.00132771	upregulated
Solyc04g063350.3	598.669546	1.10640864	0.00089542	0.0224693	upregulated
Solyc04g064510.3	1206.80559	0.43511451	0.00101911	0.02437131	upregulated
Solyc04g071610.4	3855.608	0.59397439	0.0004529	0.01424153	upregulated
Solyc04g072450.3	1427.19362	0.46286527	0.00079857	0.02078543	upregulated

Solyc04g072940.4	145.925141	0.85497871	0.00201574	0.03848204	upregulated
Solyc04g074400.1	45.4635908	2.47228251	0.00087037	0.02214745	upregulated
Solyc04g074410.2	427.92033	1.05748326	1.78E-05	0.00148163	upregulated
Solyc04g074580.1	4754.56803	0.53766435	0.00015505	0.00659019	upregulated
Solyc04g074700.4	639.126192	0.87782054	0.00037469	0.01245033	upregulated
Solyc04g074950.3	319.179032	0.90974807	0.00223162	0.04075284	upregulated
Solyc04g077140.3	1034.63975	0.82655345	7.50E-06	0.00076026	upregulated
Solyc04g077850.3	277.618023	0.9913359	0.00057789	0.01675372	upregulated
Solyc04g078620.3	1027.84921	0.61641853	2.04E-05	0.00164026	upregulated
Solyc04g079120.3	1019.45726	0.54103272	0.00056658	0.01660162	upregulated
Solyc04g079210.3	3231.24733	0.62776349	0.00185779	0.036512	upregulated
Solyc04g079890.4	114.497555	1.62088807	0.00032796	0.01114662	upregulated
Solyc04g079970.3	11639.6314	0.80987684	0.00023909	0.00892615	upregulated
Solyc04g080380.3	1334.75398	0.48165418	0.00113034	0.02605429	upregulated
Solyc04g081530.1	409.962804	1.70094558	1.92E-07	5.54E-05	upregulated
Solyc04g081700.3	196.343459	0.92586552	0.00274791	0.04657479	upregulated
Solyc04g082200.2	2337.38308	0.60972125	0.00051166	0.01546096	upregulated
Solyc04g150164.1	191.02447	1.30488199	0.00095788	0.02348686	upregulated
Solyc05g005000.4	1034.39063	0.95222957	2.08E-05	0.00164865	upregulated
Solyc05g005150.1	1417.7907	0.58866055	0.00157894	0.03262299	upregulated
Solyc05g005680.3	117.9295	1.61023189	6.63E-05	0.00354948	upregulated
Solyc05g006380.1	230.067363	0.76360657	0.0010179	0.02437131	upregulated
Solyc05g006390.1	309.431316	0.88248613	9.83E-06	0.00093651	upregulated
Solyc05g007180.3	1783.55724	0.42739413	0.00202782	0.03863654	upregulated
Solyc05g007880.4	510.977688	1.01292501	1.08E-05	0.0009865	upregulated
Solyc05g008010.3	3801.28027	0.41582077	0.000189	0.00758802	upregulated
Solyc05g008240.2	1804.56404	1.08921503	0.00090999	0.02271817	upregulated
Solyc05g008440.3	1199.591	0.63103159	0.00305332	0.04990796	upregulated
Solyc05g009550.3	56.5310332	2.01048835	0.00115911	0.02652071	upregulated
Solyc05g010720.4	187.357654	1.29882735	0.00010224	0.00483435	upregulated
Solyc05g011890.1	4361.27927	0.82715038	2.51E-05	0.00191058	upregulated
Solyc05g012030.1	257.535364	1.03958119	7.06E-05	0.00368085	upregulated
Solyc05g012950.3	639.510356	1.32987346	2.51E-05	0.00191058	upregulated
Solyc05g012955.1	352.989574	1.19692953	0.00167539	0.03399819	upregulated
Solyc05g013570.3	5504.65917	0.47345197	0.00244167	0.04325208	upregulated
Solyc05g014030.3	2443.37034	0.3838477	0.00226078	0.0409553	upregulated
Solyc05g015420.4	1050.92184	0.69821658	2.72E-05	0.00202461	upregulated
Solyc05g015530.3	1932.59281	0.4891849	0.00045835	0.01434319	upregulated
Solyc05g025900.3	1089.62693	0.84470079	0.00016043	0.00671123	upregulated
Solyc05g032680.4	127.821417	1.15225938	0.00039722	0.01302295	upregulated
Solyc05g046140.3	169.593304	1.27911225	0.00011788	0.00542767	upregulated

Solyc05g049990.4	1213.33091	0.56228188	0.00012617	0.00567455	upregulated
Solyc05g050130.4	1228.76941	1.24654987	6.39E-05	0.00350104	upregulated
Solyc05g051200.1	593.244375	1.31541964	1.32E-07	4.11E-05	upregulated
Solyc05g051560.4	564.257997	0.85083384	8.58E-05	0.00427565	upregulated
Solyc05g051750.3	2936.81833	0.59017532	7.98E-05	0.00410501	upregulated
Solyc05g051800.3	82.2850464	1.88370524	0.00102154	0.02438969	upregulated
Solyc05g052030.1	1481.52665	1.04222063	6.57E-05	0.00354948	upregulated
Solyc05g052050.1	258.622703	1.91946908	3.31E-06	0.000444	upregulated
Solyc05g052280.3	31.6410506	2.61733495	0.00299792	0.04934196	upregulated
Solyc05g052800.3	3828.9693	0.36120051	0.00241918	0.0430005	upregulated
Solyc05g053060.1	270.294947	0.65569196	0.00246823	0.04355207	upregulated
Solyc05g054315.1	8279.50616	0.52796414	0.00119637	0.027117	upregulated
Solyc05g055160.3	16697.6083	0.75465412	0.00155171	0.03222556	upregulated
Solyc05g055343.2	419.794413	1.28912781	0.00022189	0.00845425	upregulated
Solyc05g055750.3	458.581131	1.03865009	1.01E-06	0.00018031	upregulated
Solyc05g056000.3	4634.74064	0.34641081	0.00247131	0.04356661	upregulated
Solyc05g056240.3	1743.07981	0.39624096	0.00141648	0.0301781	upregulated
Solyc06g007510.3	8528.5237	0.52160348	0.00022083	0.00843999	upregulated
Solyc06g007620.3	1069.61334	0.90448548	4.27E-06	0.00052225	upregulated
Solyc06g008520.4	730.908272	0.64973513	0.00024295	0.00903536	upregulated
Solyc06g036640.4	2312.25791	0.5994729	5.20E-05	0.00306611	upregulated
Solyc06g050710.4	930.670819	0.77224335	0.00281274	0.04705492	upregulated
Solyc06g050840.3	1182.16379	0.5543279	0.00187017	0.03661768	upregulated
Solyc06g051620.3	153.876076	1.25982281	9.30E-06	0.00090774	upregulated
Solyc06g053290.1	224.882931	0.66897166	0.00171338	0.03450926	upregulated
Solyc06g053840.3	2723.20949	0.6126212	0.00212907	0.03975314	upregulated
Solyc06g054320.1	655.473681	0.7426706	1.06E-05	0.00097353	upregulated
Solyc06g054510.4	2887.90978	0.51638014	0.0003039	0.0105513	upregulated
Solyc06g059710.3	1132.83053	1.46332512	1.98E-05	0.00161279	upregulated
Solyc06g059860.3	461.802646	0.7922935	0.0013141	0.02884616	upregulated
Solyc06g059870.1	813.901793	1.13575404	2.10E-06	0.0003195	upregulated
Solyc06g059930.4	2442.17983	1.16236049	5.08E-05	0.00302381	upregulated
Solyc06g060540.3	92.9146837	1.04753216	0.00145682	0.03082435	upregulated
Solyc06g060610.2	321.836003	1.22692658	0.00013301	0.0058586	upregulated
Solyc06g060820.2	123.620272	0.98614918	0.00278786	0.04692291	upregulated
Solyc06g062510.3	3293.5696	0.44929866	0.00280375	0.04698588	upregulated
Solyc06g063320.3	1298.11439	0.37441612	0.00274218	0.04651849	upregulated
Solyc06g064610.1	175.04551	0.94045531	0.00251132	0.04385679	upregulated
Solyc06g065200.4	285.415317	0.80980344	0.00150727	0.03154657	upregulated
Solyc06g065820.3	28.5794016	2.33220884	0.00059396	0.01705745	upregulated
Solyc06g066670.4	488.74786	0.72770918	0.00188536	0.03671806	upregulated

Solyc06g068460.3	546.435165	0.84658906	4.49E-05	0.00278491	upregulated
Solyc06g068500.3	90.0343459	1.80474393	0.0005003	0.01525062	upregulated
Solyc06g068970.3	3077.73285	0.36787672	0.00096244	0.02353049	upregulated
Solyc06g069120.3	4481.26752	0.66056545	7.00E-05	0.00366034	upregulated
Solyc06g072030.1	946.572317	0.62810573	0.00031911	0.01094201	upregulated
Solyc06g073450.4	5181.20014	1.00932272	4.66E-09	3.23E-06	upregulated
Solyc06g073950.3	536.723921	0.59802341	0.00186448	0.03656922	upregulated
Solyc06g074410.4	367.756361	0.97278249	0.00164958	0.03379369	upregulated
Solyc06g082980.3	16459.4254	0.7787813	0.00266526	0.04561365	upregulated
Solyc06g084020.4	2606.41548	0.81903429	0.00070959	0.01930051	upregulated
Solyc06g084410.4	583.799614	0.72011919	2.79E-05	0.00204053	upregulated
Solyc07g005120.3	1037.3025	0.51629496	0.00013638	0.00595352	upregulated
Solyc07g006370.1	463.988711	1.1320127	0.0030215	0.04966505	upregulated
Solyc07g006560.3	4278.96197	4.10409131	0.00123558	0.02782921	upregulated
Solyc07g006670.1	328.893852	1.2283163	9.54E-05	0.00459975	upregulated
Solyc07g006710.2	1575.79558	0.73903216	0.00270773	0.04613642	upregulated
Solyc07g006855.2	547.544665	0.61793359	0.00171026	0.03448881	upregulated
Solyc07g007260.4	8447.84316	0.55644348	0.00086679	0.02208536	upregulated
Solyc07g007350.1	1683.87299	0.76536461	4.04E-07	9.73E-05	upregulated
Solyc07g016080.4	53.0600253	2.17486445	0.00023899	0.00892615	upregulated
Solyc07g017520.4	1317.98288	0.64599166	0.00019217	0.00764923	upregulated
Solyc07g018190.4	173.77499	1.09328912	0.00216083	0.04018104	upregulated
Solyc07g026680.2	415.74924	1.41911389	5.04E-09	3.31E-06	upregulated
Solyc07g042170.3	1878.38005	0.71823657	0.0027724	0.0467584	upregulated
Solyc07g042490.1	224.362598	1.90661671	1.37E-08	6.81E-06	upregulated
Solyc07g043130.3	12952.565	0.94876737	7.51E-06	0.00076026	upregulated
Solyc07g045530.2	128.889207	1.33517301	4.63E-06	0.00054238	upregulated
Solyc07g049150.2	688.653845	0.77418791	0.00237365	0.04244937	upregulated
Solyc07g049290.3	4001.54588	0.47684135	0.00271626	0.04624093	upregulated
Solyc07g049530.3	449.079378	1.86901653	7.21E-06	0.00074153	upregulated
Solyc07g052150.4	427.553161	1.52795992	5.29E-07	0.00011812	upregulated
Solyc07g054730.1	2150.90499	1.78429727	0.00285335	0.04757822	upregulated
Solyc07g054850.3	433.778424	0.60217483	0.00248764	0.04365559	upregulated
Solyc07g054900.2	406.739067	1.57822515	4.31E-05	0.00268209	upregulated
Solyc07g056200.3	95.2395089	2.98493895	2.01E-05	0.00162628	upregulated
Solyc07g056210.4	28.7567244	3.90980205	0.00101185	0.02433855	upregulated
Solyc07g056360.1	128.965777	1.41865615	0.00285386	0.04757822	upregulated
Solyc07g056480.3	1971.4	1.30716958	3.37E-06	0.00044692	upregulated
Solyc07g056500.4	145.089918	1.45803667	8.32E-07	0.00016427	upregulated
Solyc07g062510.2	110.390714	1.42261891	8.78E-05	0.00435381	upregulated
Solyc07g062710.4	1225.45177	1.25699371	3.36E-10	4.06E-07	upregulated

Solyc07g063610.4	2385.96739	0.79357768	5.05E-05	0.00302381	upregulated
Solyc07g064150.4	7796.31992	0.48095827	0.0004264	0.01360758	upregulated
Solyc07g065670.1	67.5549662	1.95978097	1.25E-05	0.00111313	upregulated
Solyc07g066650.4	2686.10387	0.51290648	0.00028714	0.01020763	upregulated
Solyc08g005450.3	2210.80382	0.70746165	0.00304552	0.04988793	upregulated
Solyc08g005630.3	1391.18099	0.54864017	0.00101776	0.02437131	upregulated
Solyc08g005670.2	694.973183	1.54261601	5.14E-07	0.00011705	upregulated
Solyc08g005677.1	602.009138	1.4760492	1.85E-05	0.00153343	upregulated
Solyc08g005680.4	992.086699	1.57617518	0.00285929	0.04758675	upregulated
Solyc08g005710.3	535.130684	1.4783459	5.92E-07	0.00012582	upregulated
Solyc08g005920.3	376.342154	0.77356885	0.00053674	0.01593963	upregulated
Solyc08g006230.4	207.445153	0.9348998	0.00027536	0.00994469	upregulated
Solyc08g006720.4	10986.821	0.34784992	0.00089476	0.0224693	upregulated
Solyc08g007460.3	105.024184	2.02753889	0.00204944	0.0389333	upregulated
Solyc08g007970.3	2386.76325	0.84069732	4.21E-05	0.00266708	upregulated
Solyc08g008220.3	7830.9635	0.50604734	0.00068303	0.01885427	upregulated
Solyc08g008420.3	87.33261	1.16697168	0.00132824	0.02904813	upregulated
Solyc08g008520.3	227.699162	1.00767688	0.00012939	0.00573925	upregulated
Solyc08g014120.3	275.893887	0.73505454	0.00156251	0.03235256	upregulated
Solyc08g014190.4	594.747549	1.28318268	0.00019973	0.00781903	upregulated
Solyc08g016210.3	136.925655	1.82244729	0.00154319	0.03212451	upregulated
Solyc08g029090.4	208.163134	0.69659815	0.00202155	0.03855501	upregulated
Solyc08g066220.4	178.083919	1.65088976	0.00014931	0.00638814	upregulated
Solyc08g066260.3	127.85664	1.05439034	0.00188035	0.03669332	upregulated
Solyc08g066890.4	830.33762	3.8866154	0.00249122	0.0436788	upregulated
Solyc08g067410.2	565.70471	0.86607633	0.00097566	0.02376348	upregulated
Solyc08g067940.3	967.090482	0.64071004	0.00212541	0.03975314	upregulated
Solyc08g068480.1	1664.1026	0.87810517	4.08E-07	9.73E-05	upregulated
Solyc08g068665.1	382.200833	1.46270966	1.04E-05	0.00096104	upregulated
Solyc08g068880.1	1782.93585	0.49785121	0.00024758	0.00916527	upregulated
Solyc08g074750.2	1625.80873	0.66943811	5.43E-05	0.00314646	upregulated
Solyc08g076860.3	560.936462	0.98068279	0.00116505	0.02656947	upregulated
Solyc08g076960.1	204.351999	0.99081689	0.00029404	0.01033904	upregulated
Solyc08g078670.2	2022.63063	0.76011054	3.05E-07	7.76E-05	upregulated
Solyc08g078940.1	330.062286	1.81500408	0.0002853	0.01017988	upregulated
Solyc08g079230.1	37.938007	4.12673403	0.00045276	0.01424153	upregulated
Solyc08g079900.3	278.793937	3.50792011	0.00025877	0.0095141	upregulated
Solyc08g080100.4	1281.68587	0.78763472	5.30E-06	0.00060661	upregulated
Solyc08g080570.4	1474.41848	1.16624915	0.00041472	0.01338936	upregulated
Solyc08g080620.1	363.753931	4.59450331	9.89E-05	0.00472114	upregulated
Solyc08g081370.1	183.554331	1.26294007	4.62E-07	0.00010764	upregulated

Solyc08g081700.1	300.626529	0.86968933	0.00170785	0.03447619	upregulated
Solyc08g083370.4	583.830255	0.67348524	0.00070306	0.01920414	upregulated
Solyc09g005940.4	378.097772	1.71055497	2.39E-07	6.24E-05	upregulated
Solyc09g007010.1	296.697646	4.4427067	0.00104342	0.02476066	upregulated
Solyc09g007150.3	5448.85666	0.89500083	0.00092287	0.02290267	upregulated
Solyc09g007240.3	1056.60181	0.6028037	0.00015597	0.0066022	upregulated
Solyc09g007880.1	38.7803795	1.64369834	0.00171485	0.03450926	upregulated
Solyc09g008080.3	808.31849	0.69872595	0.00096715	0.02358611	upregulated
Solyc09g009010.4	2274.06006	0.41849105	0.00130205	0.02864656	upregulated
Solyc09g010940.4	2892.25482	0.59659506	0.00106147	0.02509512	upregulated
Solyc09g011160.4	345.710451	1.15200398	2.62E-05	0.00197759	upregulated
Solyc09g011270.4	25.1974224	3.21602196	0.00061676	0.01741702	upregulated
Solyc09g011470.3	210.980903	1.37323965	0.00070855	0.01929944	upregulated
Solyc09g011600.3	97.0735775	1.76833842	0.00036864	0.01229163	upregulated
Solyc09g011870.3	60.6709741	1.74142203	0.00294187	0.04857292	upregulated
Solyc09g015770.3	132.052986	2.41164628	0.00034754	0.01164827	upregulated
Solyc09g018750.3	9552.82914	0.53538969	0.00255865	0.04437822	upregulated
Solyc09g072610.3	327.806151	1.11046301	0.00100971	0.0243174	upregulated
Solyc09g074675.1	33.9983529	1.934388	0.00114606	0.02635385	upregulated
Solyc09g074930.3	747.288406	0.47705904	0.00225011	0.04093594	upregulated
Solyc09g075230.1	1303.65367	0.71744175	0.00247481	0.04358858	upregulated
Solyc09g075610.3	162.492439	1.29354854	8.15E-05	0.00413833	upregulated
Solyc09g083050.3	729.924234	0.60795005	0.00059956	0.0170764	upregulated
Solyc09g084440.2	256.382432	1.42001893	0.0004186	0.01346765	upregulated
Solyc09g090430.3	2509.83693	0.56035766	0.00240193	0.04273316	upregulated
Solyc09g091170.4	3289.24669	0.34662375	0.00145297	0.03077663	upregulated
Solyc09g091700.4	612.055934	0.70720772	0.00064929	0.0181454	upregulated
Solyc09g092260.4	67.411523	1.66988733	0.00018912	0.00758802	upregulated
Solyc09g092330.3	2484.49341	0.75150475	0.00116826	0.0266112	upregulated
Solyc09g092490.3	2274.44819	0.72682729	0.00211622	0.03965665	upregulated
Solyc09g092520.3	1567.42446	0.98146671	9.15E-06	0.00089819	upregulated
Solyc09g092560.4	262.078333	1.80749511	6.91E-08	2.43E-05	upregulated
Solyc09g092725.1	819.418021	1.23901273	0.00021314	0.00824401	upregulated
Solyc09g092750.3	379.432422	1.63548911	0.00015176	0.00647862	upregulated
Solyc09g097800.2	2960.63495	1.79874095	0.00167065	0.03393776	upregulated
Solyc09g097870.4	2909.91748	0.50160463	0.00200965	0.03847987	upregulated
Solyc09g150103.1	834.787945	0.50992474	0.00029358	0.01033904	upregulated
Solyc10g005200.3	1412.9666	0.51945335	0.00068407	0.01885427	upregulated
Solyc10g005210.4	340.976164	1.08371062	6.65E-06	0.00071013	upregulated
Solyc10g005340.3	990.51983	0.79198674	1.34E-06	0.00022334	upregulated
Solyc10g005410.4	230.930166	1.561896	0.0008516	0.02187125	upregulated

Solyc10g006750.4	424.122713	1.15454251	0.00084705	0.02178339	upregulated
Solyc10g007073.1	96.5682936	1.7110706	0.00121192	0.02734819	upregulated
Solyc10g007260.3	1666.25918	0.49766321	0.00017962	0.00731285	upregulated
Solyc10g007280.4	36.4368478	1.86924409	0.0010295	0.02448886	upregulated
Solyc10g007870.3	1289.33278	1.46379401	1.14E-05	0.00102809	upregulated
Solyc10g008870.3	4016.45164	0.49108862	0.00110168	0.02570019	upregulated
Solyc10g011730.3	397.962434	1.05178776	7.12E-08	2.45E-05	upregulated
Solyc10g018305.1	105.471419	1.58569472	0.00148397	0.0312279	upregulated
Solyc10g018350.2	1394.33375	0.52197717	0.00180197	0.03580742	upregulated
Solyc10g045190.3	901.800739	0.64428789	3.40E-05	0.002356	upregulated
Solyc10g048030.2	2318.95443	1.77510863	1.59E-08	7.70E-06	upregulated
Solyc10g050160.2	742.581411	0.52434604	0.00136355	0.02952661	upregulated
Solyc10g050430.1	90.0440382	1.27466011	0.00201436	0.03848204	upregulated
Solyc10g050510.1	790.810817	1.39940343	9.80E-05	0.00470829	upregulated
Solyc10g055200.1	362.913669	1.13301797	1.28E-06	0.00021988	upregulated
Solyc10g055410.2	1316.3836	0.49724937	0.00093049	0.0230112	upregulated
Solyc10g075110.2	417.77598	1.25984505	0.00063333	0.01775066	upregulated
Solyc10g075150.2	1155.64612	4.03837603	0.00165242	0.03381594	upregulated
Solyc10g076540.1	102.950395	1.2139628	0.00148746	0.03125169	upregulated
Solyc10g078570.1	486.20486	0.62630232	0.00145964	0.03084029	upregulated
Solyc10g081580.3	2357.74307	0.39653249	0.00112459	0.02595279	upregulated
Solyc10g081850.3	678.412672	0.72231397	0.0005787	0.01675372	upregulated
Solyc10g081980.2	108.987033	1.80054145	4.01E-05	0.00257907	upregulated
Solyc10g083170.2	444.045367	0.96874057	2.77E-05	0.00204053	upregulated
Solyc10g083240.2	450.910904	0.60859617	0.00294366	0.04857292	upregulated
Solyc10g083990.2	2139.07641	0.65451046	0.00028625	0.01019498	upregulated
Solyc10g084230.2	657.178173	0.77769089	0.00173844	0.03487514	upregulated
Solyc10g084370.3	3460.42607	0.39821539	0.00221157	0.04051483	upregulated
Solyc10g084430.2	751.338922	1.44814538	6.62E-08	2.42E-05	upregulated
Solyc10g084520.1	254.925965	0.69730113	0.00091833	0.02285657	upregulated
Solyc10g084890.3	445.443225	1.49175682	0.00071638	0.01934693	upregulated
Solyc10g085010.3	120.724787	1.83115747	2.23E-06	0.00032979	upregulated
Solyc10g085200.2	1195.64828	0.56085072	0.0012719	0.02820793	upregulated
Solyc10g085215.1	1161.30791	0.49164343	0.00038792	0.01275851	upregulated
Solyc10g085300.2	630.311105	0.7464042	8.20E-06	0.00082136	upregulated
Solyc10g085830.2	7414.76644	0.48743923	8.39E-05	0.00420556	upregulated
Solyc10g085910.2	2377.39247	0.50231611	5.30E-06	0.00060661	upregulated
Solyc10g086030.2	1110.87314	0.82146946	8.23E-05	0.00415336	upregulated
Solyc10g086220.2	5643.99968	0.40129828	0.00062348	0.01752541	upregulated
Solyc10g150104.1	42.4326596	2.14411906	0.00045516	0.01426642	upregulated
Solyc10g150145.1	3518.51624	0.47505614	8.86E-05	0.00437339	upregulated

Solyc11g006780.2	1451.72481	0.42743235	0.00050011	0.01525062	upregulated
Solyc11g008270.2	4514.77508	0.72322457	3.63E-05	0.00245214	upregulated
Solyc11g009030.1	1067.41284	0.42538763	0.0019408	0.03745823	upregulated
Solyc11g010170.2	898.619282	1.1579499	0.00161729	0.03330864	upregulated
Solyc11g010230.2	15465.1899	0.37692665	0.00260951	0.04485801	upregulated
Solyc11g010270.2	13043.7808	0.40259412	0.00124474	0.02789343	upregulated
Solyc11g010670.1	146.72533	1.20151666	0.00218118	0.04034378	upregulated
Solyc11g011030.2	3831.65543	0.74905967	0.00132931	0.02904813	upregulated
Solyc11g011170.2	6486.87167	0.48396494	8.70E-05	0.00432668	upregulated
Solyc11g012220.1	176.785509	0.96473783	0.00137336	0.02967535	upregulated
Solyc11g012260.3	2764.99877	0.58369171	0.00023693	0.00889219	upregulated
Solyc11g012840.2	852.886758	0.53480443	0.00125203	0.02795964	upregulated
Solyc11g013100.2	2130.98597	0.44143318	0.00082481	0.02135339	upregulated
Solyc11g013450.2	348.816134	1.2347793	2.22E-06	0.00032979	upregulated
Solyc11g019910.1	3761.65745	0.72094681	0.00190915	0.03699502	upregulated
Solyc11g020670.1	208.193798	1.54548348	6.79E-05	0.00359367	upregulated
Solyc11g020960.2	207.056641	1.51606528	1.96E-06	0.00030109	upregulated
Solyc11g030380.2	1485.98736	0.48434064	0.00152504	0.03188399	upregulated
Solyc11g045225.1	1090.85545	0.52504351	0.00228833	0.04124329	upregulated
Solyc11g065600.2	514.752675	1.17800685	9.76E-06	0.00093418	upregulated
Solyc11g066320.2	343.421045	0.67555949	0.00280373	0.04698588	upregulated
Solyc11g067010.2	813.569266	0.71807055	0.00023403	0.00882257	upregulated
Solyc11g068430.3	735.4197	0.99413206	0.00015282	0.00650948	upregulated
Solyc11g068515.1	31813.8308	0.4521047	0.00091779	0.02285657	upregulated
Solyc11g068710.3	72.7977454	1.4777729	0.00225864	0.0409553	upregulated
Solyc11g069070.3	771.304139	0.66327024	0.00106533	0.02512483	upregulated
Solyc11g069650.2	678.851279	0.56272609	0.00252903	0.04403338	upregulated
Solyc11g069940.1	220.103379	1.00838545	0.00013699	0.00596698	upregulated
Solyc11g069960.2	3776.02253	1.23511255	3.68E-07	9.24E-05	upregulated
Solyc11g072110.2	2858.45018	0.51678585	0.00086117	0.02200014	upregulated
Solyc12g005270.2	3503.09789	0.43570116	0.00068717	0.0188566	upregulated
Solyc12g006050.2	1550.80359	1.06262637	3.32E-09	2.57E-06	upregulated
Solyc12g006280.3	23.2898587	2.04413115	0.00285675	0.04758544	upregulated
Solyc12g008530.2	563.987878	1.08471143	1.84E-06	0.00028763	upregulated
Solyc12g008560.1	1929.56105	0.91907227	0.00178622	0.03561202	upregulated
Solyc12g008600.2	123.03232	1.29144374	0.00254084	0.04418818	upregulated
Solyc12g008800.3	1614.49345	1.45205271	5.40E-12	1.36E-08	upregulated
Solyc12g009880.1	121.246901	1.56916998	0.00019879	0.00780749	upregulated
Solyc12g009920.1	539.528951	0.82078802	0.00071382	0.01934327	upregulated
Solyc12g010790.2	1387.93103	0.38861224	0.00289972	0.04801165	upregulated
Solyc12g010800.2	277.91794	1.19378648	9.70E-07	0.00017865	upregulated

Solyc12g011160.2	1570.88603	0.55593512	0.00025309	0.00934057	upregulated
Solyc12g013540.2	2574.24285	0.48633035	0.00067235	0.01860159	upregulated
Solyc12g014100.2	362.736363	0.89478293	0.00013349	0.0058586	upregulated
Solyc12g014310.2	462.375208	0.69706733	0.00060186	0.01709148	upregulated
Solyc12g015860.2	9067.93198	0.88755833	0.00012326	0.00560899	upregulated
Solyc12g019550.2	32447.7896	0.51160391	0.00013612	0.00595352	upregulated
Solyc12g036390.2	126.814371	1.81300508	9.19E-05	0.00448764	upregulated
Solyc12g042110.3	1011.49568	0.80609501	6.49E-05	0.00353513	upregulated
Solyc12g042480.3	34.2212106	2.60591242	0.00146076	0.03084029	upregulated
Solyc12g044300.2	2833.51667	0.44580289	0.00019739	0.00777476	upregulated
Solyc12g049030.1	26.1646007	3.82031477	0.00248396	0.04365406	upregulated
Solyc12g049530.2	378.218031	0.82459155	0.00027178	0.00986101	upregulated
Solyc12g056100.3	2012.34287	0.40431209	0.00071301	0.01934327	upregulated
Solyc12g056510.3	2031.5752	0.45597775	0.00289493	0.04797351	upregulated
Solyc12g056610.3	380.664258	1.69626311	5.73E-06	0.00063729	upregulated
Solyc12g056710.3	745.638206	1.61923487	2.30E-07	6.09E-05	upregulated
Solyc12g087840.1	278.499122	1.16384812	9.47E-06	0.00091123	upregulated
Solyc12g088250.2	1411.91691	0.70432145	3.45E-06	0.00045378	upregulated
Solyc12g088460.3	428.915215	0.82995219	0.00217399	0.04034378	upregulated
Solyc12g094630.2	6125.34579	0.34666075	0.00215039	0.04002547	upregulated
Solyc12g096770.1	7689.85952	0.76317479	0.00078779	0.02064373	upregulated
Solyc12g098510.1	375.430866	0.58823949	0.00218627	0.04034378	upregulated
Solyc12g100060.1	4101.31837	0.73036466	0.00013106	0.00578673	upregulated
Solyc12g100280.3	69.2430173	1.35594939	0.00206251	0.03906654	upregulated
Solyc12g150113.1	1177.64604	0.8948753	1.01E-05	0.00095463	upregulated

Supplementary Material 7.8. Table of differentially expressed genes between self-grafted and heterografted conditions: Tomato/RS-2 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Gene ID	baseMean	log2FC	pvalue	padj	expression
Solyc01g005300.4	406.78223	-2.5704296	1.66E-24	3.91E-21	downregulated
Solyc01g005470.3	421.990524	-0.8781508	0.00063366	0.01421146	downregulated
Solyc01g005560.3	12337.2558	-0.69203	1.09E-09	2.77E-07	downregulated
Solyc01g005720.3	367.450776	-0.9433917	5.83E-05	0.00229687	downregulated
Solyc01g005930.3	700.270261	-0.5565362	0.00198698	0.03308823	downregulated
Solyc01g006020.4	1636.21399	-0.9319891	1.21E-08	2.03E-06	downregulated
Solyc01g006555.1	4114.41073	-0.7998942	0.00134665	0.02505438	downregulated
Solyc01g006830.3	9024.18728	-0.9586064	1.02E-25	3.21E-22	downregulated
Solyc01g007860.3	4746.7745	-0.3516433	0.00116109	0.02269782	downregulated
Solyc01g008790.4	2978.45352	-0.5156599	0.00112502	0.02217635	downregulated

Solyc01g008940.2	155.754158	-1.2272438	4.15E-05	0.00181154	downregulated
Solyc01g009380.3	615.596881	-0.521366	0.00052969	0.01247216	downregulated
Solyc01g009850.4	888.085477	-0.467903	0.00123663	0.02360217	downregulated
Solyc01g010480.3	10437.7995	-1.5383949	7.90E-06	0.00048275	downregulated
Solyc01g049880.3	412.01887	-0.884314	3.88E-06	0.00027222	downregulated
Solyc01g066290.2	78.0818987	-1.1114871	0.00332797	0.0483055	downregulated
Solyc01g067680.3	764.152614	-0.6664727	5.22E-06	0.00034972	downregulated
Solyc01g068060.4	1499.62609	-0.5932253	1.33E-05	0.00073609	downregulated
Solyc01g073970.3	79.1848832	-1.7551298	8.17E-05	0.0029912	downregulated
Solyc01g079470.4	17076.6723	-1.0433496	7.73E-06	0.00047381	downregulated
Solyc01g080220.3	1322.25738	-0.5796572	0.00249541	0.03917153	downregulated
Solyc01g081450.3	1393.55485	-0.4437737	0.00188566	0.03190755	downregulated
Solyc01g081510.4	127.779875	-0.9634807	4.29E-05	0.00185143	downregulated
Solyc01g086710.4	627.430966	-0.5293825	0.00283223	0.04313207	downregulated
Solyc01g087270.3	474.850044	-1.1349252	0.00313788	0.04632972	downregulated
Solyc01g087620.3	3423.30666	-0.5546219	3.66E-05	0.00164576	downregulated
Solyc01g087680.4	2447.17953	-0.4634358	4.66E-05	0.00197872	downregulated
Solyc01g087710.2	2100.52148	-0.4985061	0.00055937	0.01299271	downregulated
Solyc01g087810.2	95.4971922	-1.5915036	0.00045108	0.01113488	downregulated
Solyc01g090500.4	599.338423	-0.5714204	0.00069578	0.01528808	downregulated
Solyc01g090680.3	1058.13247	-0.8375622	0.00132806	0.02486227	downregulated
Solyc01g091690.3	493.572561	-1.170164	2.77E-09	6.09E-07	downregulated
Solyc01g091830.3	231.533349	-1.4288922	1.08E-06	9.13E-05	downregulated
Solyc01g091900.3	553.852098	-0.4181732	0.00243335	0.03848528	downregulated
Solyc01g094370.3	2186.48373	-0.5160445	0.00258756	0.04018376	downregulated
Solyc01g094830.4	1257.60898	-0.4342467	0.00056965	0.01313438	downregulated
Solyc01g095270.3	904.779829	-0.9671149	3.86E-06	0.00027222	downregulated
Solyc01g095530.2	12384.478	-0.8571668	2.80E-07	2.92E-05	downregulated
Solyc01g095740.4	1987.3468	-0.5881565	0.00025207	0.00708777	downregulated
Solyc01g096050.4	667.487538	-0.7947077	0.00165475	0.02912234	downregulated
Solyc01g096400.4	537.799851	-0.8753221	6.90E-06	0.00043573	downregulated
Solyc01g097000.3	947.928956	-0.6608828	8.95E-05	0.00322981	downregulated
Solyc01g097020.4	1162.04707	-0.6338824	5.19E-05	0.00213321	downregulated
Solyc01g097610.3	561.975992	-0.5021475	0.00120071	0.02316349	downregulated
Solyc01g097860.4	31888.8638	-0.3874317	0.0007734	0.01655891	downregulated
Solyc01g098920.4	2329.99796	-0.3037984	0.00285099	0.04331124	downregulated
Solyc01g099010.3	1927.21278	-0.6079593	0.00051313	0.0121935	downregulated
Solyc01g099750.2	664.222056	-0.7988254	0.00030646	0.00826743	downregulated
Solyc01g099800.4	117.004345	-0.9795989	0.00182129	0.03112512	downregulated
Solyc01g100230.3	2966.66741	-1.3382784	0.00039295	0.00997364	downregulated
Solyc01g100780.3	74.9706258	-1.1292404	0.00158065	0.02802837	downregulated

Solyc01g103390.3	109.24213	-1.0129885	0.0028548	0.04331124	downregulated
Solyc01g103540.3	18512.2118	-0.5657534	0.00148031	0.0268045	downregulated
Solyc01g104650.3	512.10649	-0.7124217	0.00248717	0.03907459	downregulated
Solyc01g105030.3	164141.034	-0.3221554	0.00286234	0.04331124	downregulated
Solyc01g105710.3	1821.42054	-0.572534	6.49E-06	0.00041528	downregulated
Solyc01g106000.4	2433.30209	-0.8491652	3.81E-06	0.0002707	downregulated
Solyc01g106400.3	727.594061	-0.510501	0.00104848	0.02106339	downregulated
Solyc01g106450.3	1869.71707	-0.4564123	0.00030616	0.00826743	downregulated
Solyc01g108300.3	2263.99341	-0.5376158	0.00016468	0.00512779	downregulated
Solyc01g108560.4	143.195697	-0.9062069	0.00044264	0.01095527	downregulated
Solyc01g108570.3	413.371439	-0.6889433	0.00157532	0.02801156	downregulated
Solyc01g108910.4	489.283359	-1.2535272	5.34E-12	2.59E-09	downregulated
Solyc01g109090.2	330.429841	-1.9891301	7.44E-22	1.28E-18	downregulated
Solyc01g109100.2	697.076866	-1.5873403	4.66E-09	9.46E-07	downregulated
Solyc01g109630.4	713.55627	-0.3800175	0.00229676	0.03703843	downregulated
Solyc01g109660.2	45964.4893	-1.2707075	9.72E-15	8.34E-12	downregulated
Solyc01g110390.2	3600.79019	-0.3662015	0.00095381	0.01953543	downregulated
Solyc01g110400.2	404.020828	-0.760172	5.07E-05	0.00210338	downregulated
Solyc01g111170.3	50649.4985	-0.6121643	5.44E-07	5.16E-05	downregulated
Solyc01g111300.4	6056.10109	-1.4761827	2.01E-16	2.38E-13	downregulated
Solyc01g111600.3	2279.20545	-0.7586296	1.00E-12	6.29E-10	downregulated
Solyc01g112100.3	1080.93663	-0.5770671	0.00217326	0.03534863	downregulated
Solyc01g150144.1	219.380538	-0.8524552	0.00117836	0.02291669	downregulated
Solyc01g150166.1	1521.3199	-0.4129171	0.00126034	0.02384798	downregulated
Solyc02g014310.4	4573.58907	-0.4615534	2.92E-05	0.00136674	downregulated
Solyc02g014860.3	72.3177251	-2.8431086	2.66E-05	0.00127265	downregulated
Solyc02g021400.2	3082.11783	-0.5788145	0.0023138	0.03721782	downregulated
Solyc02g021440.4	2729.78074	-0.528167	0.00080321	0.01708088	downregulated
Solyc02g030170.4	28086.2065	-0.3410855	0.00014153	0.00456085	downregulated
Solyc02g031850.1	259.000637	-1.0129891	5.77E-05	0.00229104	downregulated
Solyc02g031900.3	601.321802	-0.696969	7.96E-06	0.00048512	downregulated
Solyc02g036470.4	2069.85814	-0.3710428	0.00150947	0.02712164	downregulated
Solyc02g043940.1	302.967623	-0.7936869	0.00036416	0.00940735	downregulated
Solyc02g063220.3	1792.31251	-0.7631007	9.62E-07	8.33E-05	downregulated
Solyc02g063410.3	356.767056	-1.319863	6.26E-05	0.00241092	downregulated
Solyc02g063450.4	5593.54432	-1.2182457	0.0008201	0.01736176	downregulated
Solyc02g063510.1	232.245046	-0.9186453	0.00046158	0.01133475	downregulated
Solyc02g064690.3	91.3212239	-1.8293202	0.00039193	0.00996112	downregulated
Solyc02g064730.3	8132.97464	-0.5666372	2.17E-05	0.0010866	downregulated
Solyc02g064950.3	5648.38439	-0.539045	0.00011239	0.00379661	downregulated
Solyc02g065400.3	308209.716	-0.3536579	0.00085853	0.01797065	downregulated

Solyc02g065780.1	743.787379	-1.0121573	6.42E-05	0.00246982	downregulated
Solyc02g066930.3	355.473489	-0.9407609	5.69E-09	1.06E-06	downregulated
Solyc02g067420.3	1287.70142	-0.4111279	0.00077043	0.01651404	downregulated
Solyc02g067690.3	515.596935	-0.7759681	0.00010513	0.00360951	downregulated
Solyc02g068270.4	3941.53083	-0.3961685	0.00062267	0.0140316	downregulated
Solyc02g068710.3	1124.57616	-0.7676168	2.62E-07	2.78E-05	downregulated
Solyc02g068760.4	2716.65242	-0.5830846	4.20E-05	0.00182835	downregulated
Solyc02g069100.4	2969.04881	-0.4041695	0.00083261	0.0175873	downregulated
Solyc02g070240.3	395.262217	-0.5571705	0.00036178	0.00938436	downregulated
Solyc02g070560.3	882.184257	-0.5458629	0.00266897	0.04109188	downregulated
Solyc02g070820.1	74.1701139	-1.9401698	2.11E-07	2.36E-05	downregulated
Solyc02g070990.1	98313.0933	-0.7393206	0.0005757	0.01319354	downregulated
Solyc02g071020.3	77.9851702	-1.2992187	0.00067024	0.01483791	downregulated
Solyc02g071150.3	3544.24373	-0.3917039	0.00052432	0.01236113	downregulated
Solyc02g071280.3	1037.05701	-0.4920963	0.00060559	0.0137764	downregulated
Solyc02g071750.3	75.2622662	-2.0367287	2.23E-05	0.00111157	downregulated
Solyc02g071870.4	245.506892	-0.8204193	9.52E-05	0.00338716	downregulated
Solyc02g076690.3	3450.47357	-1.9967347	4.13E-31	2.60E-27	downregulated
Solyc02g076720.3	4471.66577	-0.4057371	0.00324945	0.0474943	downregulated
Solyc02g077770.3	254.322534	-1.1022561	5.89E-05	0.00230182	downregulated
Solyc02g078450.3	1734.93379	-0.8293217	1.74E-06	0.00013656	downregulated
Solyc02g078460.3	928.667733	-0.5180941	0.00174857	0.03023433	downregulated
Solyc02g079570.4	390.07173	-0.5343918	0.00202235	0.03350007	downregulated
Solyc02g079770.3	5577.18994	-0.472149	0.00184314	0.03141308	downregulated
Solyc02g079790.3	99.1254651	-1.1288831	0.00021359	0.0061863	downregulated
Solyc02g080070.3	2916.10118	-0.4470369	0.00020603	0.00606029	downregulated
Solyc02g080140.4	676.214645	-0.5171924	0.00315775	0.04658669	downregulated
Solyc02g080420.4	2998.77187	-0.4759575	6.95E-07	6.28E-05	downregulated
Solyc02g081060.4	307.963258	-1.3969038	2.37E-08	3.70E-06	downregulated
Solyc02g081880.3	2282.44246	-0.6322533	1.07E-06	9.09E-05	downregulated
Solyc02g082000.3	2369.66817	-0.7287684	0.00172322	0.02996431	downregulated
Solyc02g082700.3	7676.35757	-0.4630745	0.00032676	0.00869091	downregulated
Solyc02g083310.3	1858.67085	-0.5542359	1.94E-05	0.00098039	downregulated
Solyc02g083340.4	2408.06111	-0.3336255	0.00336836	0.04877916	downregulated
Solyc02g084020.3	626.186608	-0.4853229	0.00186871	0.03167753	downregulated
Solyc02g084240.3	515.307046	-1.1659636	0.00036352	0.00940364	downregulated
Solyc02g085300.4	2353.88173	-0.5504502	0.00238045	0.03780695	downregulated
Solyc02g085540.1	2783.6376	-0.3433823	0.00033369	0.00882549	downregulated
Solyc02g086380.1	249.319208	-0.7610191	0.00057117	0.01313438	downregulated
Solyc02g086660.4	1288.23319	-0.5187251	0.00127297	0.02396679	downregulated
Solyc02g087060.4	2041.97537	-0.540162	4.41E-05	0.00188755	downregulated

Solyc02g087110.3	2211.16153	-0.6460547	0.00242397	0.03840118	downregulated
Solyc02g087400.1	11476.3354	-0.3225125	0.00296295	0.04444759	downregulated
Solyc02g087560.1	1432.56986	-0.544465	0.00131747	0.02475539	downregulated
Solyc02g087850.1	3271.3042	-0.5466959	0.00080576	0.01711242	downregulated
Solyc02g088790.3	395.043086	-0.6564964	0.00234356	0.03745015	downregulated
Solyc02g089065.1	14614.3987	-0.3971767	0.00143208	0.02624254	downregulated
Solyc02g089820.4	2058.09657	-0.3693256	0.00174232	0.03015756	downregulated
Solyc02g090100.1	10692.5814	-0.4524636	4.82E-07	4.67E-05	downregulated
Solyc02g090390.4	1147.21885	-0.8513362	5.65E-06	0.0003738	downregulated
Solyc02g090430.3	2419.18499	-0.541783	0.00064505	0.01437691	downregulated
Solyc02g090840.3	4206.57495	-0.6140407	1.03E-07	1.26E-05	downregulated
Solyc02g090890.4	45333.4696	-0.3122346	0.00190582	0.03219097	downregulated
Solyc02g090900.3	2864.15646	-0.3586737	0.00158071	0.02802837	downregulated
Solyc02g092270.3	3841.74437	-0.3880316	1.82E-05	0.00093115	downregulated
Solyc02g092590.3	844.882981	-0.9899227	5.35E-09	1.04E-06	downregulated
Solyc02g092845.1	164.107768	-1.0164642	0.0001489	0.00473358	downregulated
Solyc02g093110.3	4562.29917	-0.3530402	0.0009833	0.02001254	downregulated
Solyc02g094030.3	1418.45858	-0.4580657	0.00085675	0.01795658	downregulated
Solyc03g005740.3	1151.32562	-0.6621774	3.78E-08	5.49E-06	downregulated
Solyc03g005780.3	277259.8	-0.4056202	0.00018945	0.00566079	downregulated
Solyc03g005820.3	2021.92884	-0.5748621	0.00028013	0.00772255	downregulated
Solyc03g006410.3	2963.00247	-0.9091862	4.69E-08	6.37E-06	downregulated
Solyc03g006550.4	163.666759	-1.2761011	0.00195444	0.03271258	downregulated
Solyc03g007220.3	1444.49166	-0.7573921	2.60E-06	0.00019749	downregulated
Solyc03g019650.3	1900.22867	-0.8177795	7.35E-08	9.38E-06	downregulated
Solyc03g019890.3	2154.8135	-0.3026976	0.00144756	0.02642097	downregulated
Solyc03g025600.3	1768.80343	-0.3545464	0.00244867	0.03863052	downregulated
Solyc03g025910.3	2280.16878	-0.5100548	0.00136012	0.02523043	downregulated
Solyc03g026130.3	207.84039	-1.0333925	6.93E-06	0.00043635	downregulated
Solyc03g026240.4	1742.04976	-0.3206663	0.00312998	0.04624918	downregulated
Solyc03g026320.4	1763.54873	-0.740616	7.02E-08	9.08E-06	downregulated
Solyc03g031600.3	1721.00129	-0.7356662	4.31E-08	6.12E-06	downregulated
Solyc03g031840.3	822.278098	-0.6264846	1.37E-05	0.00074552	downregulated
Solyc03g031980.4	214.574926	-0.7444193	0.00049253	0.01183336	downregulated
Solyc03g031990.4	904.646608	-1.342023	2.85E-09	6.19E-07	downregulated
Solyc03g033500.4	460.252778	-0.5335158	0.00101456	0.02051273	downregulated
Solyc03g043860.2	107.726167	-1.5261496	0.00166506	0.02917757	downregulated
Solyc03g044630.2	504.474151	-1.2067124	9.66E-05	0.00340974	downregulated
Solyc03g051920.4	784.089999	-0.357051	0.00226422	0.03667024	downregulated
Solyc03g059170.2	8981.71009	-0.4444301	0.00089893	0.01865432	downregulated
Solyc03g078610.3	1810.74059	-0.5953011	6.01E-06	0.00038997	downregulated

Solyc03g078720.4	247.621649	-0.6050472	0.00346937	0.04973264	downregulated
Solyc03g078730.3	179.695447	-1.1217075	0.00010921	0.00371575	downregulated
Solyc03g081240.3	111.074492	-1.7306412	4.83E-06	0.00033383	downregulated
Solyc03g082570.4	226.977665	-1.0009193	0.00148824	0.02689376	downregulated
Solyc03g082620.4	4639.9545	-0.6855848	0.0001354	0.00440835	downregulated
Solyc03g083090.4	3509.30145	-0.7776035	4.65E-09	9.46E-07	downregulated
Solyc03g083250.3	3225.11928	-0.7902109	1.56E-11	6.25E-09	downregulated
Solyc03g083520.4	2296.10193	-0.3462498	0.00013929	0.00451173	downregulated
Solyc03g093510.2	1380.8775	-0.4409672	0.00169197	0.02950248	downregulated
Solyc03g093540.1	146.190532	-1.1640875	0.00124541	0.02370802	downregulated
Solyc03g093800.1	989.845405	-1.2045696	2.92E-13	2.04E-10	downregulated
Solyc03g094060.4	163.818375	-0.9539139	0.0006875	0.01514917	downregulated
Solyc03g095730.4	1527.58748	-0.3706678	0.00275993	0.04223538	downregulated
Solyc03g096390.3	780.336297	-0.556385	0.002617	0.04047454	downregulated
Solyc03g097140.3	1806.00698	-0.3593872	0.00296083	0.04444759	downregulated
Solyc03g098240.3	475.064588	-1.0740828	3.39E-07	3.43E-05	downregulated
Solyc03g110860.3	3547.80689	-0.6485989	6.20E-05	0.00240282	downregulated
Solyc03g111260.3	2012.15823	-0.5033043	0.00021036	0.00615896	downregulated
Solyc03g111330.4	1135.75138	-0.4706584	9.38E-05	0.00335156	downregulated
Solyc03g111850.3	2616.80227	-0.4288832	2.84E-06	0.00021251	downregulated
Solyc03g112210.1	673.253127	-0.6233484	3.68E-05	0.00164704	downregulated
Solyc03g112900.3	5415.35689	-0.3822623	5.69E-05	0.00226271	downregulated
Solyc03g113060.3	2288.2952	-0.7973706	1.21E-08	2.03E-06	downregulated
Solyc03g113460.1	765.04074	-0.7550794	7.45E-09	1.34E-06	downregulated
Solyc03g113730.3	2651.81762	-0.6100981	0.00048965	0.01177894	downregulated
Solyc03g113920.4	8162.23027	-0.5049637	0.00022223	0.00635853	downregulated
Solyc03g114130.1	478.940774	-1.2633402	9.01E-09	1.58E-06	downregulated
Solyc03g114150.3	7775.88758	-0.5526844	0.00229448	0.03703323	downregulated
Solyc03g114510.4	1645.57754	-0.4424648	0.00125614	0.02382379	downregulated
Solyc03g114580.4	1940.0647	-0.6910951	0.00023503	0.00666919	downregulated
Solyc03g114970.3	1118.88013	-0.613247	1.74E-05	0.00089813	downregulated
Solyc03g115020.3	19107.3038	-0.6132675	5.80E-05	0.00229296	downregulated
Solyc03g115815.1	271.728052	-1.445754	2.85E-05	0.00134259	downregulated
Solyc03g115900.4	344650.495	-0.3125481	0.00221281	0.0359301	downregulated
Solyc03g116670.3	9070.63368	-1.0791076	9.09E-09	1.58E-06	downregulated
Solyc03g116800.4	1829.54658	-0.3925249	9.52E-05	0.00338716	downregulated
Solyc03g116820.4	206.377428	-0.7515975	0.00210386	0.03451744	downregulated
Solyc03g117430.3	3838.88889	-0.5088247	0.00029831	0.00812879	downregulated
Solyc03g117510.4	478.866389	-0.6308527	0.00113664	0.02235857	downregulated
Solyc03g117810.4	2138.57037	-0.7920869	7.11E-05	0.00267973	downregulated
Solyc03g118170.3	3949.16679	-1.1861574	4.36E-20	6.86E-17	downregulated

Solyc03g118300.1	380.970935	-1.4370993	5.44E-10	1.45E-07	downregulated
Solyc03g118630.3	304.39573	-0.9024919	1.33E-06	0.00010846	downregulated
Solyc03g118770.4	55.0773574	-1.9172773	0.00017312	0.00532059	downregulated
Solyc03g118810.1	513.498986	-0.604027	0.00093489	0.01925908	downregulated
Solyc03g119080.4	7315.48086	-0.5689047	3.81E-08	5.49E-06	downregulated
Solyc03g119150.4	7953.08092	-0.3611528	0.0010775	0.02148629	downregulated
Solyc03g119250.4	314.330917	-0.6174779	0.00173043	0.03003445	downregulated
Solyc03g119930.1	4397.82779	-0.9374998	3.60E-05	0.00162751	downregulated
Solyc03g119970.3	4130.96846	-0.4139076	0.00194299	0.0325857	downregulated
Solyc03g120490.3	1365.6264	-0.3408804	0.00248657	0.03907459	downregulated
Solyc03g120640.3	101554.877	-0.5286187	1.40E-06	0.00011212	downregulated
Solyc03g120740.1	111.113454	-0.8243554	0.00235893	0.03760388	downregulated
Solyc03g121070.3	2468.06898	-0.8059907	2.57E-12	1.43E-09	downregulated
Solyc03g122340.3	1235.27073	-0.6215957	0.00029098	0.00798979	downregulated
Solyc03g123610.4	3572.97379	-0.2903354	0.00259867	0.04025707	downregulated
Solyc03g123710.3	112.04449	-1.2379231	0.00168294	0.02939937	downregulated
Solyc03g123860.4	362.239625	-0.5732742	0.00058814	0.01344614	downregulated
Solyc04g005555.1	411.888213	-1.4644927	9.60E-10	2.52E-07	downregulated
Solyc04g007780.3	365.287183	-1.4761201	2.69E-05	0.00128027	downregulated
Solyc04g007790.3	46415.3983	-0.8698162	2.53E-07	2.72E-05	downregulated
Solyc04g007990.1	654.507868	-0.8055913	9.57E-06	0.00056294	downregulated
Solyc04g008040.4	7736.88227	-0.6748159	1.75E-11	6.88E-09	downregulated
Solyc04g008280.2	2529.975	-0.5453161	8.47E-06	0.00050909	downregulated
Solyc04g008300.1	699.177054	-0.4737575	0.00291095	0.04397635	downregulated
Solyc04g008730.3	1000.59921	-0.7267806	2.66E-05	0.00127265	downregulated
Solyc04g010100.2	649.449659	-0.9018787	1.54E-07	1.78E-05	downregulated
Solyc04g010190.1	8477.23308	-0.4191331	0.00177284	0.03043487	downregulated
Solyc04g014510.3	2383.40206	-0.6352402	0.00088527	0.0184315	downregulated
Solyc04g014645.1	30.3956219	-1.784788	0.00345744	0.04965048	downregulated
Solyc04g015040.3	5849.79114	-0.3635235	0.00230761	0.03714999	downregulated
Solyc04g015560.4	1953.14158	-0.6903602	0.00015669	0.00491516	downregulated
Solyc04g017690.3	3894.11259	-0.6081116	0.00133064	0.02486227	downregulated
Solyc04g050560.4	337.038384	-0.5082336	0.00155385	0.02773426	downregulated
Solyc04g050620.3	889.488086	-1.1036599	1.52E-05	0.00080887	downregulated
Solyc04g054370.1	2753.36658	-0.623784	6.67E-07	6.15E-05	downregulated
Solyc04g054980.3	8794.87501	-0.6085921	7.67E-06	0.00047298	downregulated
Solyc04g058050.1	44.7289123	-1.2982732	0.00330774	0.04812274	downregulated
Solyc04g058150.3	11440.6083	-0.9602687	9.11E-09	1.58E-06	downregulated
Solyc04g063380.3	1226.15187	-0.6030586	6.42E-06	0.00041253	downregulated
Solyc04g064870.3	261.835254	-0.8426775	0.00110292	0.02184213	downregulated
Solyc04g071140.3	3894.96122	-1.0877715	3.13E-07	3.21E-05	downregulated

Solyc04g071800.3	18939.0751	-0.8405756	1.16E-06	9.62E-05	downregulated
Solyc04g071900.4	485.025972	-0.7446909	0.00145002	0.02643062	downregulated
Solyc04g071990.3	2392.4482	-0.6607111	1.12E-07	1.36E-05	downregulated
Solyc04g072034.1	837.963711	-0.4574502	0.00029561	0.00806685	downregulated
Solyc04g072240.3	1885.03118	-0.3505168	0.00033918	0.00888358	downregulated
Solyc04g072380.3	226.680433	-0.6574802	0.0014984	0.026962	downregulated
Solyc04g074920.2	434.508413	-0.766967	0.0015472	0.02766793	downregulated
Solyc04g076780.4	495.32058	-0.6885382	1.72E-05	0.00089091	downregulated
Solyc04g077000.3	116.513965	-1.1426849	0.00186648	0.03166809	downregulated
Solyc04g077030.3	461.778242	-0.5889974	0.00345239	0.04964701	downregulated
Solyc04g077120.4	1768.07115	-0.4677623	8.69E-06	0.00051927	downregulated
Solyc04g078070.4	6027.92459	-0.5219003	1.54E-05	0.00081095	downregulated
Solyc04g078195.1	5849.44604	-0.8391806	2.60E-05	0.00125189	downregulated
Solyc04g079040.4	2160.91037	-0.6567295	1.15E-09	2.86E-07	downregulated
Solyc04g079640.3	1440.05633	-0.9949007	4.92E-08	6.63E-06	downregulated
Solyc04g080390.4	1529.57012	-0.4348411	5.57E-05	0.00222788	downregulated
Solyc04g080700.4	1803.80182	-1.4519328	3.19E-12	1.63E-09	downregulated
Solyc04g080730.3	3849.31867	-0.322895	0.00126899	0.02396476	downregulated
Solyc04g080870.1	4031.86394	-0.7953976	1.53E-09	3.63E-07	downregulated
Solyc04g080960.4	32064.2102	-0.7719761	0.00067761	0.01498363	downregulated
Solyc04g081550.3	784.649952	-1.0686755	4.71E-10	1.31E-07	downregulated
Solyc04g081590.4	2376.24426	-0.7337051	9.39E-05	0.00335156	downregulated
Solyc04g081880.4	10250.2579	-0.4652051	0.00057553	0.01319354	downregulated
Solyc04g082000.4	1540.82404	-1.1696285	1.78E-15	1.76E-12	downregulated
Solyc04g082010.1	9545.11819	-0.8145566	0.00064382	0.01437691	downregulated
Solyc04g082040.3	1136.64307	-0.7201066	7.10E-06	0.00044423	downregulated
Solyc04g082050.3	168.726815	-1.4257849	1.26E-05	0.00070581	downregulated
Solyc04g082235.1	2262.96122	-0.7333121	1.74E-10	5.31E-08	downregulated
Solyc04g082740.4	756.784601	-0.6538637	5.12E-05	0.00211981	downregulated
Solyc04g082910.1	1012.32481	-0.9046733	5.21E-05	0.00213321	downregulated
Solyc04g150159.1	900.586539	-0.8664659	0.00023517	0.00666919	downregulated
Solyc04g150163.1	91.9339774	-1.0907316	0.00127135	0.02396476	downregulated
Solyc05g006850.4	1751.53913	-0.6043559	5.40E-05	0.00218183	downregulated
Solyc05g007070.2	3570.97565	-0.7176565	2.90E-07	3.01E-05	downregulated
Solyc05g007140.3	1501.58661	-0.4850562	3.30E-05	0.0015136	downregulated
Solyc05g007770.3	138.674828	-2.0063426	0.00029539	0.00806685	downregulated
Solyc05g008010.3	3801.28027	-0.3146532	0.00143203	0.02624254	downregulated
Solyc05g008105.1	972.093772	-0.742006	0.00038856	0.00990217	downregulated
Solyc05g008120.4	51.3759814	-1.4540089	0.00163965	0.02891059	downregulated
Solyc05g008290.4	4544.73878	-0.7435355	5.61E-09	1.06E-06	downregulated
Solyc05g008810.4	2109.55552	-0.5216202	0.00057173	0.01313438	downregulated

Solyc05g009260.1	87.2039137	-1.0632604	0.00185385	0.03153885	downregulated
Solyc05g009630.4	817.762228	-0.419005	0.00069624	0.01528808	downregulated
Solyc05g010240.4	824.579792	-1.9142771	4.63E-30	2.19E-26	downregulated
Solyc05g010340.3	324.404025	-0.8791419	7.52E-05	0.00281036	downregulated
Solyc05g010590.4	2072.13212	-0.5694596	2.22E-06	0.00017092	downregulated
Solyc05g010685.1	1239.40121	-0.6001134	0.00064933	0.01444273	downregulated
Solyc05g012200.3	706.133319	-0.7188077	0.00025983	0.0072477	downregulated
Solyc05g012580.1	33508.1239	-0.6665337	4.94E-05	0.00206808	downregulated
Solyc05g013480.4	6038.27981	-0.4539729	6.46E-05	0.00247591	downregulated
Solyc05g013560.3	679.419512	-1.0909648	8.64E-11	2.77E-08	downregulated
Solyc05g014051.1	30.5984197	-6.0510163	1.04E-05	0.00060379	downregulated
Solyc05g014790.3	1271.09517	-0.3821116	0.00253579	0.03964066	downregulated
Solyc05g015150.3	1475.38002	-0.4384527	0.00073861	0.01600302	downregulated
Solyc05g026490.3	4465.73375	-0.6469167	1.82E-05	0.00093115	downregulated
Solyc05g046390.3	3064.60097	-0.5322221	1.33E-05	0.00073546	downregulated
Solyc05g047680.4	479.423467	-2.0916148	3.20E-09	6.80E-07	downregulated
Solyc05g050120.3	6156.26951	-0.7496778	3.02E-05	0.00139914	downregulated
Solyc05g050380.4	535.739621	-0.8181177	0.00106966	0.02142042	downregulated
Solyc05g052470.3	630.543036	-0.837491	2.06E-05	0.00103658	downregulated
Solyc05g052520.3	740.876882	-0.5610794	0.00309728	0.04587378	downregulated
Solyc05g052890.3	179.806161	-1.8340219	1.35E-05	0.00074074	downregulated
Solyc05g053100.3	6074.87545	-0.3947922	0.00012028	0.00403446	downregulated
Solyc05g054120.1	929.581752	-0.9084821	2.12E-08	3.34E-06	downregulated
Solyc05g054350.3	7464.01202	-0.6509662	5.35E-05	0.00216821	downregulated
Solyc05g054560.3	149.535556	-0.9426354	0.00203418	0.03361948	downregulated
Solyc05g054850.1	42.5715856	-1.5025992	0.00261156	0.04042348	downregulated
Solyc05g055250.2	594.752626	-0.6276889	0.00059394	0.01354589	downregulated
Solyc05g055310.3	3666.09388	-0.821093	3.49E-07	3.48E-05	downregulated
Solyc05g056060.4	155974.766	-0.4324938	7.19E-06	0.00044781	downregulated
Solyc05g056200.1	72.7515432	-1.1877472	0.00149742	0.026962	downregulated
Solyc05g056350.3	5956.53193	-0.3581853	0.00038795	0.00989995	downregulated
Solyc06g005970.2	555.4641	-0.4925286	0.00165819	0.0291557	downregulated
Solyc06g006000.3	123.522224	-1.4282144	2.75E-05	0.0013005	downregulated
Solyc06g006080.3	12600.7669	-1.1827273	6.99E-17	8.80E-14	downregulated
Solyc06g006100.3	1321.34961	-0.6680124	5.66E-07	5.30E-05	downregulated
Solyc06g007210.3	2282.22698	-0.8946604	2.49E-05	0.00122574	downregulated
Solyc06g007220.4	2136.16084	-0.9391861	6.73E-05	0.00255736	downregulated
Solyc06g007440.4	9847.31704	-0.4691451	0.00126972	0.02396476	downregulated
Solyc06g008030.3	301.0631	-1.1580598	5.28E-05	0.00214463	downregulated
Solyc06g009140.3	193.603177	-1.4229771	0.00017946	0.0054484	downregulated
Solyc06g009630.1	22763.1759	-0.6168735	4.06E-10	1.14E-07	downregulated

Solyc06g031680.2	462.585349	-0.8188157	6.93E-07	6.28E-05	downregulated
Solyc06g031690.4	704.7504	-0.5835589	0.00051945	0.01229246	downregulated
Solyc06g034290.3	923.787385	-0.9273173	8.39E-06	0.00050755	downregulated
Solyc06g035870.3	2632.13203	-0.5917009	2.90E-09	6.21E-07	downregulated
Solyc06g036520.1	895.640127	-0.7770225	0.00106742	0.02139833	downregulated
Solyc06g036540.1	994.398857	-0.8127266	4.96E-09	9.97E-07	downregulated
Solyc06g048410.4	27095.7139	-0.7940745	0.00148784	0.02689376	downregulated
Solyc06g051250.1	200.398951	-1.4858155	5.34E-10	1.44E-07	downregulated
Solyc06g051680.1	84.3628677	-1.5465534	0.00032631	0.00869091	downregulated
Solyc06g053180.4	819.431206	-0.8428677	3.62E-05	0.00163	downregulated
Solyc06g053810.3	1534.03848	-0.3951387	0.00337819	0.0488841	downregulated
Solyc06g053980.3	524.566299	-1.0561961	2.68E-08	4.15E-06	downregulated
Solyc06g054250.4	1745.57291	-0.5031305	9.85E-05	0.00345207	downregulated
Solyc06g054260.1	235878.651	-0.3460644	0.00021902	0.00628562	downregulated
Solyc06g054370.2	46.5227481	-1.7232583	0.00042215	0.01054488	downregulated
Solyc06g060080.2	2302.40783	-0.4971367	0.00032521	0.00867409	downregulated
Solyc06g060140.4	2369.71669	-0.4258692	0.0032029	0.04692287	downregulated
Solyc06g063370.3	605965.715	-0.331672	0.00035514	0.00922489	downregulated
Solyc06g065330.4	2141.04204	-0.3416145	0.00108263	0.02153934	downregulated
Solyc06g065650.3	1177.2096	-0.8964008	8.94E-09	1.58E-06	downregulated
Solyc06g066640.3	44129.67	-0.4830865	9.09E-05	0.00326867	downregulated
Solyc06g068050.3	101.980723	-0.9790273	0.00175532	0.03029926	downregulated
Solyc06g068080.4	771.736275	-0.4500077	0.00050636	0.01205817	downregulated
Solyc06g068600.3	201.615077	-1.3238861	1.48E-05	0.00079463	downregulated
Solyc06g068620.3	1055.33923	-1.5712401	2.54E-25	6.85E-22	downregulated
Solyc06g069150.1	816.181598	-1.4846174	6.96E-09	1.26E-06	downregulated
Solyc06g069410.3	1243.17672	-0.6157281	7.69E-05	0.00285092	downregulated
Solyc06g071050.4	1699.68399	-0.68556	1.72E-05	0.00089091	downregulated
Solyc06g071380.3	102.222476	-1.074478	0.00295409	0.04444759	downregulated
Solyc06g071820.3	992.076082	-1.0604145	1.01E-15	1.06E-12	downregulated
Solyc06g073170.1	616.48982	-0.6047461	0.00014106	0.00455343	downregulated
Solyc06g073740.3	691.318192	-0.5592286	4.02E-05	0.00176197	downregulated
Solyc06g074200.4	180094.667	-0.5264895	4.95E-05	0.00207008	downregulated
Solyc06g075460.4	159.00394	-1.0455637	0.00094326	0.0193405	downregulated
Solyc06g075810.3	2234.53166	-0.5452511	4.24E-05	0.00184185	downregulated
Solyc06g075830.2	2298.39911	-0.51465	1.50E-06	0.00011977	downregulated
Solyc06g075960.1	1456.8167	-0.44723	0.00053616	0.01256826	downregulated
Solyc06g076140.4	26560.7806	-0.7573966	6.81E-07	6.21E-05	downregulated
Solyc06g076470.3	4175.2378	-0.8704137	8.93E-12	4.00E-09	downregulated
Solyc06g076520.1	794.055236	-0.5450462	0.0003851	0.00984057	downregulated
Solyc06g076850.3	11731.0085	-0.5379952	6.72E-07	6.16E-05	downregulated

Solyc06g076890.1	841.659123	-0.3678635	0.00118762	0.02304939	downregulated
Solyc06g082190.3	137.80435	-1.2316748	2.89E-05	0.00135588	downregulated
Solyc06g082220.4	4439.61189	-0.3704589	0.00031129	0.0083738	downregulated
Solyc06g082910.3	4518.97359	-0.3749326	0.00107346	0.02146049	downregulated
Solyc06g082950.4	95331.4712	-0.4052662	0.00286012	0.04331124	downregulated
Solyc06g083340.3	2320.02725	-0.6847177	5.44E-05	0.00219075	downregulated
Solyc06g083830.4	1459.66985	-0.3607018	0.00343503	0.04951686	downregulated
Solyc06g084050.4	33866.808	-0.5552108	7.00E-06	0.00043887	downregulated
Solyc06g084140.4	2094.9882	-0.4154309	0.00035304	0.00918282	downregulated
Solyc06g084320.1	560.247386	-0.6406796	1.22E-05	0.00069437	downregulated
Solyc06g150130.1	11089.8952	-0.5402245	1.27E-05	0.00070758	downregulated
Solyc07g005720.3	675.765363	-0.8911353	1.07E-09	2.77E-07	downregulated
Solyc07g005790.4	174.809419	-0.7528301	0.00251788	0.03945866	downregulated
Solyc07g005930.4	1050.88524	-1.1349278	7.72E-07	6.87E-05	downregulated
Solyc07g005945.1	126.161534	-1.3452875	3.65E-06	0.00026185	downregulated
Solyc07g007050.1	222.271436	-0.8179675	0.00204003	0.03366412	downregulated
Solyc07g007130.1	284.662395	-0.7420752	0.00177915	0.03051536	downregulated
Solyc07g007150.1	404.026879	-1.2322719	1.16E-05	0.00066227	downregulated
Solyc07g007180.4	901.822381	-0.6149081	0.00207181	0.03410996	downregulated
Solyc07g007330.1	1661.09011	-0.5913376	0.0009106	0.01883427	downregulated
Solyc07g007680.4	1315.26618	-0.3787938	0.0018615	0.03161209	downregulated
Solyc07g007790.3	9165.6321	-0.4078475	0.00329672	0.04809147	downregulated
Solyc07g008200.3	355.669767	-0.7344582	0.00192834	0.03244507	downregulated
Solyc07g008310.3	473.233164	-0.7086753	0.00074112	0.016013	downregulated
Solyc07g008440.3	556.742823	-1.1593062	9.20E-06	0.00054284	downregulated
Solyc07g008770.4	1336.07779	-0.5038325	3.98E-05	0.00174686	downregulated
Solyc07g009437.1	43.2072851	-1.4276978	0.00124049	0.02363822	downregulated
Solyc07g014730.3	713.626079	-1.7793775	2.06E-13	1.49E-10	downregulated
Solyc07g020860.3	8716.56847	-0.3212233	0.00238774	0.03789076	downregulated
Solyc07g024000.3	1351.83648	-0.7719186	9.49E-12	4.07E-09	downregulated
Solyc07g032670.3	94.2941741	-1.0979847	0.0003519	0.00916582	downregulated
Solyc07g041900.3	1817.02958	-1.7466885	2.15E-17	2.90E-14	downregulated
Solyc07g042190.3	2611.10084	-0.4380746	0.00152696	0.02735786	downregulated
Solyc07g043230.3	557.049293	-0.9779814	5.17E-05	0.00213321	downregulated
Solyc07g044760.3	2466.38205	-0.5135364	1.24E-07	1.49E-05	downregulated
Solyc07g045080.3	4383.19376	-0.7518476	9.11E-12	4.00E-09	downregulated
Solyc07g045250.1	687.554496	-0.4708948	0.00244667	0.03863052	downregulated
Solyc07g045470.3	579.423249	-0.6531378	0.00021774	0.00625842	downregulated
Solyc07g045540.4	8577.33812	-0.3170446	0.00340965	0.0492639	downregulated
Solyc07g047700.4	785.058483	-0.5087588	6.23E-05	0.00240636	downregulated
Solyc07g047840.2	819.839904	-0.5350093	0.00196366	0.03281574	downregulated

Solyc07g048040.1	458.071329	-0.4670567	0.00146861	0.02669215	downregulated
Solyc07g049360.3	5417.49592	-0.6239868	6.78E-08	8.83E-06	downregulated
Solyc07g052350.3	13443.4901	-0.4989383	2.82E-06	0.00021232	downregulated
Solyc07g052885.1	130.800488	-0.7712183	0.00234689	0.03746296	downregulated
Solyc07g052950.3	1838.78045	-0.9881071	9.51E-09	1.63E-06	downregulated
Solyc07g053140.3	1224.98039	-0.724826	2.53E-05	0.00123293	downregulated
Solyc07g054300.3	1358.23076	-0.4576781	0.00054757	0.01275009	downregulated
Solyc07g054430.3	1002.76367	-1.0133222	5.26E-05	0.00214405	downregulated
Solyc07g055050.3	6165.05677	-1.0293057	8.49E-06	0.00050909	downregulated
Solyc07g055640.1	1318.53676	-0.9164882	1.25E-05	0.0007053	downregulated
Solyc07g055720.4	158.796248	-3.3504654	2.38E-16	2.64E-13	downregulated
Solyc07g056420.4	24892.8346	-0.5976759	3.15E-07	3.22E-05	downregulated
Solyc07g056430.3	460.196676	-1.1080366	2.36E-05	0.00116702	downregulated
Solyc07g056490.4	3218.57718	-0.3509257	0.00190889	0.03221405	downregulated
Solyc07g056570.1	3365.70247	-0.6585052	0.00015016	0.00475765	downregulated
Solyc07g061930.1	163.378805	-1.6852788	5.32E-08	7.02E-06	downregulated
Solyc07g062060.3	2865.45908	-0.3458639	0.00296499	0.04444759	downregulated
Solyc07g062260.3	698.788462	-0.5875402	0.00054541	0.01274688	downregulated
Solyc07g062700.3	24632.2836	-0.5876048	0.00021637	0.00623794	downregulated
Solyc07g062970.3	679.268232	-0.4943703	0.00153876	0.02754314	downregulated
Solyc07g063220.4	169.323476	-0.7629891	0.00293308	0.0442398	downregulated
Solyc07g063250.3	380.751924	-0.9312225	3.10E-06	0.00022963	downregulated
Solyc07g063530.3	3348.12757	-0.4730522	0.0001907	0.00567997	downregulated
Solyc07g063870.3	2756.61128	-0.4519362	0.00242921	0.03845204	downregulated
Solyc07g064020.4	470.332101	-0.7836404	5.58E-07	5.26E-05	downregulated
Solyc07g064150.4	7796.31992	-0.4118576	0.0006392	0.01430178	downregulated
Solyc07g064160.3	162828.061	-0.8192186	1.28E-10	3.97E-08	downregulated
Solyc07g064620.2	1415.30001	-0.6676734	5.46E-05	0.00219359	downregulated
Solyc07g064680.3	2047.57321	-0.5442766	0.00239532	0.03797923	downregulated
Solyc07g064940.3	3333.95984	-0.4544072	5.66E-06	0.0003738	downregulated
Solyc07g065200.3	2304.02455	-0.568595	3.45E-07	3.46E-05	downregulated
Solyc07g065270.1	5309.12248	-0.4229914	0.00029171	0.00799512	downregulated
Solyc07g065275.1	1630.1525	-0.4870864	3.92E-05	0.0017383	downregulated
Solyc07g065380.4	676.575482	-0.4809373	0.00163301	0.02885736	downregulated
Solyc07g065500.2	5652.8148	-0.7230683	8.02E-08	1.01E-05	downregulated
Solyc07g065940.1	173.791443	-0.8233342	0.00111266	0.02195559	downregulated
Solyc07g066150.1	197419.031	-0.3769598	0.00021346	0.0061863	downregulated
Solyc07g066310.3	396480.121	-0.4845963	3.32E-06	0.0002429	downregulated
Solyc07g066630.4	3037.90139	-0.3306861	0.00214246	0.03502882	downregulated
Solyc07g150140.1	254.804381	-0.8021524	0.00090515	0.01874223	downregulated
Solyc08g005560.3	474.959554	-0.8586063	0.00139453	0.02564198	downregulated

Solyc08g005580.3	332.948533	-0.7327731	0.0003656	0.00943178	downregulated
Solyc08g005960.2	6766.5694	-1.5392118	2.98E-12	1.56E-09	downregulated
Solyc08g006320.4	1574.11708	-0.5713526	1.52E-05	0.00080887	downregulated
Solyc08g006570.4	417.155826	-0.5882369	0.00016757	0.00517898	downregulated
Solyc08g006770.3	659.890943	-1.3735445	5.43E-11	1.87E-08	downregulated
Solyc08g007240.4	1138.61355	-1.932192	2.04E-11	7.67E-09	downregulated
Solyc08g008170.4	1030.42799	-0.649006	1.37E-06	0.00011088	downregulated
Solyc08g008410.3	1215.3458	-0.4302536	0.00341488	0.04930163	downregulated
Solyc08g013900.3	1055.56692	-0.42434	0.00201402	0.03339899	downregulated
Solyc08g013910.4	69.2649228	-1.2595138	0.00210387	0.03451744	downregulated
Solyc08g042120.1	78.8253492	-1.0696314	0.002172	0.03534863	downregulated
Solyc08g060920.4	366.634432	-1.307065	3.02E-05	0.00139914	downregulated
Solyc08g060925.1	126.815584	-1.331136	1.02E-05	0.0005919	downregulated
Solyc08g062960.4	132.574984	-1.8008953	1.28E-08	2.11E-06	downregulated
Solyc08g063090.2	2506.27417	-0.9417021	2.80E-06	0.00021142	downregulated
Solyc08g065260.4	744.846814	-0.6775891	0.00016639	0.0051648	downregulated
Solyc08g066110.3	3357.37987	-0.3683261	0.00138792	0.02554526	downregulated
Solyc08g067320.3	4588.96721	-1.2568864	2.57E-27	9.71E-24	downregulated
Solyc08g067430.4	870.127718	-0.6631714	1.22E-05	0.00069437	downregulated
Solyc08g068070.3	430.049371	-0.7221201	0.00021073	0.00616018	downregulated
Solyc08g068180.3	3618.25622	-0.3707495	0.00054745	0.01275009	downregulated
Solyc08g068220.3	528.108262	-0.5663666	0.00156047	0.02780354	downregulated
Solyc08g069060.4	841.868495	-0.6936194	0.00098346	0.02001254	downregulated
Solyc08g075280.4	1431.91642	-0.7734504	1.05E-05	0.00060637	downregulated
Solyc08g075370.3	3575.65615	-0.7444012	4.45E-08	6.22E-06	downregulated
Solyc08g075500.4	940.11725	-0.9661198	0.00014334	0.00460358	downregulated
Solyc08g075710.3	1189.54243	-0.7268471	1.54E-09	3.63E-07	downregulated
Solyc08g075890.3	8341.14607	-0.3466308	0.00024779	0.00698554	downregulated
Solyc08g075920.4	502.418846	-0.9362468	6.62E-05	0.00252363	downregulated
Solyc08g076870.1	159.604897	-1.0259387	0.00120877	0.02322675	downregulated
Solyc08g076880.3	7584.34578	-0.6461789	5.82E-07	5.41E-05	downregulated
Solyc08g077130.2	80.3074029	-1.8997373	0.00031472	0.00845409	downregulated
Solyc08g078090.1	1315.24387	-0.5114097	0.00299304	0.04471567	downregulated
Solyc08g078210.3	3786.15653	-0.5982037	5.33E-07	5.09E-05	downregulated
Solyc08g079010.1	261.858623	-0.9842836	0.00012224	0.00406416	downregulated
Solyc08g079280.3	13359.5542	-0.419772	0.00025606	0.00716357	downregulated
Solyc08g080250.4	984.24576	-0.5542347	0.00010806	0.00369013	downregulated
Solyc08g080380.4	1048.9248	-0.6327288	0.00071201	0.01555511	downregulated
Solyc08g082090.1	1517.02091	-0.6148607	0.00030135	0.0081682	downregulated
Solyc08g082110.4	193.424155	-1.195499	0.00300828	0.04490772	downregulated
Solyc08g082120.2	2348.63897	-0.9782769	0.00021266	0.0061863	downregulated

Solyc08g082190.3	38180.9492	-0.6263832	1.88E-05	0.00095886	downregulated
Solyc08g082640.2	4419.03038	-0.8065222	3.67E-10	1.05E-07	downregulated
Solyc08g082660.2	1558.62464	-0.8637465	0.00043578	0.01084213	downregulated
Solyc08g082800.3	63.6494031	-1.4726522	0.00054713	0.01275009	downregulated
Solyc08g083060.3	5905.62768	-0.3340225	0.00046846	0.01142953	downregulated
Solyc08g083380.2	667.895083	-0.7274871	0.00329795	0.04809147	downregulated
Solyc09g008320.4	1629.68058	-0.8416419	1.65E-05	0.0008649	downregulated
Solyc09g010120.2	4925.95138	-0.4194541	0.00096586	0.01971819	downregulated
Solyc09g010220.4	2006.50741	-0.9729837	1.35E-06	0.00010967	downregulated
Solyc09g010430.1	196.44652	-1.2820895	4.58E-08	6.27E-06	downregulated
Solyc09g010800.5.1	124322.066	-0.57269	3.00E-05	0.00139762	downregulated
Solyc09g010860.4	1703.34965	-0.4890067	0.00120248	0.02316349	downregulated
Solyc09g011340.3	2648.74852	-0.4589991	1.17E-06	9.66E-05	downregulated
Solyc09g014300.3	3866.95087	-0.3358229	0.00119218	0.02311406	downregulated
Solyc09g014520.3	474002.077	-0.3631643	0.00032802	0.0087013	downregulated
Solyc09g018010.3	1710.97295	-0.9148505	5.52E-05	0.00221233	downregulated
Solyc09g056390.1	1331.69429	-0.7670524	0.00062135	0.01401866	downregulated
Solyc09g059970.3	2108.66018	-0.585055	0.0001046	0.00360951	downregulated
Solyc09g063130.3	133130.342	-0.3560611	8.82E-05	0.00319608	downregulated
Solyc09g064720.3	1885.69502	-0.5416785	7.41E-05	0.00277462	downregulated
Solyc09g065620.3	807.344672	-1.0564004	0.00015457	0.00488118	downregulated
Solyc09g065840.3	833.989456	-0.7542847	1.75E-05	0.00089893	downregulated
Solyc09g065910.3	101608.882	-0.6060381	1.03E-05	0.00059839	downregulated
Solyc09g066150.2	561.180554	-0.8498563	0.00055548	0.01291842	downregulated
Solyc09g072590.3	575.08215	-0.5936769	0.0009322	0.01923891	downregulated
Solyc09g072900.4	1430.79188	-0.3332603	0.00306397	0.04555905	downregulated
Solyc09g075320.1	282.922758	-1.1789404	1.33E-05	0.00073546	downregulated
Solyc09g075860.3	2096.59835	-0.4588055	8.66E-05	0.00315175	downregulated
Solyc09g075880.3	66.4299993	-1.3964005	0.00198259	0.03304441	downregulated
Solyc09g082060.3	10421.7983	-0.5815183	1.37E-07	1.61E-05	downregulated
Solyc09g082480.2	109.752719	-1.4799802	0.0007953	0.01693182	downregulated
Solyc09g083120.3	884.741161	-0.5050937	3.80E-05	0.00169445	downregulated
Solyc09g083350.3	2164.39794	-0.3839306	0.00076945	0.01651178	downregulated
Solyc09g089860.4	348.55716	-1.0004138	2.06E-06	0.00015986	downregulated
Solyc09g090120.3	915.604803	-0.4408853	0.00123735	0.02360217	downregulated
Solyc09g090400.4	40.7313735	-1.6272205	0.0012152	0.02329726	downregulated
Solyc09g091050.4	638.770179	-0.6447904	0.00089492	0.01859147	downregulated
Solyc09g091660.3	4034.14712	-0.6898342	2.23E-05	0.00111268	downregulated
Solyc09g091830.4	2139.84952	-0.5944962	2.75E-08	4.22E-06	downregulated
Solyc09g091940.2	3801.42548	-0.7956615	6.09E-12	2.88E-09	downregulated
Solyc09g097780.2	8879.89459	-0.8981547	5.65E-05	0.00225179	downregulated

Solyc10g006230.3	455075.865	-0.3081768	0.00327678	0.0478567	downregulated
Solyc10g006410.3	690.147067	-0.5106752	0.0033069	0.04812274	downregulated
Solyc10g006700.1	222.809772	-0.7311917	0.00120906	0.02322675	downregulated
Solyc10g006900.3	69811.3129	-0.5463392	0.00017673	0.00538292	downregulated
Solyc10g007350.4	2460.38284	-0.7602607	2.21E-09	4.97E-07	downregulated
Solyc10g008270.3	921.059135	-0.7317693	5.87E-06	0.00038505	downregulated
Solyc10g008500.4	497.917159	-0.7663415	2.24E-06	0.00017159	downregulated
Solyc10g008790.3	774.775431	-0.3911285	0.00308184	0.04575266	downregulated
Solyc10g009020.3	190.413067	-0.8245217	0.0007435	0.01603613	downregulated
Solyc10g009080.4	1787.0975	-0.5063563	9.20E-05	0.00329558	downregulated
Solyc10g009110.1	365.941848	-0.8872209	2.63E-05	0.00126549	downregulated
Solyc10g009190.1	991.118748	-0.6778443	0.00304978	0.04541958	downregulated
Solyc10g009340.1	1605.70013	-0.741418	0.00012125	0.00405274	downregulated
Solyc10g011700.4	310.449858	-0.556408	0.0013832	0.02548322	downregulated
Solyc10g012030.4	2073.98891	-0.5175712	0.00014705	0.00469269	downregulated
Solyc10g024410.2	3674.35575	-0.4456936	5.03E-06	0.00034425	downregulated
Solyc10g045320.2	1148.46398	-0.3863811	0.00265351	0.04093856	downregulated
Solyc10g047130.2	1543.28318	-0.4804229	0.00231683	0.03723484	downregulated
Solyc10g049210.3	1722.69179	-0.4187323	5.41E-05	0.00218183	downregulated
Solyc10g051200.2	3812.42055	-0.3062823	0.00285801	0.04331124	downregulated
Solyc10g051215.1	52.7433687	-1.3543866	0.00274594	0.04208949	downregulated
Solyc10g051373.1	5467.72217	-1.0097256	5.27E-08	7.01E-06	downregulated
Solyc10g051377.1	6666.84932	-1.1292076	3.75E-34	7.08E-30	downregulated
Solyc10g055780.1	471.635286	-1.3296338	1.12E-12	6.82E-10	downregulated
Solyc10g055800.2	1170.08237	-1.3057214	0.00317896	0.04675354	downregulated
Solyc10g077065.1	368.593109	-0.9667954	5.96E-08	7.81E-06	downregulated
Solyc10g078510.3	64.0714613	-2.3856533	0.00275712	0.04222658	downregulated
Solyc10g078590.2	3182.58835	-0.713348	2.97E-06	0.00022105	downregulated
Solyc10g078600.3	1225.77287	-0.643154	0.00082222	0.01738724	downregulated
Solyc10g078630.2	9572.94305	-0.9110635	2.07E-11	7.67E-09	downregulated
Solyc10g078690.3	4981.01999	-0.4405756	6.86E-05	0.00259715	downregulated
Solyc10g078750.2	1130.43959	-0.4706434	0.00211175	0.03461653	downregulated
Solyc10g078860.2	238.784807	-1.1013067	1.39E-05	0.00075521	downregulated
Solyc10g078920.3	458.599801	-0.5554427	0.00159462	0.02824845	downregulated
Solyc10g079460.1	42.3582111	-1.7492195	0.00046729	0.01142953	downregulated
Solyc10g079755.1	2881.38306	-0.5784417	5.21E-05	0.00213321	downregulated
Solyc10g079820.2	13527.0585	-0.7354683	1.35E-05	0.00074074	downregulated
Solyc10g079840.2	349.870406	-0.8179802	4.79E-05	0.00202192	downregulated
Solyc10g080190.1	1787.10439	-0.5342178	0.00018847	0.00564044	downregulated
Solyc10g080240.1	48.2153587	-1.61659	0.00027388	0.00757249	downregulated
Solyc10g080620.1	117.965367	-1.9003185	9.72E-07	8.38E-05	downregulated

Solyc10g080670.2	535.790955	-1.041865	0.00010493	0.00360951	downregulated
Solyc10g081170.2	15548.1438	-0.5637902	2.30E-05	0.00113832	downregulated
Solyc10g081470.2	4549.08688	-0.3010106	0.00193413	0.03249482	downregulated
Solyc10g081770.3	337.10396	-0.8210639	0.00019423	0.0057581	downregulated
Solyc10g083280.4	176.729315	-0.9066673	0.0001426	0.00458735	downregulated
Solyc10g083730.2	376.758289	-0.8371091	0.00012483	0.00413552	downregulated
Solyc10g086430.3	105.907497	-0.9420778	0.0031959	0.04689311	downregulated
Solyc11g005360.2	1257.92396	-0.6489859	3.67E-05	0.00164704	downregulated
Solyc11g005650.1	141.076666	-0.9546412	0.00048676	0.01175456	downregulated
Solyc11g005880.2	1441.24026	-0.5113354	0.00068587	0.01513083	downregulated
Solyc11g006060.2	11540.5412	-0.4129999	0.00123495	0.02360217	downregulated
Solyc11g006190.3	2018.58149	-0.457926	1.11E-05	0.0006365	downregulated
Solyc11g006200.2	272.351037	-1.1179306	4.56E-08	6.27E-06	downregulated
Solyc11g007945.1	70.5055954	-1.2990651	0.00324178	0.04741892	downregulated
Solyc11g008020.2	97.9461347	-1.2741256	0.00015818	0.00495374	downregulated
Solyc11g010680.4	401.11862	-0.8377829	1.68E-05	0.00087433	downregulated
Solyc11g011060.3	299.9968	-0.6673304	0.00173222	0.03003785	downregulated
Solyc11g011920.2	18361.8354	-0.4231451	0.00020179	0.00595403	downregulated
Solyc11g012930.2	842.585727	-0.7275098	8.47E-06	0.00050909	downregulated
Solyc11g013020.2	538.644543	-0.6130738	0.00026104	0.00727059	downregulated
Solyc11g017010.2	15385.338	-0.3449216	0.00066615	0.01476472	downregulated
Solyc11g017470.2	672.526459	-0.5491611	0.00115631	0.0226748	downregulated
Solyc11g027840.2	264.816557	-1.3201807	1.25E-09	3.07E-07	downregulated
Solyc11g042880.3	128.656005	-1.2489497	5.03E-05	0.00209052	downregulated
Solyc11g045250.1	521.77383	-0.565906	0.00151646	0.02722128	downregulated
Solyc11g065030.3	358.968953	-0.7796903	0.00224276	0.03638516	downregulated
Solyc11g065870.3	2429.9285	-0.4897249	0.00010242	0.00354234	downregulated
Solyc11g066020.2	2415.83	-0.7832641	2.64E-10	7.79E-08	downregulated
Solyc11g066330.2	177.426786	-0.7613031	0.00347107	0.04973264	downregulated
Solyc11g067110.2	138.549698	-1.1560101	7.56E-05	0.00282319	downregulated
Solyc11g067140.2	774.789759	-0.8832047	1.46E-08	2.36E-06	downregulated
Solyc11g067200.2	524.739693	-0.5677243	0.00207747	0.03417324	downregulated
Solyc11g068515.1	31813.8308	-0.6662045	3.12E-08	4.72E-06	downregulated
Solyc11g069910.2	1439.0117	-0.3582533	0.00127159	0.02396476	downregulated
Solyc11g070050.2	1078.61352	-0.5262647	0.00021457	0.00620498	downregulated
Solyc11g071460.2	1574.59963	-1.4610238	4.65E-24	9.76E-21	downregulated
Solyc11g071620.3	1916.80969	-0.5111972	0.00024785	0.00698554	downregulated
Solyc11g072480.2	2480.72545	-0.5997483	7.24E-08	9.30E-06	downregulated
Solyc12g005660.2	1337.17654	-0.5970253	0.00013133	0.00430328	downregulated
Solyc12g005750.1	133.773102	-2.1822074	7.31E-06	0.00045408	downregulated
Solyc12g006003.1	2383.38764	-0.7242414	4.24E-09	8.79E-07	downregulated

Solyc12g006140.2	247085.59	-0.6218305	8.17E-05	0.0029912	downregulated
Solyc12g006290.2	2491.92407	-0.4134886	0.00084586	0.01778745	downregulated
Solyc12g006440.2	154.087625	-1.8828623	7.71E-08	9.78E-06	downregulated
Solyc12g006590.3	298.057978	-1.7986307	4.82E-05	0.00203018	downregulated
Solyc12g006695.1	143.179712	-1.4797255	4.35E-05	0.00186707	downregulated
Solyc12g006850.2	588.139562	-0.5479244	0.00330311	0.04812274	downregulated
Solyc12g007030.3	2706.66414	-0.5896522	1.36E-05	0.00074177	downregulated
Solyc12g007060.1	245.320699	-1.0674302	0.00236675	0.03767265	downregulated
Solyc12g007170.3	1395.18514	-0.4383024	9.99E-05	0.00348022	downregulated
Solyc12g008560.1	1929.56105	-0.8307039	0.00142316	0.02614299	downregulated
Solyc12g009180.2	989.555198	-0.6135894	0.00016684	0.0051648	downregulated
Solyc12g009380.2	654.69098	-0.6295587	5.86E-05	0.00230106	downregulated
Solyc12g009440.2	12886.509	-0.5141541	0.00042176	0.01054488	downregulated
Solyc12g009480.2	444.1757	-0.8842969	9.75E-05	0.00343366	downregulated
Solyc12g011280.2	93751.5152	-0.4113518	0.00135119	0.02511396	downregulated
Solyc12g013550.2	1308.02018	-0.4857404	0.00014711	0.00469269	downregulated
Solyc12g013710.2	133330.195	-0.5880649	0.0001471	0.00469269	downregulated
Solyc12g013810.2	25144.6875	-0.4455702	0.00012218	0.00406416	downregulated
Solyc12g013920.2	637.864348	-0.599604	0.0034515	0.04964701	downregulated
Solyc12g014090.2	138.28619	-1.0655529	3.60E-05	0.00162751	downregulated
Solyc12g014140.3	6836.19996	-0.7402609	3.93E-06	0.00027362	downregulated
Solyc12g014160.3	211.677959	-0.8127571	0.00034804	0.00907797	downregulated
Solyc12g014290.2	2084.14174	-0.4796555	1.93E-05	0.00097604	downregulated
Solyc12g015970.3	2733.601	-0.7353361	0.0001117	0.00378684	downregulated
Solyc12g017690.3	236.801748	-1.2087032	2.20E-09	4.97E-07	downregulated
Solyc12g021160.1	133.355598	-1.1837922	0.00048435	0.01171116	downregulated
Solyc12g021327.1	259.198027	-1.3656418	3.32E-08	4.89E-06	downregulated
Solyc12g021330.1	207.405985	-1.4058623	2.16E-09	4.97E-07	downregulated
Solyc12g040790.2	13129.7309	-0.6135218	0.00011984	0.00402692	downregulated
Solyc12g042770.3	21576.6858	-0.9056955	2.75E-11	1.00E-08	downregulated
Solyc12g042950.2	2793.06087	-1.041897	2.66E-07	2.81E-05	downregulated
Solyc12g055760.2	2953.76562	-0.4661916	4.51E-05	0.00192339	downregulated
Solyc12g055970.3	1851.06913	-0.6124415	0.00023865	0.00674648	downregulated
Solyc12g056650.2	5038.14954	-0.9233905	5.44E-15	5.13E-12	downregulated
Solyc12g088840.1	698.754731	-0.6119975	0.00047192	0.01148415	downregulated
Solyc12g089140.2	836.281573	-0.8958163	1.62E-05	0.00084826	downregulated
Solyc12g089220.3	1111.84089	-1.1098051	0.00015415	0.00487609	downregulated
Solyc12g094520.2	929.912162	-0.5964386	0.000176	0.00536925	downregulated
Solyc12g094620.3	46235.0968	-0.8113261	0.00038303	0.00980108	downregulated
Solyc12g094630.2	6125.34579	-0.3479492	0.00049592	0.01188446	downregulated
Solyc12g095910.2	4538.93064	-0.8959906	1.19E-14	9.79E-12	downregulated

Solyc12g098340.2	123.637285	-1.8454184	2.47E-07	2.68E-05	downregulated
Solyc12g098880.2	241.698744	-0.9788879	0.00020518	0.00604476	downregulated
Solyc12g098900.2	91.1209163	-1.8537789	0.00167843	0.02934774	downregulated
Solyc12g098910.2	2241.97965	-0.5057591	0.00332176	0.04825236	downregulated
Solyc12g099400.2	403.951703	-0.4812999	0.00195576	0.03271258	downregulated
Solyc12g099650.2	104748.268	-0.6877297	1.03E-07	1.26E-05	downregulated
Solyc01g005120.3	1385.09164	0.61917378	5.85E-06	0.00038505	upregulated
Solyc01g005257.1	508.765058	0.55727987	0.00117737	0.02291669	upregulated
Solyc01g005690.3	1971.75211	0.39325045	0.00020044	0.00593265	upregulated
Solyc01g005830.4	1491.75108	0.44448177	6.84E-05	0.00259446	upregulated
Solyc01g005985.1	4747.76819	0.51977876	3.36E-05	0.00153515	upregulated
Solyc01g006820.2	2845.8771	0.47191848	0.00028822	0.007934	upregulated
Solyc01g006900.3	14959.1377	0.65926818	7.72E-05	0.00285268	upregulated
Solyc01g007010.2	223.271363	1.12670973	0.00011049	0.00375263	upregulated
Solyc01g008110.4	55084.605	0.72454423	0.00039057	0.00994	upregulated
Solyc01g008600.4	236.200029	0.63905165	0.00075573	0.01625412	upregulated
Solyc01g009010.3	3469.08661	0.54620603	0.00043682	0.01084421	upregulated
Solyc01g009300.3	1132.76792	0.4872485	0.00119793	0.02315417	upregulated
Solyc01g010910.2	73.9305002	1.66239923	0.00199468	0.03315802	upregulated
Solyc01g011465.1	45.7529054	2.08197173	0.00172585	0.0299824	upregulated
Solyc01g011510.4	1818.10611	0.50598881	0.00010885	0.00371034	upregulated
Solyc01g057770.3	1103.99061	0.5631905	7.65E-05	0.0028425	upregulated
Solyc01g058720.4	1904.81721	0.75738127	0.00098299	0.02001254	upregulated
Solyc01g065530.3	807.51179	0.55594668	0.00032807	0.0087013	upregulated
Solyc01g066640.2	183.333722	1.4514795	1.99E-07	2.25E-05	upregulated
Solyc01g067660.3	4244.92572	0.45858844	4.27E-05	0.00184889	upregulated
Solyc01g068080.4	211.275454	1.12417163	0.00050058	0.01198091	upregulated
Solyc01g068560.3	6150.10522	0.34144145	0.00285629	0.04331124	upregulated
Solyc01g079240.3	5516.10934	0.50226826	0.00076338	0.01640018	upregulated
Solyc01g079410.3	3146.03157	0.70661101	0.0034849	0.04989297	upregulated
Solyc01g079580.3	773.016082	0.59678735	6.87E-06	0.00043547	upregulated
Solyc01g079620.4	192.882108	1.08750134	6.10E-05	0.002376	upregulated
Solyc01g080790.3	51.303929	1.16298991	0.00253116	0.039601	upregulated
Solyc01g081440.3	987.013164	0.5920706	7.78E-05	0.00286924	upregulated
Solyc01g081540.4	1192.20866	0.58715375	0.00041776	0.01049062	upregulated
Solyc01g088400.4	1035.9956	1.22824546	2.76E-05	0.0013019	upregulated
Solyc01g088430.4	834.588047	0.96359487	0.00086355	0.01803913	upregulated
Solyc01g089850.4	1762.19948	0.72069049	0.00010062	0.00349944	upregulated
Solyc01g090270.4	2097.01626	0.35471351	0.00184195	0.03141308	upregulated
Solyc01g090410.3	813.799747	0.86264286	0.00026947	0.00746153	upregulated
Solyc01g090910.3	1179.11451	0.42349616	0.00219201	0.03562293	upregulated

Solyc01g091200.4	1532.50279	0.4257144	0.00084467	0.01778226	upregulated
Solyc01g091320.3	24194.0026	0.41936591	0.00104212	0.02095791	upregulated
Solyc01g091530.4	9561.95257	0.62785896	5.65E-09	1.06E-06	upregulated
Solyc01g091610.1	48.5401949	1.44832369	0.00120331	0.02316349	upregulated
Solyc01g091660.3	214.06916	1.45603842	3.08E-07	3.18E-05	upregulated
Solyc01g091860.4	1041.60401	0.45602086	4.57E-05	0.00194499	upregulated
Solyc01g091870.3	727.87331	0.6043457	1.93E-06	0.00015146	upregulated
Solyc01g093970.4	1148.47537	0.56304259	7.36E-06	0.00045573	upregulated
Solyc01g094070.3	315.233238	1.01052198	0.00200412	0.03328575	upregulated
Solyc01g094090.4	452.112065	0.94882989	0.00023521	0.00666919	upregulated
Solyc01g094700.4	8302.62201	0.40005289	0.00043701	0.01084421	upregulated
Solyc01g094750.4	958.824102	0.86482686	1.24E-07	1.49E-05	upregulated
Solyc01g094790.3	1153.06146	0.49877856	0.00073435	0.01595794	upregulated
Solyc01g094870.3	28.6456633	2.40461492	0.00157421	0.02801156	upregulated
Solyc01g094940.4	986.781276	0.67827821	1.19E-06	9.75E-05	upregulated
Solyc01g095610.4	282.731091	1.04166272	1.62E-06	0.00012901	upregulated
Solyc01g095670.4	8830.71965	0.3630012	0.00297705	0.04454718	upregulated
Solyc01g096270.3	2941.28755	0.44329274	0.00064493	0.01437691	upregulated
Solyc01g096630.3	1307.53714	0.48932357	0.00041232	0.01038159	upregulated
Solyc01g096730.2	203.228214	0.91782665	0.00062793	0.01411645	upregulated
Solyc01g096740.4	1080.5952	0.91668994	0.0009041	0.01874094	upregulated
Solyc01g097930.3	99.2116014	1.43885734	0.0002167	0.00623794	upregulated
Solyc01g098410.4	718.562551	0.51189801	0.00022634	0.00645652	upregulated
Solyc01g099870.3	174.401908	1.73787778	4.38E-06	0.00030441	upregulated
Solyc01g100110.4	2923.62151	0.39101679	0.00133106	0.02486227	upregulated
Solyc01g100610.3	2621.06663	0.44567485	5.80E-05	0.00229296	upregulated
Solyc01g100750.2	307.713458	0.85852184	0.00025952	0.0072477	upregulated
Solyc01g102310.3	3099.72563	0.82153203	6.25E-11	2.11E-08	upregulated
Solyc01g102350.3	1589.84842	0.57075546	3.17E-06	0.0002327	upregulated
Solyc01g102580.3	7605.88598	0.56599671	2.22E-06	0.00017092	upregulated
Solyc01g102700.4	1301.86726	0.4316676	0.00110544	0.02185873	upregulated
Solyc01g103150.3	520.966841	0.43850246	0.0021141	0.03462507	upregulated
Solyc01g103200.4	1320.58605	0.70426496	1.72E-06	0.00013557	upregulated
Solyc01g103310.4	68.2012124	1.49937419	0.00056524	0.01309626	upregulated
Solyc01g103590.4	858.683625	1.05481653	9.56E-05	0.00339171	upregulated
Solyc01g104770.4	987.641402	0.47858795	0.00101804	0.02056105	upregulated
Solyc01g105680.4	2696.53039	0.40076087	0.0003375	0.00886416	upregulated
Solyc01g105920.3	721.269789	0.88372131	0.00047826	0.01159595	upregulated
Solyc01g106690.3	1416.30013	0.5142661	0.00032312	0.00864269	upregulated
Solyc01g107340.4	653.32697	0.65663242	0.00023367	0.00665556	upregulated
Solyc01g108660.4	3842.60454	0.44872519	0.00338577	0.04895625	upregulated

Solyc01g109180.4	583.425332	0.4941531	0.00061654	0.01396012	upregulated
Solyc01g110290.3	12181.3062	0.46053719	0.00071334	0.01555511	upregulated
Solyc01g110370.4	1421.81917	0.54812844	5.20E-05	0.00213321	upregulated
Solyc01g111090.3	1700.77633	0.43336855	0.00042303	0.0105529	upregulated
Solyc01g111160.3	28337.203	0.52159795	0.00132751	0.02486227	upregulated
Solyc01g111560.3	5813.03232	0.34861183	5.62E-05	0.00224377	upregulated
Solyc01g111660.4	11450.4141	0.48306831	0.0002536	0.00710543	upregulated
Solyc01g112260.4	2022.84872	0.56871363	1.19E-06	9.75E-05	upregulated
Solyc02g020910.4	6399.42787	0.35969411	3.01E-05	0.00139849	upregulated
Solyc02g021420.3	3637.21825	0.36003297	0.00316618	0.04660212	upregulated
Solyc02g031985.1	49.086602	1.2950277	0.00094171	0.01932963	upregulated
Solyc02g036370.3	353.665409	0.59660114	0.00074389	0.01603613	upregulated
Solyc02g037490.1	54.1948675	1.77856187	9.57E-05	0.00339171	upregulated
Solyc02g061760.4	4162.13819	0.5556575	0.0002942	0.00805165	upregulated
Solyc02g063000.4	6940.85613	0.72897732	1.93E-05	0.00097604	upregulated
Solyc02g063390.4	1569.44873	0.85007413	0.00084142	0.0177337	upregulated
Solyc02g065240.3	2188.04704	0.58178692	0.00059473	0.01354741	upregulated
Solyc02g065280.3	3739.17781	0.37003215	0.00115755	0.0226755	upregulated
Solyc02g065765.1	7198.55759	0.33314865	7.70E-05	0.00285092	upregulated
Solyc02g067050.3	619.71198	1.00060364	3.98E-05	0.00174686	upregulated
Solyc02g067230.3	124.389053	0.88200712	0.00318549	0.04677667	upregulated
Solyc02g068600.3	377.910875	1.01944156	5.97E-06	0.00038876	upregulated
Solyc02g068610.2	106.050083	1.02178562	0.00114058	0.02241281	upregulated
Solyc02g070050.3	2358.97096	0.58244643	5.22E-08	6.99E-06	upregulated
Solyc02g070580.1	1211.36265	0.78625054	0.00017935	0.0054484	upregulated
Solyc02g071320.4	8179.58642	0.31622301	0.00257443	0.04001278	upregulated
Solyc02g071520.3	755.925109	0.6097166	0.00014872	0.00473358	upregulated
Solyc02g071610.3	2366.45367	0.56115027	0.00025222	0.00708777	upregulated
Solyc02g071710.3	1229.11102	0.85190746	0.00016656	0.0051648	upregulated
Solyc02g072240.3	1265.7271	0.68057134	2.04E-06	0.00015944	upregulated
Solyc02g076670.3	208.427749	0.86468415	0.00033504	0.00884771	upregulated
Solyc02g076680.3	1010.18341	0.69025585	6.73E-05	0.00255736	upregulated
Solyc02g077090.4	2110.86298	0.42699049	0.0002753	0.00760058	upregulated
Solyc02g077330.3	3069.95228	0.55264569	0.00063477	0.01421938	upregulated
Solyc02g078400.3	2569.25895	0.54096159	0.00080651	0.01711242	upregulated
Solyc02g080260.4	556.008611	0.57748369	0.00294019	0.04431165	upregulated
Solyc02g080330.4	2504.72502	0.83602744	4.73E-05	0.0020043	upregulated
Solyc02g080500.3	2000.78035	0.36115616	0.00063148	0.01417936	upregulated
Solyc02g080660.3	1550.3801	0.43583208	0.00192041	0.03237955	upregulated
Solyc02g080670.3	458.754778	1.74023097	6.36E-12	2.93E-09	upregulated
Solyc02g081340.3	80.6007411	2.16338965	0.00123699	0.02360217	upregulated

Solyc02g081770.2	212.147029	1.15390378	0.00204117	0.03366412	upregulated
Solyc02g082140.3	1784.08059	0.55577628	0.0013389	0.02495935	upregulated
Solyc02g082510.1	853.520103	0.51717614	0.00075201	0.01619264	upregulated
Solyc02g082760.3	70679.0861	0.24826185	0.00202805	0.03356498	upregulated
Solyc02g082850.3	1716.81272	0.62575388	0.00070361	0.01541407	upregulated
Solyc02g083860.3	883.184298	0.71241582	0.0032001	0.04691816	upregulated
Solyc02g084370.2	182.21678	1.27723918	2.67E-05	0.00127498	upregulated
Solyc02g084390.3	3177.95808	0.56730947	2.59E-07	2.77E-05	upregulated
Solyc02g085020.4	36.0293393	1.91464213	0.0034509	0.04964701	upregulated
Solyc02g085320.1	71.6127698	1.41525125	0.0027627	0.04224365	upregulated
Solyc02g085400.3	2787.83663	0.48265773	0.00146807	0.02669215	upregulated
Solyc02g085870.3	7502.15249	0.41577283	5.25E-05	0.00214405	upregulated
Solyc02g086650.3	56253.4362	0.5639048	0.00103942	0.0209258	upregulated
Solyc02g086840.3	920.94395	0.67054556	6.40E-06	0.00041239	upregulated
Solyc02g087180.4	786.316126	0.49563479	0.00296457	0.04444759	upregulated
Solyc02g087190.1	1637.2523	0.54475464	0.00031046	0.00836339	upregulated
Solyc02g087770.3	847.36185	0.83649662	0.00100051	0.02029283	upregulated
Solyc02g088190.4	797.086886	0.50413129	0.00262935	0.04063233	upregulated
Solyc02g088390.4	1468.75092	0.44864275	0.00174995	0.03023433	upregulated
Solyc02g088560.4	7778.72015	0.35804949	0.00037561	0.00963737	upregulated
Solyc02g088820.4	1772.345	0.43725725	0.00019168	0.00569128	upregulated
Solyc02g088910.3	585.688053	0.73568809	0.0003987	0.01009267	upregulated
Solyc02g089170.4	117.498646	1.41323422	0.00015544	0.00490023	upregulated
Solyc02g089250.4	6137.19254	0.57004922	3.96E-05	0.00174623	upregulated
Solyc02g089540.3	2258.77794	0.62707769	0.00160792	0.02845735	upregulated
Solyc02g089610.2	7046.10347	0.45366851	0.00033602	0.00884771	upregulated
Solyc02g089620.3	1037.27745	2.78496103	3.33E-31	2.60E-27	upregulated
Solyc02g090070.3	1375.247	0.45580632	0.00011845	0.00399433	upregulated
Solyc02g090360.3	688.265627	0.64647119	0.00046267	0.01133531	upregulated
Solyc02g090580.3	1326.21151	0.63635064	3.15E-08	4.72E-06	upregulated
Solyc02g090930.3	156.324271	1.05221418	0.00018663	0.00560292	upregulated
Solyc02g090960.1	488.322985	0.70439976	0.00012933	0.00426241	upregulated
Solyc02g091020.3	127.397901	1.01275495	0.00173662	0.03008663	upregulated
Solyc02g091690.3	219.899237	0.89416952	0.00196889	0.03287402	upregulated
Solyc02g091780.1	1629.77048	0.41461929	0.00030521	0.0082574	upregulated
Solyc02g091890.3	2678.17681	0.51140367	5.02E-05	0.00209052	upregulated
Solyc02g092210.1	385.60069	0.67310304	0.00166183	0.02917757	upregulated
Solyc02g092220.1	264.429213	0.76914961	4.31E-05	0.00185326	upregulated
Solyc02g092470.3	1168.27573	0.50284811	0.00060624	0.0137764	upregulated
Solyc02g092790.3	6287.50573	1.42582585	1.55E-11	6.25E-09	upregulated
Solyc02g092930.1	844.543473	0.71300918	0.00053076	0.0124818	upregulated

Solyc02g093100.3	1013.47392	0.67140866	9.16E-07	8.01E-05	upregulated
Solyc02g093270.4	427.274483	0.91070093	0.00026715	0.00741891	upregulated
Solyc02g093290.3	4973.64856	0.32549505	0.00134363	0.02502287	upregulated
Solyc02g093310.3	109.560939	1.02425784	0.00232244	0.03726169	upregulated
Solyc02g093970.4	2504.94157	0.44795959	0.00012855	0.00424383	upregulated
Solyc02g094190.3	248.829178	0.69384158	0.00306378	0.04555905	upregulated
Solyc02g094390.3	601.746548	0.46574651	0.00309421	0.04586423	upregulated
Solyc02g150130.1	2187.63279	0.62064545	0.0004554	0.0112123	upregulated
Solyc02g150147.1	2217.05984	0.63350033	1.69E-05	0.00087845	upregulated
Solyc03g005320.3	920.125028	1.28204105	4.08E-18	5.93E-15	upregulated
Solyc03g005900.4	1009.40123	0.50995191	6.23E-05	0.00240636	upregulated
Solyc03g006050.4	885.21821	0.66600996	5.07E-06	0.00034429	upregulated
Solyc03g006240.3	639.801408	0.78717229	0.00013151	0.00430328	upregulated
Solyc03g006250.2	2035.4002	0.71882992	0.00163816	0.02891059	upregulated
Solyc03g006500.3	579.155979	0.84765292	8.12E-05	0.00298441	upregulated
Solyc03g006910.3	51.2772664	3.72047923	4.28E-05	0.00185093	upregulated
Solyc03g007240.3	14546.898	1.29271554	0.00107393	0.02146049	upregulated
Solyc03g007760.3	2674.79631	0.87848022	1.39E-11	5.84E-09	upregulated
Solyc03g007920.4	976.975997	0.64532498	0.00291775	0.04404383	upregulated
Solyc03g019760.4	2687.22138	0.45820068	0.00192892	0.03244507	upregulated
Solyc03g019800.4	620.205664	0.50797297	0.00096358	0.01969285	upregulated
Solyc03g025510.3	1154.74039	0.47433921	0.0017676	0.03042792	upregulated
Solyc03g025830.4	553.140878	0.52251266	0.00049487	0.01187444	upregulated
Solyc03g026040.4	559.665104	0.76844596	9.04E-05	0.00325718	upregulated
Solyc03g026070.4	520.742074	0.57291542	0.0003361	0.00884771	upregulated
Solyc03g031800.3	585.413458	0.87434722	2.08E-09	4.86E-07	upregulated
Solyc03g031860.3	5603.40239	0.5370005	0.00164756	0.02902282	upregulated
Solyc03g044200.3	276.619383	0.7239613	0.00065939	0.01463217	upregulated
Solyc03g044660.3	1079.30846	0.80354049	0.00103865	0.0209258	upregulated
Solyc03g045140.4	174.143785	1.32079297	0.00017361	0.00532205	upregulated
Solyc03g058950.3	688.714041	0.5191722	0.00088103	0.01836344	upregulated
Solyc03g078580.3	1414.22354	0.39322399	0.0020453	0.03370282	upregulated
Solyc03g078640.1	2611.35521	0.45748946	1.49E-05	0.00079682	upregulated
Solyc03g082660.3	6015.30306	0.32699825	0.00272931	0.04186864	upregulated
Solyc03g083400.3	449.733215	0.57234856	0.00093903	0.01929554	upregulated
Solyc03g093790.3	544.150389	0.48937155	0.00116108	0.02269782	upregulated
Solyc03g095490.3	1185.51059	0.48142698	0.00013092	0.0042996	upregulated
Solyc03g096380.3	1892.36722	0.48017222	0.00041909	0.01051	upregulated
Solyc03g097030.3	880.575799	0.6319226	1.26E-05	0.00070581	upregulated
Solyc03g097170.3	396.192246	0.99303342	0.00154971	0.02768656	upregulated
Solyc03g110940.3	4892.30525	0.35851734	0.00023568	0.00667253	upregulated

Solyc03g111620.1	154.916263	1.0281173	5.86E-05	0.00230106	upregulated
Solyc03g111670.3	4477.65568	0.3073263	0.00108241	0.02153934	upregulated
Solyc03g111815.1	6715.36728	1.11617243	8.84E-06	0.00052585	upregulated
Solyc03g111970.4	1022.54659	0.43219946	0.0031662	0.04660212	upregulated
Solyc03g112010.4	371.016153	0.75266031	0.00085933	0.01797065	upregulated
Solyc03g112130.1	373.617847	0.86060781	1.50E-05	0.00080115	upregulated
Solyc03g112540.4	195.668399	0.8609759	0.00085619	0.01795658	upregulated
Solyc03g112620.4	862.081245	0.70154979	0.0005659	0.01309626	upregulated
Solyc03g113910.3	153.01247	1.13618111	0.00026875	0.00745231	upregulated
Solyc03g114320.4	2485.23569	0.47139654	1.11E-06	9.30E-05	upregulated
Solyc03g114330.3	891.921654	0.63665502	5.09E-06	0.00034476	upregulated
Solyc03g114460.3	2428.59314	0.50318397	0.0024809	0.03904104	upregulated
Solyc03g114560.2	664.197065	0.62510654	0.00201448	0.03339899	upregulated
Solyc03g114730.3	3429.19948	0.59556619	4.09E-12	2.03E-09	upregulated
Solyc03g115740.2	1185.91002	0.45117835	4.13E-05	0.00180719	upregulated
Solyc03g115870.3	134.730829	1.75578418	5.91E-06	0.0003862	upregulated
Solyc03g116200.2	1438.51014	0.85803371	0.00107708	0.02148629	upregulated
Solyc03g116270.3	197.381247	0.7653135	0.00146306	0.02664268	upregulated
Solyc03g116320.3	316.567367	0.91038884	0.00143332	0.02624254	upregulated
Solyc03g116590.3	3659.88946	0.78267547	0.00184479	0.03141308	upregulated
Solyc03g116740.3	1111.46196	1.38790246	1.81E-11	6.99E-09	upregulated
Solyc03g117600.3	4024.02959	0.85982827	2.29E-05	0.00113832	upregulated
Solyc03g117800.4	860.337748	0.63571541	0.00214638	0.03503224	upregulated
Solyc03g117870.3	11744.2066	0.72128948	0.00135838	0.02522279	upregulated
Solyc03g118540.4	202.29494	0.98932181	0.0015802	0.02802837	upregulated
Solyc03g119110.4	2400.45515	0.34147447	0.00074054	0.016013	upregulated
Solyc03g119520.4	746.996297	0.67983286	0.00113334	0.02231699	upregulated
Solyc03g121170.3	1715.24118	0.50526344	0.00100153	0.02029283	upregulated
Solyc03g121270.3	2487.75445	0.70222862	0.00136904	0.0253709	upregulated
Solyc03g121600.4	5479.84557	1.21652451	9.44E-13	6.15E-10	upregulated
Solyc03g121610.3	518.498566	0.5662753	0.00012999	0.00427655	upregulated
Solyc03g121660.3	1263.08211	0.48716649	0.00116316	0.02271479	upregulated
Solyc03g122140.3	500.681896	0.79793864	0.00110344	0.02184213	upregulated
Solyc03g122270.4	1241.48532	0.34508603	0.00197918	0.03301659	upregulated
Solyc03g123420.1	284.839909	0.55619733	0.00301983	0.04504453	upregulated
Solyc03g123590.4	92.2984139	1.26163973	0.00052226	0.01234255	upregulated
Solyc03g123740.4	2612.80897	0.39879606	0.00018157	0.00548614	upregulated
Solyc03g150113.1	33.5439729	1.58695604	0.00041478	0.0104298	upregulated
Solyc04g005070.3	10287.1297	0.77925391	0.00018278	0.0055051	upregulated
Solyc04g005100.3	955.24863	0.93523912	3.95E-05	0.00174503	upregulated
Solyc04g005600.3	482.760758	0.92654493	0.00099392	0.02018192	upregulated

Solyc04g006980.1	224.301312	0.93995721	0.00149784	0.026962	upregulated
Solyc04g007530.3	816.008068	0.57975648	0.00116821	0.02276621	upregulated
Solyc04g007640.3	1237.51194	0.37752605	0.00078932	0.01684539	upregulated
Solyc04g007710.3	4525.37349	0.30144592	0.00250326	0.03926213	upregulated
Solyc04g007823.1	292.248244	1.1138715	5.27E-05	0.00214405	upregulated
Solyc04g008210.2	1880.30855	1.22398872	5.02E-10	1.37E-07	upregulated
Solyc04g008940.4	28.0921589	2.40437637	0.00252643	0.03955983	upregulated
Solyc04g009040.4	50.9345646	1.75898309	0.00018324	0.00551013	upregulated
Solyc04g009180.3	1236.37657	0.43535035	0.00247783	0.03902532	upregulated
Solyc04g009900.4	2896.97794	0.9104553	4.31E-07	4.24E-05	upregulated
Solyc04g015270.3	5882.33904	0.34225113	0.00040258	0.01016386	upregulated
Solyc04g017720.3	2796.20738	0.5119226	0.00122144	0.02339316	upregulated
Solyc04g040160.4	8006.01068	0.46772057	7.48E-07	6.73E-05	upregulated
Solyc04g050440.3	2482.85412	0.94166239	3.89E-06	0.00027238	upregulated
Solyc04g050570.3	171.7966	1.7122712	0.00034485	0.00900716	upregulated
Solyc04g053130.4	1769.59611	0.63782197	0.00105175	0.02110647	upregulated
Solyc04g054220.3	83.3328703	1.29549572	0.00171561	0.0298596	upregulated
Solyc04g055253.1	114.336934	1.47441687	0.00234411	0.03745015	upregulated
Solyc04g056390.3	9458.47691	1.04967489	0.00345457	0.04964701	upregulated
Solyc04g064610.3	556.463624	0.67844999	0.00277068	0.0423313	upregulated
Solyc04g071360.4	2546.78405	0.33595633	0.00232486	0.03726878	upregulated
Solyc04g071480.1	3341.68083	0.48427613	9.49E-08	1.19E-05	upregulated
Solyc04g071650.4	12657.7497	0.42009105	7.33E-05	0.00275193	upregulated
Solyc04g072740.3	5895.4066	0.54369606	1.45E-09	3.51E-07	upregulated
Solyc04g072760.3	548.931208	1.54215096	3.13E-08	4.72E-06	upregulated
Solyc04g074310.4	288.104	1.50385384	2.78E-12	1.50E-09	upregulated
Solyc04g074410.2	427.92033	1.20197698	3.27E-08	4.86E-06	upregulated
Solyc04g074450.1	176.201553	1.06312807	0.00016837	0.0051867	upregulated
Solyc04g074570.1	974.959283	0.64665529	9.98E-06	0.00058348	upregulated
Solyc04g074730.1	2449.67988	0.53183588	0.00093898	0.01929554	upregulated
Solyc04g074980.3	2423.88396	0.42410394	0.00310379	0.04593408	upregulated
Solyc04g076190.1	290.266272	0.76791962	0.00277701	0.04239377	upregulated
Solyc04g077140.3	1034.63975	0.84753303	1.96E-07	2.23E-05	upregulated
Solyc04g077190.4	762.814024	0.55493182	0.0004889	0.01177894	upregulated
Solyc04g077510.4	548.549069	0.7301475	0.00144809	0.02642097	upregulated
Solyc04g077670.3	1612.07502	0.46779989	0.00156067	0.02780354	upregulated
Solyc04g078590.3	488.806277	0.93732611	2.50E-05	0.00122774	upregulated
Solyc04g078750.3	4668.03584	0.47396078	0.00215688	0.03517324	upregulated
Solyc04g078810.4	1462.91575	0.56065732	2.71E-05	0.00128682	upregulated
Solyc04g079120.3	1019.45726	0.80497726	5.64E-09	1.06E-06	upregulated
Solyc04g079340.3	2089.35981	0.51294362	0.00096264	0.01969285	upregulated

Solyc04g080450.1	4541.28583	0.47057514	0.00016138	0.00504547	upregulated
Solyc04g080490.4	399.053134	0.70590014	0.00227842	0.03686868	upregulated
Solyc04g080740.1	1544.52026	0.79109192	0.00208811	0.03431841	upregulated
Solyc04g081260.3	8288.33101	0.34034055	0.00015665	0.00491516	upregulated
Solyc04g082140.3	4096.43165	0.97049446	1.32E-08	2.16E-06	upregulated
Solyc04g082490.3	4219.18282	0.58945879	0.0004628	0.01133531	upregulated
Solyc04g082710.4	2842.9229	0.57454843	3.40E-05	0.00155274	upregulated
Solyc04g082970.4	399.818916	0.71684425	0.00051851	0.01228544	upregulated
Solyc04g150164.1	191.02447	1.04928884	0.00270811	0.04161104	upregulated
Solyc05g005000.4	1034.39063	1.02195431	2.26E-07	2.50E-05	upregulated
Solyc05g005140.4	1145.58464	0.50554999	0.00080919	0.0171502	upregulated
Solyc05g005170.4	1544.12412	0.60734693	3.64E-06	0.00026185	upregulated
Solyc05g005680.3	117.9295	1.68067628	2.59E-06	0.00019734	upregulated
Solyc05g005810.4	129.605826	1.17042269	0.00270306	0.04156721	upregulated
Solyc05g005990.3	2670.137	0.78898854	0.00092661	0.01914459	upregulated
Solyc05g006490.4	2836.07705	0.43483912	0.00229366	0.03703323	upregulated
Solyc05g006510.2	279.102682	1.18640031	6.45E-05	0.00247524	upregulated
Solyc05g007180.3	1783.55724	0.55034682	6.51E-06	0.00041563	upregulated
Solyc05g007880.4	510.977688	1.23629585	1.13E-09	2.83E-07	upregulated
Solyc05g007980.3	3371.60602	0.449932	9.78E-05	0.00343366	upregulated
Solyc05g008895.1	788.477774	0.75623301	0.00036341	0.00940364	upregulated
Solyc05g009420.1	274.404988	1.13173093	4.41E-08	6.21E-06	upregulated
Solyc05g009820.4	3527.4781	0.40544801	4.47E-05	0.0019098	upregulated
Solyc05g010320.4	3294.59592	0.58433161	0.00147732	0.02679902	upregulated
Solyc05g010420.2	167749.467	0.61999656	0.0023432	0.03745015	upregulated
Solyc05g011890.1	4361.27927	0.90950925	1.49E-07	1.74E-05	upregulated
Solyc05g011920.3	1711.10877	0.72061627	0.00022035	0.00631438	upregulated
Solyc05g012450.4	1569.57022	0.32418423	0.00119741	0.02315417	upregulated
Solyc05g012680.3	438.387387	0.75555095	0.00077615	0.01659893	upregulated
Solyc05g012950.3	639.510356	1.16149275	3.09E-05	0.00142897	upregulated
Solyc05g012955.1	352.989574	1.01490145	0.00256579	0.04001278	upregulated
Solyc05g013220.2	471.573616	0.68949971	0.00045026	0.01112921	upregulated
Solyc05g013440.3	20068.3313	0.92275587	0.00013171	0.00430328	upregulated
Solyc05g013510.4	20531.0284	0.39136267	0.00185808	0.03158234	upregulated
Solyc05g013870.4	1253.6967	0.54910657	0.00043078	0.01073208	upregulated
Solyc05g014490.3	1075.20773	0.42873362	0.00056793	0.01311106	upregulated
Solyc05g015980.3	2030.35792	0.41819746	0.0006191	0.01398465	upregulated
Solyc05g016030.3	2251.70317	0.44742638	0.00036723	0.00946081	upregulated
Solyc05g032680.4	127.821417	0.85823526	0.00302781	0.04512798	upregulated
Solyc05g046030.4	80.0487823	1.40016081	0.00078946	0.01684539	upregulated
Solyc05g047710.3	58.9553503	1.24381634	0.00188331	0.03189636	upregulated

Solyc05g050240.3	400.282905	0.8240631	2.60E-05	0.00125189	upregulated
Solyc05g050280.3	3317.74766	0.50495978	0.00017328	0.00532059	upregulated
Solyc05g051460.3	430.543706	0.87733089	0.00119402	0.02312598	upregulated
Solyc05g052240.3	2181.86466	0.5784314	1.20E-05	0.00068265	upregulated
Solyc05g053060.1	270.294947	0.79266452	3.29E-05	0.00151002	upregulated
Solyc05g053550.3	7151.55428	0.57968446	0.00029109	0.00798979	upregulated
Solyc05g054090.3	261.911933	1.07721961	0.00056694	0.01310415	upregulated
Solyc05g054405.1	1805.36752	0.39542026	0.00259323	0.04023879	upregulated
Solyc05g055730.4	466.377317	0.71991999	0.00133857	0.02495935	upregulated
Solyc05g055750.3	458.581131	0.91499815	1.14E-06	9.51E-05	upregulated
Solyc05g056120.3	2210.06281	0.58295312	2.54E-07	2.72E-05	upregulated
Solyc05g056170.3	2609.82908	1.22105897	9.07E-07	7.97E-05	upregulated
Solyc06g007170.4	874.244255	1.15961548	6.65E-11	2.16E-08	upregulated
Solyc06g007620.3	1069.61334	0.59781934	0.00058895	0.0134482	upregulated
Solyc06g009110.3	245.07356	0.59745116	0.00085627	0.01795658	upregulated
Solyc06g009670.3	183.821923	1.16282517	8.96E-06	0.00053052	upregulated
Solyc06g018100.4	1468.75091	0.43277522	0.00192945	0.03244507	upregulated
Solyc06g030470.4	336.784095	0.8222757	5.12E-06	0.00034554	upregulated
Solyc06g035970.3	10000.6208	0.29744075	0.00216074	0.03520576	upregulated
Solyc06g036130.4	891.951563	0.77882779	0.00052288	0.01234255	upregulated
Solyc06g036260.3	14825.663	0.60762127	0.00015584	0.00490496	upregulated
Solyc06g036290.3	294.23117	1.27945414	1.88E-07	2.15E-05	upregulated
Solyc06g036555.1	148.086155	0.83137932	0.00306686	0.04556608	upregulated
Solyc06g048620.3	1095.53785	0.40091592	0.00152055	0.02726876	upregulated
Solyc06g050840.3	1182.16379	0.66417896	2.37E-05	0.00117017	upregulated
Solyc06g050920.4	356.782211	0.59773072	0.00048931	0.01177894	upregulated
Solyc06g051010.1	1046.18703	0.48374613	0.00072827	0.01586229	upregulated
Solyc06g051620.3	153.876076	0.76606526	0.00256912	0.04001278	upregulated
Solyc06g053300.3	3000.24156	0.66570829	0.0009934	0.02018192	upregulated
Solyc06g053870.4	146.441109	1.65112677	0.0002133	0.0061863	upregulated
Solyc06g059930.4	2442.17983	0.97289202	0.00012126	0.00405274	upregulated
Solyc06g060610.2	321.836003	0.84505362	0.00296794	0.04444759	upregulated
Solyc06g061023.1	478.773474	0.91106209	0.0023597	0.03760388	upregulated
Solyc06g061027.1	5896.07137	0.6553364	0.00244077	0.03857028	upregulated
Solyc06g062490.3	43.9518153	1.3934689	0.00181529	0.03107494	upregulated
Solyc06g062580.3	2169.64675	0.58491597	0.00010138	0.0035192	upregulated
Solyc06g062600.3	431.857749	0.92051764	3.73E-05	0.00166414	upregulated
Solyc06g063240.3	3603.48002	0.44568966	7.52E-07	6.73E-05	upregulated
Solyc06g064820.3	394.080205	1.30177352	1.17E-06	9.66E-05	upregulated
Solyc06g064940.3	3134.79099	0.39871664	0.00010238	0.00354234	upregulated
Solyc06g065190.1	263.749964	0.82504894	0.00125015	0.02377427	upregulated

Solyc06g065260.3	1857.38151	0.44459284	0.00034094	0.00891739	upregulated
Solyc06g065530.4	84.246244	1.42372569	8.74E-05	0.00317288	upregulated
Solyc06g065560.2	1370.81892	0.65948215	1.55E-08	2.48E-06	upregulated
Solyc06g065970.1	24691.9325	0.61930216	2.19E-07	2.43E-05	upregulated
Solyc06g066600.3	365.454614	0.5568349	0.00183396	0.03131321	upregulated
Solyc06g066800.2	1152.99056	0.53985721	0.001143	0.02243705	upregulated
Solyc06g068650.4	4896.45461	0.84778736	2.51E-05	0.00122817	upregulated
Solyc06g068840.3	1263.17614	0.48839401	0.00022299	0.00637047	upregulated
Solyc06g068880.3	318.252065	0.77626889	0.00036837	0.00947717	upregulated
Solyc06g068980.4	2604.24465	0.71260737	3.54E-06	0.0002579	upregulated
Solyc06g072740.1	655.84208	0.53677671	0.00309111	0.04585428	upregulated
Solyc06g073450.4	5181.20014	0.63963786	2.59E-05	0.00125189	upregulated
Solyc06g073760.3	108.460415	1.42851345	0.00021258	0.0061863	upregulated
Solyc06g073920.3	1203.19314	0.55061243	0.00045712	0.01123982	upregulated
Solyc06g074000.1	3074.03494	0.64590346	0.00310868	0.04597052	upregulated
Solyc06g074070.3	575.442104	0.55743971	0.0001635	0.00510333	upregulated
Solyc06g074630.4	566.289484	0.61028688	1.82E-05	0.00093115	upregulated
Solyc06g074670.4	3827.3259	0.38685038	0.00137773	0.02540723	upregulated
Solyc06g076020.3	751.000266	0.76562838	0.00214532	0.03503224	upregulated
Solyc06g082610.4	2372.57862	0.47199577	0.00190463	0.03219097	upregulated
Solyc06g083030.3	731.450186	0.9391323	1.26E-05	0.00070581	upregulated
Solyc06g083040.3	28880.0177	0.8070821	0.00056007	0.01299303	upregulated
Solyc06g083440.3	678.994385	0.49906921	0.00318214	0.04676389	upregulated
Solyc06g083460.4	1385.79937	0.40089389	0.00014364	0.0046051	upregulated
Solyc06g083560.3	228.083729	0.66764263	0.0017103	0.02979453	upregulated
Solyc06g083580.4	2395.98764	0.5232439	0.00011914	0.00401052	upregulated
Solyc06g083720.2	157.033244	1.03042663	0.00111176	0.02195559	upregulated
Solyc06g084120.4	193.225337	0.94439216	0.00125503	0.02382379	upregulated
Solyc06g084290.3	506.694853	0.58883572	0.00296804	0.04444759	upregulated
Solyc07g005250.1	414.113676	0.87744148	3.43E-05	0.0015609	upregulated
Solyc07g005510.3	38382.3237	0.38657905	0.00016794	0.00518195	upregulated
Solyc07g005840.2	1291.73242	0.50155048	7.62E-05	0.00283819	upregulated
Solyc07g006300.4	2445.93879	0.7389851	1.54E-05	0.00081095	upregulated
Solyc07g006560.3	4278.96197	4.49287589	6.08E-05	0.00237254	upregulated
Solyc07g006670.1	328.893852	1.5809833	1.23E-08	2.03E-06	upregulated
Solyc07g006680.1	2093.30601	0.63927724	3.88E-06	0.00027222	upregulated
Solyc07g006855.2	547.544665	0.56326769	0.00121046	0.02322997	upregulated
Solyc07g006870.4	322.495819	0.81196252	0.00266997	0.04109188	upregulated
Solyc07g007260.4	8447.84316	0.52807207	0.00033896	0.00888358	upregulated
Solyc07g007350.1	1683.87299	0.42877682	0.00133013	0.02486227	upregulated
Solyc07g008410.4	5098.25112	1.21620915	0.00264207	0.04079548	upregulated

Solyc07g009380.4	3854.85276	0.61587109	0.00020749	0.00609361	upregulated
Solyc07g016080.4	53.0600253	1.86773685	0.00040259	0.01016386	upregulated
Solyc07g018240.1	2475.78259	0.61265948	0.00149445	0.026962	upregulated
Solyc07g019460.3	25209.7346	0.8519075	8.86E-06	0.00052585	upregulated
Solyc07g026680.2	415.74924	2.09135272	1.28E-22	2.41E-19	upregulated
Solyc07g041730.4	263.604414	0.64932896	0.0004684	0.01142953	upregulated
Solyc07g042490.1	224.362598	1.87206142	3.24E-10	9.40E-08	upregulated
Solyc07g042500.4	1518.61449	0.57949471	0.00073412	0.01595794	upregulated
Solyc07g042590.4	1130.18642	0.45008694	0.00108358	0.02153934	upregulated
Solyc07g043130.3	12952.565	0.58381744	0.00178242	0.03054377	upregulated
Solyc07g043500.1	25781.7763	0.6625877	0.00128206	0.02411394	upregulated
Solyc07g043560.4	1836.17973	0.51084178	0.00166577	0.02917757	upregulated
Solyc07g045180.4	259.535047	1.01924829	6.87E-06	0.00043547	upregulated
Solyc07g045350.4	705.834654	0.99570654	0.00131947	0.0247682	upregulated
Solyc07g045440.1	5834.04809	0.5087583	1.94E-08	3.08E-06	upregulated
Solyc07g049300.3	643.67506	0.57221943	0.00012205	0.00406416	upregulated
Solyc07g049370.2	998.927124	0.63851862	9.78E-05	0.00343366	upregulated
Solyc07g049610.1	1250.32041	0.44181762	0.00050265	0.01200316	upregulated
Solyc07g052230.3	145.357391	1.34718745	8.37E-07	7.39E-05	upregulated
Solyc07g052240.3	372.69256	0.708706	0.00101968	0.02057234	upregulated
Solyc07g052490.4	38.6007562	2.23895961	1.45E-05	0.00078003	upregulated
Solyc07g053540.1	1776.18076	0.89209104	3.77E-06	0.00026882	upregulated
Solyc07g054580.3	5601.88293	0.9246504	1.23E-07	1.49E-05	upregulated
Solyc07g054900.2	406.739067	1.03894634	0.00234203	0.03745015	upregulated
Solyc07g055700.2	1028.67736	0.37317405	0.00224927	0.0364594	upregulated
Solyc07g055950.3	5568.43337	0.91000524	6.24E-07	5.78E-05	upregulated
Solyc07g056050.1	4379.82588	0.315144	0.00041203	0.01038159	upregulated
Solyc07g056480.3	1971.4	0.78089631	0.00166716	0.02917757	upregulated
Solyc07g061750.4	464.409515	0.83026553	0.00194681	0.03262076	upregulated
Solyc07g062130.3	8717.73729	0.4620393	0.00118465	0.02301532	upregulated
Solyc07g062710.4	1225.45177	0.90059987	3.61E-07	3.59E-05	upregulated
Solyc07g063120.4	4368.48833	0.64493303	4.15E-08	5.93E-06	upregulated
Solyc07g063350.3	350.4529	0.63157043	0.00346921	0.04973264	upregulated
Solyc07g064670.3	1893.43223	0.40371764	8.43E-05	0.00307788	upregulated
Solyc07g065120.3	6028.58531	0.55657222	2.05E-07	2.31E-05	upregulated
Solyc08g005050.4	5188.29219	0.52674062	0.00296503	0.04444759	upregulated
Solyc08g005130.1	213.172537	0.92529564	0.00053438	0.01255122	upregulated
Solyc08g005630.3	1391.18099	0.4896348	0.00089356	0.01858372	upregulated
Solyc08g005670.2	694.973183	1.36556241	4.90E-07	4.70E-05	upregulated
Solyc08g005677.1	602.009138	1.55278998	3.34E-07	3.39E-05	upregulated
Solyc08g005710.3	535.130684	1.15850797	9.71E-06	0.00056935	upregulated

Solyc08g006310.3	1816.80364	0.47736361	4.92E-05	0.00206538	upregulated
Solyc08g007130.4	648.881034	1.07817017	5.27E-09	1.04E-06	upregulated
Solyc08g007210.4	541.334464	0.78113014	5.29E-06	0.00035276	upregulated
Solyc08g007970.3	2386.76325	0.680019	0.00017429	0.00532569	upregulated
Solyc08g008380.4	407.876934	0.73238749	0.00019049	0.00567997	upregulated
Solyc08g008480.4	209.007235	1.33472205	0.00051579	0.01223637	upregulated
Solyc08g023440.3	994.258643	0.45555878	0.0004694	0.01143764	upregulated
Solyc08g062760.1	146.746313	0.90953883	0.00010503	0.00360951	upregulated
Solyc08g065140.1	730.383729	0.61758909	0.00064561	0.01437691	upregulated
Solyc08g066740.3	268.944093	0.80392643	0.00050278	0.01200316	upregulated
Solyc08g066890.4	830.33762	4.32739341	0.00013535	0.00440835	upregulated
Solyc08g067260.4	4422.375	0.60572419	1.82E-07	2.10E-05	upregulated
Solyc08g067940.3	967.090482	0.73707931	6.14E-05	0.00238455	upregulated
Solyc08g068490.3	5779.55295	0.59545809	0.0003364	0.00884771	upregulated
Solyc08g068665.1	382.200833	1.0965954	0.00018827	0.00564044	upregulated
Solyc08g068800.4	128.731041	0.93866791	0.0020349	0.03361948	upregulated
Solyc08g074620.3	4038.85697	1.5723819	0.0013772	0.02540723	upregulated
Solyc08g074630.2	730.465418	1.15630806	0.00057151	0.01313438	upregulated
Solyc08g075240.3	645.742274	1.0582861	9.87E-05	0.00345243	upregulated
Solyc08g075470.3	3364.1766	0.40541999	8.21E-06	0.00049874	upregulated
Solyc08g076370.3	877.55463	0.75172866	1.28E-07	1.52E-05	upregulated
Solyc08g077210.4	3557.64939	0.38739048	0.00014026	0.00453545	upregulated
Solyc08g077240.3	7699.72496	0.28237415	0.00334377	0.04849756	upregulated
Solyc08g077430.3	3118.2769	0.66915307	9.48E-07	8.25E-05	upregulated
Solyc08g078030.4	397.058536	0.6671654	8.53E-05	0.00311123	upregulated
Solyc08g078670.2	2022.63063	0.74829448	1.12E-08	1.90E-06	upregulated
Solyc08g078940.1	330.062286	2.92610307	3.18E-11	1.13E-08	upregulated
Solyc08g078960.4	1860.42758	0.39101236	0.00143414	0.02624254	upregulated
Solyc08g079060.4	528.798561	1.60962435	5.90E-09	1.09E-06	upregulated
Solyc08g079090.4	4222.14195	0.83958588	2.49E-09	5.53E-07	upregulated
Solyc08g079750.3	2501.62515	0.44926943	4.90E-06	0.00033635	upregulated
Solyc08g079790.1	1444.18438	0.34589013	0.00265766	0.04096919	upregulated
Solyc08g080160.4	39.756408	2.22810616	0.00068428	0.01511327	upregulated
Solyc08g080470.3	454.966009	0.63139601	0.00032221	0.00863053	upregulated
Solyc08g081220.1	3677.3081	0.45750801	1.53E-05	0.00081095	upregulated
Solyc08g082010.3	3623.13248	0.55771054	2.50E-10	7.48E-08	upregulated
Solyc08g082060.3	1340.51109	0.3797338	0.00032474	0.00867393	upregulated
Solyc08g082450.3	476.924643	0.8049791	0.00271792	0.04172782	upregulated
Solyc09g005940.4	378.097772	1.08742044	0.0002122	0.0061863	upregulated
Solyc09g007110.3	1874.28218	0.4699007	0.00030148	0.0081682	upregulated
Solyc09g007150.3	5448.85666	0.76235755	0.0013775	0.02540723	upregulated

Solyc09g007660.1	321.282123	0.61038981	0.00137231	0.02540666	upregulated
Solyc09g007790.1	37.2926485	1.87212293	0.00026561	0.00738701	upregulated
Solyc09g007910.4	2564.1526	1.56406414	0.00073562	0.01596727	upregulated
Solyc09g008840.4	2192.39893	0.81787345	0.00045203	0.01114376	upregulated
Solyc09g009010.4	2274.06006	0.38869446	0.00071193	0.01555511	upregulated
Solyc09g009220.4	752.855031	1.4269557	6.55E-11	2.16E-08	upregulated
Solyc09g011040.1	137.505676	0.8384802	0.0012603	0.02384798	upregulated
Solyc09g011080.3	24658.0224	0.94435578	7.69E-06	0.00047298	upregulated
Solyc09g014350.3	5709.69555	0.65014629	2.33E-07	2.54E-05	upregulated
Solyc09g014970.4	100.678127	1.42135312	0.00012317	0.00408779	upregulated
Solyc09g015040.1	1018.29669	0.46699319	0.00015002	0.00475765	upregulated
Solyc09g015170.4	217.152832	0.8265375	0.00245715	0.03873195	upregulated
Solyc09g015520.3	520.570532	0.52298254	0.00033212	0.00879636	upregulated
Solyc09g015830.3	4380.16572	0.55411185	4.33E-07	4.24E-05	upregulated
Solyc09g015840.4	953.524011	0.66066147	5.35E-06	0.00035572	upregulated
Solyc09g019980.3	148.32955	0.82901286	0.00053643	0.01256826	upregulated
Solyc09g031517.1	530.440011	0.45163536	0.00120295	0.02316349	upregulated
Solyc09g059170.3	1416.6581	1.03876634	1.26E-05	0.00070581	upregulated
Solyc09g063030.4	4050.84143	0.5179718	3.60E-06	0.00026137	upregulated
Solyc09g065660.4	192.449294	1.5220129	0.00029981	0.00814623	upregulated
Solyc09g065870.4	498.96382	0.60501765	0.00343412	0.04951686	upregulated
Solyc09g072820.4	1850.96303	0.66467791	6.38E-06	0.00041239	upregulated
Solyc09g074060.3	2517.47303	0.51885261	3.77E-06	0.00026882	upregulated
Solyc09g075280.2	1615.06559	0.38858394	0.00038241	0.00979842	upregulated
Solyc09g075400.4	85.2980051	2.37493139	0.00018222	0.00549694	upregulated
Solyc09g076000.3	2125.09384	0.36127279	0.00257427	0.04001278	upregulated
Solyc09g082510.3	6399.11611	0.36879265	0.00144612	0.02642097	upregulated
Solyc09g083050.3	729.924234	0.79140847	3.96E-07	3.91E-05	upregulated
Solyc09g083390.3	1832.01876	0.547054	1.07E-05	0.00061383	upregulated
Solyc09g090680.3	915.8397	0.9349644	0.0008704	0.01816198	upregulated
Solyc09g091270.3	235.068842	0.76963586	0.00148046	0.0268045	upregulated
Solyc09g092460.4	1052.09162	0.42401346	0.00236834	0.03767265	upregulated
Solyc09g092490.3	2274.44819	0.83232961	6.59E-05	0.00251848	upregulated
Solyc09g092520.3	1567.42446	1.37371663	1.86E-12	1.07E-09	upregulated
Solyc09g092560.4	262.078333	1.4492652	1.09E-06	9.22E-05	upregulated
Solyc10g005080.3	7122.77981	0.84654717	1.30E-14	1.02E-11	upregulated
Solyc10g005200.3	1412.9666	0.51444934	0.0001381	0.00448077	upregulated
Solyc10g005210.4	340.976164	1.117607	1.48E-07	1.73E-05	upregulated
Solyc10g005330.3	3857.16468	0.4363787	0.00061797	0.01397585	upregulated
Solyc10g005960.1	11090.081	0.43735539	0.00253909	0.03965931	upregulated
Solyc10g006870.1	1140.14001	0.46070343	0.00071282	0.01555511	upregulated

Solyc10g007110.3	3150.1027	0.39992016	0.00013637	0.00443247	upregulated
Solyc10g007290.4	1471.36383	0.49667155	0.00280589	0.04280005	upregulated
Solyc10g008620.3	135.989586	1.05905844	0.00336149	0.04871714	upregulated
Solyc10g009240.3	373.117188	0.90734491	3.13E-06	0.00023094	upregulated
Solyc10g009380.3	237.730633	1.16196476	0.00177024	0.03043487	upregulated
Solyc10g011820.4	3700.27388	0.56647327	2.57E-05	0.00124816	upregulated
Solyc10g018305.1	105.471419	1.51152352	0.00062458	0.01405785	upregulated
Solyc10g049580.2	1219.98566	0.51055185	0.00051334	0.0121935	upregulated
Solyc10g050160.2	742.581411	0.72781799	4.44E-07	4.32E-05	upregulated
Solyc10g052490.2	1305.22017	0.79334574	0.00050457	0.01203069	upregulated
Solyc10g052500.2	46.1872209	2.51998644	1.58E-05	0.00083326	upregulated
Solyc10g054010.1	278.451564	0.75669011	0.00193915	0.03255021	upregulated
Solyc10g054440.3	10055.1772	0.6663009	1.64E-12	9.69E-10	upregulated
Solyc10g055410.2	1316.3836	0.61328984	3.61E-06	0.00026137	upregulated
Solyc10g074540.1	1375.86817	1.02276017	1.08E-10	3.39E-08	upregulated
Solyc10g075110.2	417.77598	1.35860563	2.98E-05	0.00139438	upregulated
Solyc10g076360.1	887.252817	0.7269634	1.69E-06	0.00013371	upregulated
Solyc10g078240.2	2292.09216	0.69242521	0.00020175	0.00595403	upregulated
Solyc10g078470.2	215.819242	1.46859679	7.85E-05	0.00288973	upregulated
Solyc10g078910.3	3526.53678	0.42285013	2.50E-06	0.00019125	upregulated
Solyc10g079300.2	158.495949	0.97557831	0.00083529	0.01762419	upregulated
Solyc10g079350.3	2144.52094	1.94734171	4.89E-06	0.00033635	upregulated
Solyc10g080150.2	933.329714	0.91263009	0.00042159	0.01054488	upregulated
Solyc10g080870.3	414.414279	0.93608787	0.00137445	0.02540723	upregulated
Solyc10g081420.2	1037.11244	0.55209016	4.83E-05	0.00203018	upregulated
Solyc10g081720.2	7115.86017	0.28363829	0.00163358	0.02885736	upregulated
Solyc10g083170.2	444.045367	1.20313231	3.54E-09	7.43E-07	upregulated
Solyc10g083440.2	952.196992	1.28643303	5.02E-09	9.97E-07	upregulated
Solyc10g083670.3	1601.42352	0.55669629	5.05E-06	0.00034429	upregulated
Solyc10g084230.2	657.178173	0.82252876	0.00017423	0.00532569	upregulated
Solyc10g084280.2	2364.74595	0.41320298	0.00070172	0.01539049	upregulated
Solyc10g084370.3	3460.42607	0.6103441	1.02E-07	1.26E-05	upregulated
Solyc10g084380.1	2662.23564	0.74032387	0.00069164	0.01522261	upregulated
Solyc10g084430.2	751.338922	0.91943811	0.00010666	0.0036507	upregulated
Solyc10g084530.1	583.989468	0.56798752	0.00018062	0.00547488	upregulated
Solyc10g084890.3	445.443225	1.35981079	0.00047861	0.01159595	upregulated
Solyc10g085020.3	5289.75305	0.35736954	0.00149916	0.026962	upregulated
Solyc10g085220.3	6508.01253	0.73464222	0.00125654	0.02382379	upregulated
Solyc10g085610.2	692.139465	0.62610966	0.00237	0.03767265	upregulated
Solyc10g085670.2	415.774369	0.64280111	0.00018134	0.00548614	upregulated
Solyc10g085830.2	7414.76644	0.33307583	0.00232084	0.03726169	upregulated

Solyc10g086030.2	1110.87314	0.5663534	0.00212433	0.03476236	upregulated
Solyc10g086060.2	3633.17286	0.39603535	0.0019934	0.03315802	upregulated
Solyc10g086180.2	26412.7862	1.17985081	0.00257123	0.04001278	upregulated
Solyc10g150142.1	555.332146	0.52124346	0.00100895	0.02042132	upregulated
Solyc11g005150.3	334.498182	1.00204541	4.88E-07	4.70E-05	upregulated
Solyc11g006040.2	3779.94577	0.52223769	0.00043828	0.01086146	upregulated
Solyc11g006250.2	11078.2687	0.51332993	0.00073897	0.01600302	upregulated
Solyc11g008540.3	8070.4359	0.86586706	3.90E-05	0.00173148	upregulated
Solyc11g008630.3	7364.38744	0.44433652	0.0003181	0.00853272	upregulated
Solyc11g008870.2	10018.614	0.34577614	0.00282873	0.04311353	upregulated
Solyc11g010170.2	898.619282	0.95218002	0.00331225	0.04815131	upregulated
Solyc11g010380.2	4422.39451	0.69086284	1.07E-06	9.09E-05	upregulated
Solyc11g011020.2	1930.4196	0.52823578	3.20E-05	0.00147546	upregulated
Solyc11g011030.2	3831.65543	0.86661262	2.55E-05	0.00124063	upregulated
Solyc11g012240.1	488.739839	0.59664349	0.00061489	0.01393956	upregulated
Solyc11g013170.2	4829.23753	0.51564799	0.00288399	0.04360388	upregulated
Solyc11g020670.1	208.193798	1.15434621	0.00079045	0.01684754	upregulated
Solyc11g033283.1	1688.12131	0.62412511	7.91E-07	7.02E-05	upregulated
Solyc11g044250.3	7026.47136	0.45249681	1.41E-05	0.00076435	upregulated
Solyc11g065090.2	2408.79528	0.44306849	5.16E-06	0.00034701	upregulated
Solyc11g065220.2	263.496959	1.16663216	4.54E-08	6.27E-06	upregulated
Solyc11g066320.2	343.421045	0.75140132	0.00016483	0.00512779	upregulated
Solyc11g066390.2	32714.5637	0.88634458	0.00029952	0.00814623	upregulated
Solyc11g066490.1	442.311317	0.57229901	0.00020961	0.00614625	upregulated
Solyc11g066880.2	80.895213	1.6185979	0.00256655	0.04001278	upregulated
Solyc11g069650.2	678.851279	0.65209677	7.23E-05	0.00271805	upregulated
Solyc11g069960.2	3776.02253	1.40941537	4.75E-11	1.66E-08	upregulated
Solyc11g071850.1	931.387578	0.50459877	0.00177254	0.03043487	upregulated
Solyc11g072030.3	2780.29063	0.60629372	0.00019168	0.00569128	upregulated
Solyc11g072110.2	2858.45018	0.70745769	2.28E-07	2.50E-05	upregulated
Solyc11g072580.2	239.132755	0.61020191	0.00259777	0.04025707	upregulated
Solyc11g072990.1	1448.96501	0.56186392	1.39E-05	0.0007562	upregulated
Solyc12g005230.3	385.209351	0.62392354	0.00116555	0.02273784	upregulated
Solyc12g005430.1	450.504706	1.96987712	0.00025336	0.00710543	upregulated
Solyc12g006050.2	1550.80359	1.23409206	6.88E-15	6.19E-12	upregulated
Solyc12g006380.2	1402.43219	1.13807036	9.16E-05	0.00328994	upregulated
Solyc12g006460.2	27016.5696	0.48033322	0.00147428	0.02676943	upregulated
Solyc12g006805.1	4144.21363	0.37826214	0.00039824	0.01009267	upregulated
Solyc12g006980.2	1011.55104	0.81194174	3.76E-08	5.49E-06	upregulated
Solyc12g007100.2	2631.69309	0.31189615	0.00175958	0.03033066	upregulated
Solyc12g007110.2	4233.086	0.30257332	0.00110226	0.02184213	upregulated

Solyc12g008490.2	858.332719	0.47687224	0.00037143	0.00954295	upregulated
Solyc12g008530.2	563.987878	0.74534756	0.00021534	0.00621787	upregulated
Solyc12g008600.2	123.03232	1.93625114	2.68E-07	2.81E-05	upregulated
Solyc12g008800.3	1614.49345	1.35545388	3.16E-13	2.13E-10	upregulated
Solyc12g009650.2	84687.2343	0.53665291	7.02E-05	0.00265142	upregulated
Solyc12g010800.2	277.91794	1.01229487	2.85E-06	0.00021297	upregulated
Solyc12g011010.2	5110.71612	0.65573097	5.87E-05	0.00230122	upregulated
Solyc12g011023.1	99.3727186	1.89067146	0.00284191	0.0432447	upregulated
Solyc12g011160.2	1570.88603	0.65474312	1.02E-06	8.77E-05	upregulated
Solyc12g014400.3	2093.02222	0.36846446	0.00316238	0.04660212	upregulated
Solyc12g015770.3	1157.03154	0.96874015	0.00012816	0.00423848	upregulated
Solyc12g015860.2	9067.93198	0.79934499	8.84E-05	0.0031974	upregulated
Solyc12g017970.1	156.410613	0.71790086	0.00229029	0.03702894	upregulated
Solyc12g019320.2	3977.39326	0.72154846	0.00110077	0.02184213	upregulated
Solyc12g038520.3	425.080213	1.01091962	0.00011206	0.00379253	upregulated
Solyc12g038550.1	683.809444	0.5336009	0.00181671	0.03107494	upregulated
Solyc12g042500.2	365.874849	0.87964721	0.00047897	0.01159595	upregulated
Solyc12g044600.3	14297.2545	0.3403661	0.00168743	0.02945042	upregulated
Solyc12g056580.2	6926.09344	0.72818056	1.39E-14	1.05E-11	upregulated
Solyc12g056600.3	535.800507	1.19210487	0.00093521	0.01925908	upregulated
Solyc12g056610.3	380.664258	1.04134561	0.00166656	0.02917757	upregulated
Solyc12g056630.3	382.831044	0.62130158	0.00065883	0.01463217	upregulated
Solyc12g056710.3	745.638206	0.95191766	0.00058638	0.01342215	upregulated
Solyc12g056800.2	5605.04732	0.44247131	0.00010671	0.0036507	upregulated
Solyc12g057040.2	3930.10675	0.36559345	0.00323844	0.04740678	upregulated
Solyc12g057080.2	4044.79262	0.53001983	0.0023072	0.03714999	upregulated
Solyc12g088220.2	165.697012	1.23895521	5.67E-07	5.30E-05	upregulated
Solyc12g088250.2	1411.91691	0.39863754	0.00298049	0.04456346	upregulated
Solyc12g088370.2	593.015318	0.49524829	0.00284525	0.04326062	upregulated
Solyc12g088870.1	885.211923	0.63871161	0.00176035	0.03033066	upregulated
Solyc12g096130.2	338.574335	1.01355033	3.52E-05	0.00159813	upregulated
Solyc12g096770.1	7689.85952	1.16369141	6.43E-09	1.18E-06	upregulated
Solyc12g096780.2	3709.01842	2.28816772	0.00054197	0.01268215	upregulated
Solyc12g096860.3	149.778582	0.83381838	0.00061267	0.01390576	upregulated
Solyc12g096900.2	2524.29453	0.54969002	9.65E-05	0.00340974	upregulated
Solyc12g098590.3	92.2078666	2.19624464	0.00047563	0.01155948	upregulated
Solyc12g098603.1	68.2501195	1.68501587	2.08E-05	0.00104704	upregulated
Solyc12g100280.3	69.2430173	1.51519528	9.97E-05	0.00347894	upregulated

Supplementary Material 7.9. Table of mobile mRNAs locates in tomato scions produced by the RS-1 rootstock in heterograft conditions: Tomato/RS-1 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

mRNA	Locus	FPKM_RS-1_rep1	FPKM_RS-1_rep2
Shab01g004760	B_Sly01:5972515-5978275	0.00316605	0.00339958
Shab01g008600	B_Sly01:60035397-60047699	0.0044476	0.00159188
Shab01g013330	B_Sly01:78868620-78878402	0.00186442	0.00200194
Shab01g016410	B_Sly01:82049115-82052118	0.00607177	0.00651963
Shab01g024980	B_Sly01:89937933-89948813	0.01005767	0.00539977
Shab02g003440	B_Sly02:29185905-29187331	0.01278177	0.05489827
Shab02g012750	B_Sly02:43302519-43307821	0.00687897	0.00369318
Shab02g014830	B_Sly02:45071341-45078386	0.00258864	0.00833876
Shab02g021500	B_Sly02:50442121-50444486	0.00770904	0.00827767
Shab02g028060	B_Sly02:55682980-55684771	0.02035668	0.02185821
Shab02g028630	B_Sly02:56074611-56079830	0.00698835	0.00375191
Shab03g003210	B_Sly03:2929226-2934116	0.00372921	0.00400428
Shab03g009190	B_Sly03:21926161-21926397	0.07696029	0.08263695
Shab03g016360	B_Sly03:54858327-54859613	0.01417217	0.01521753
Shab03g023150	B_Sly03:61151935-61154788	0.00639089	0.00686228
Shab04g006880	B_Sly04:6325465-6340191	0.00123851	0.00132987
Shab04g008460	B_Sly04:12107707-12108169	0.07878872	0.04230012
Shab04g019620	B_Sly04:61214444-61228588	0.00386842	0.00138459
Shab04g025710	B_Sly04:66893834-66898764	0.00369896	0.0039718
Shab05g021200	B_Sly05:70048099-70050870	0.00657994	0.00706528
Shab06g004370	B_Sly06:15110410-15117120	0.00271786	0.00291834
Shab06g005360	B_Sly06:26579441-26582146	0.00674042	0.0072376
Shab06g009280	B_Sly06:37199322-37207914	0.00212261	0.00683753
Shab06g011670	B_Sly06:40332649-40346864	0.0038491	0.00137767
Shab06g014420	B_Sly06:42924386-42928488	0.00444543	0.01431998
Shab06g014650	B_Sly06:43170419-43173487	0.01188634	0.03190772
Shab07g013320	B_Sly07:61786181-61792061	0.00310144	0.00333021
Shab07g020450	B_Sly07:69206398-69210350	0.00461411	0.00990891
Shab07g020670	B_Sly07:69363083-69367732	0.00392249	0.00421182
Shab07g021250	B_Sly07:69748259-69748797	0.03383968	0.10900718
Shab08g013160	B_Sly08:54278415-54280728	0.01576455	0.00846368
Shab08g018000	B_Sly08:60198977-60199393	0.13122006	0.14089897
Shab08g021360	B_Sly08:63245776-63251024	0.00347487	0.00746236
Shab09g016450	B_Sly09:72623677-72636907	0.00137855	0.00740116
Shab10g003540	B_Sly10:3002339-3002966	0.02904393	0.09355871
Shab10g015070	B_Sly10:62718883-62724112	0.00697499	0.0112342
Shab10g017190	B_Sly10:64969954-64972517	0.02134117	0.00763844
Shab10g021560	B_Sly10:68460329-68466322	0.00608595	0.00326743
Shab10g022180	B_Sly10:68908680-68912157	0.00524427	0.0056311
Shab10g023440	B_Sly10:69821975-69823082	0.01646172	0.12373167

Shab11g001880	B_Sly11:1495694-1497829	0.01707827	0.00916899
Shab11g004830	B_Sly11:4442378-4444362	0.00918871	0.00986648
Shab12g019590	B_Sly12:66884987-66887950	0.01230741	0.01321522
Shab12g020290	B_Sly12:67381158-67384923	0.00484323	0.00520047
Shabxxg002040	B_Contig00248:494235-499134	0.02233419	0.00399693
Shabxxg002490	B_Contig00296:20031-21392	0.0401753	0.01437956
Shabxxg004120	B_Contig00535:26038-26256	0.08328579	0.08942902
Shabxxg018280	B_Contig02234:186236-190350	0.00443246	0.00475941
Shabxxg019140	B_Contig02349:17640-20080	0.00747218	0.00802333

Supplementary Material 7.10. Table of mobile mRNAs locates in tomato scions produced by the RS-2 rootstock in heterograft conditions: Tomato/RS-2 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

mRNA	Locus	FPKM_RS-2_rep1	FPKM_RS-2_rep2	FPKM_RS-2_rep3	FPKM_RS-2_rep4
Shab02g014830	B_Sly02:45071341-45078386	0.00261485	0.00266007	0.00144749	0.00267987
Shab03g013970	B_Sly03:50487420-50490727	0.0055696	0.00566591	0	0.0057081
Shab03g022550	B_Sly03:60704786-60710012	0.00352482	0.00358577	0	0.00722494
Shab04g013000	B_Sly04:48249703-48251596	0.00972768	0.0098959	0	0.00996958
Shab04g023540	B_Sly04:65286651-65288037	0.01328351	0.12161899	0	0.01361384
Shab05g005810	B_Sly05:5519736-5522115	0.00774127	0.00787514	0.01714116	0.00793378
Shab08g005180	B_Sly08:8418438-8427294	0.00208019	0.0105808	0	0.00426383
Shab08g006200	B_Sly08:18406686-18421322	0.00251749	0.00384153	0	0.00516018
Shab08g009540	B_Sly08:47049758-47074362	0.0007488	0.00076175	0.00124353	0.00076742
Shab09g000830	B_Sly09:678393-681436	0.01210527	0.00615731	0	0.00620315
Shab10g003230	B_Sly10:2689849-2696004	0.00598578	0.00304465	0	0.00613463
Shab10g017190	B_Sly10:64969954-64972517	0.02155721	0.02193	0	0.01472885
Shab10g021990	B_Sly10:68787393-68787824	0.04264868	0.0433862	0	0.04370923
Shab10g023440	B_Sly10:69821975-69823082	0.03325673	0.11841143	0	0.03408374
Shab12g000040	B_Sly12:53471-56671	0.00575577	0.01171061	0	0.0058989
Shabxxg006490	B_Contig00750:37739-38926	0.03101722	0.15776799	0.06009506	0.14304841

Supplementary Material 7.11. Table of mobile sRNAs locates in tomato scions produced by the RS-1 rootstock in heterograft conditions: Tomato/RS-1 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Locus	RPM_RS-1_rep1	RPM_RS-1_rep2	DicerCall Consensus
B_Contig00505:102007-102029	13.0948724	1.37822183	N
B_Contig00513:33054-33070	7.55473405	1.10257747	N
B_Contig00760:22981-22999	13.5985213	0.27564437	N
B_Contig00917:162295-162311	15.1094681	0.55128873	N
B_Contig01210:27551-27573	22.6642021	1.92951057	N
B_Sly01:75232888-75232907	7.05108511	0.8269331	N
B_Sly01:77961824-77961844	11.0802766	0.27564437	N
B_Sly01:89382364-89382392	3.52554256	7.44239791	N
B_Sly01:95947860-95947889	8.05838298	1.6538662	N
B_Sly02:19825988-19826003	7.05108511	0.27564437	N
B_Sly02:29203654-29203673	11.0802766	1.10257747	N
B_Sly02:46326360-46326396	10.0729787	1.37822183	N
B_Sly03:2475834-2475856	7.55473405	0.27564437	N
B_Sly03:54637466-54637493	8.05838298	19.5707501	N
B_Sly03:63405898-63405923	8.56203192	2.75644367	N
B_Sly03:64341317-64341341	8.56203192	1.10257747	N
B_Sly04:218436-218465	11.5839255	4.68595424	N
B_Sly04:36019077-36019091	0.50364894	0.55128873	N
B_Sly04:54039571-54039597	6.54743618	0.27564437	N
B_Sly04:57923663-57923687	7.55473405	2.20515494	N
B_Sly04:60749647-60749669	3.52554256	3.3077324	N
B_Sly04:62299053-62299075	9.06568086	0.8269331	N
B_Sly04:63001537-63001556	7.55473405	0.27564437	N
B_Sly05:44231241-44231316	1.51094681	3.3077324	N
B_Sly06:1265297-1265322	7.05108511	1.92951057	N
B_Sly06:2989386-2989409	4.53284043	3.85902114	N
B_Sly06:35316480-35316502	8.56203192	1.10257747	N
B_Sly07:31242026-31242045	1.00729787	0.27564437	N
B_Sly07:33924052-33924069	16.116766	1.92951057	N
B_Sly07:43932830-43932845	2.01459575	3.58337677	N
B_Sly07:66369446-66369477	6.04378724	3.85902114	N
B_Sly08:3264300-3264334	3.52554256	4.68595424	N
B_Sly08:9364814-9364836	10.0729787	2.20515494	N
B_Sly08:44722460-44722478	7.55473405	1.10257747	N
B_Sly08:45797639-45797656	8.05838298	0.55128873	N
B_Sly09:1550918-1550942	15.1094681	7.16675354	N
B_Sly09:5468258-5468284	6.54743618	2.75644367	N

B_Sly09:10630091-10630115	5.03648937	3.58337677	N
B_Sly09:16335537-16335560	7.55473405	0.27564437	N
B_Sly09:22571575-22571593	8.56203192	0.8269331	N
B_Sly09:22872564-22872583	9.06568086	1.10257747	N
B_Sly09:23564994-23565016	13.0948724	0.55128873	N
B_Sly09:44623098-44623133	1.00729787	4.1346655	N
B_Sly09:66118411-66118521	9.06568086	0.8269331	N
B_Sly09:75821077-75821099	8.56203192	0.8269331	N
B_Sly10:601382-601403	6.54743618	1.92951057	N
B_Sly10:24904870-24904892	6.54743618	2.20515494	N
B_Sly10:51695090-51695113	9.56932979	1.37822183	N
B_Sly11:12791855-12791876	2.51824468	0.55128873	N
B_Sly11:55211255-55211283	7.05108511	0.55128873	N
B_Sly11:58165289-58165321	6.54743618	1.10257747	N
B_Sly12:40134521-40134536	10.0729787	0.27564437	N

Supplementary Material 7.12. Table of mobile sRNAs locates in tomato scions produced by the RS-2 rootstock in heterograft conditions: Tomato/RS-2 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Locus	RPM_RS-2_rep1	RPM_RS-2_rep2	RPM_RS-2_rep3	RPM_RS-2_rep4	DicerCall Consensus
B_Contig00054:22647-22661	0	0.47279848	0	0.81408033	N
B_Contig00760:22981-22999	0.54842662	0.47279848	0	0.81408033	N
B_Contig01877:26453-26484	0	0	0.63498353	4.884482	N
B_Sly01:4967960-4967984	4.38741295	0	1.26996706	0	N
B_Sly01:23996583-23996606	0	0.47279848	0	6.1056025	24
B_Sly01:89382364-89382392	0	1.41839545	0	0.40704017	N
B_Sly01:90073954-90073981	25.7760511	14.1839545	18.4145223	9.768964	24
B_Sly01:95947860-95947889	0	0.94559697	0	1.62816067	N
B_Sly03:2475834-2475856	0.54842662	0	0	1.2211205	N
B_Sly03:49820867-49820897	0.54842662	0	0	57.7997037	24
B_Sly03:54637466-54637493	4.38741295	6.1463803	4.4448847	6.91968283	24
B_Sly03:63405898-63405923	1.09685324	0.94559697	0	0.40704017	24
B_Sly04:36019077-36019091	0	0	0.63498353	0.81408033	N
B_Sly04:57923663-57923687	0	0	0.63498353	1.2211205	24
B_Sly05:66786631-66786655	4.93583957	0.47279848	0	0	N
B_Sly07:43932830-43932845	1.09685324	0.47279848	0	0	N
B_Sly07:66369446-66369477	1.64527986	1.41839545	2.53993411	0.40704017	24
B_Sly11:12791855-12791876	4.93583957	0	0	0.40704017	N
B_Sly11:36745806-36745831	0	0	0.63498353	5.69856233	N

B_Sly11:58165289-58165321	0	0	1.26996706	0.40704017	N

Supplementary Material 7.13. Table of mobile sRNA sequences. Tomato/RS-1 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Mobile sRNA	Consensus Sequence
B_Contig00505:102007-102029	UUUUAAGUAGAUCUAAUCGUUU
B_Contig00513:33054-33070	GUGUGACUUGAACUAA
B_Contig00760:22981-22999	CUCCGAUUCGUAAAAAA
B_Contig00917:162295-162311	AUUGUAGAGGGAAGA
B_Sly01:75232888-75232907	UUUCUAUGAUUUCUGAAUUU
B_Sly01:77961824-77961844	UUGAUUGAUCGAACCACA
B_Sly01:89382364-89382392	AGAAGAUAUGAAUGCUGAAUUGAG
B_Sly01:95947860-95947889	AUGAGUCUAACUGUAAUAUACUAC
B_Sly02:19825988-19826003	GUCUCUGAGAUCUCAA
B_Sly02:29203654-29203673	AAUGUCUUUGAUUGUGUUCA
B_Sly03:2475834-2475856	AUCAAGUGUGUGUGAAUUCA
B_Sly04:218436-218465	AUGUGACAAAUCUGAAAUAUAUC
B_Sly04:36019077-36019091	GAUGGGUGCUCUCCU
B_Sly04:60749647-60749669	UUAAGGCUCAAAGUAAUUCUUG
B_Sly04:62299053-62299075	AGCUAUAGAUACACUGU
B_Sly06:1265297-1265322	AAGAAUCUCAUGAACCUACAAGA
B_Sly06:2989386-2989409	UUAGACAUCUCAAUUAGACUUUG
B_Sly07:33924052-33924069	CUUGUCGGUUGUGAACA
B_Sly07:43932830-43932845	GCGGAUAUGGACGAAU
B_Sly08:44722460-44722478	UCUUAUUACCCCUGAACA
B_Sly08:45797639-45797656	CUUGUUUGACUUGGAACA
B_Sly09:1550918-1550942	AAAGAUCUCUGAUUUAAAUUUCA
B_Sly09:16335537-16335560	UAACCUAUGAAACUCCUAAGACA
B_Sly09:22872564-22872583	UCCGGAUAUGAUUCAGC
B_Sly09:44623098-44623133	AACUGUAGCCUAUAUUUUAGGAAC
B_Sly09:66118411-66118521	UUCCGAAGACUACUUAGUUA
B_Sly09:75821077-75821099	CUUACGUCUUAUGAAUCUACA
B_Sly10:601382-601403	AUAAGAUUGUGUCACUUGUCCC
B_Sly10:24904870-24904892	AGGACAAAUAAAACCCAACAACA
B_Sly10:51695090-51695113	AUUCCAUCUGUAUAAAACUCUACA
B_Sly11:12791855-12791876	UCCUGAACUUAUUUUAUAUU
B_Sly11:55211255-55211283	AAAGUCUGACUAAAUUUUGAUUU
B_Sly11:58165289-58165321	UACAUGGAUCUCUAUCAGUUG
B_Sly12:40134521-40134536	GGGCCUGUAGCUCAGG

Supplementary Material 7.14. Table of mobile sRNA sequences. Tomato/RS-2 heterografted samples in comparison to Tomato/Tomato self-grafted samples.

Mobile sRNA	Consensus sequence
B_Contig00054:22647-22661	CGUUGAGUUCUUAACA
B_Sly01:4967960-4967984	AAGAUACCUGUCACCUCUCACCAGU
B_Sly01:23996583-23996606	AGGUGUGUCUCGGAGAUUUUGGUC
B_Sly01:90073954-90073981	AGAGCAUGUCAUCUUGGGUCUAGU
B_Sly03:49820867-49820897	AAUAUGGGGACCUUUGGAGUGAUU
B_Sly03:54637466-54637493	AAAGCUAGUGGAUUCAUCCGAACC
B_Sly04:36019077-36019091	GAUGGGUGCUCUCCU
B_Sly04:57923663-57923687	AUUUUAAACGUGAACGUCUGAAGC
B_Sly05:66786631-66786655	ACUUUUAUCAUUGUAGGGCAGAAAA
B_Sly07:43932830-43932845	GCGGAUAUGGACGAA

LIST OF REFERENCES

Abdel-Ghany, S. E. and M. Pilon (2008). "MicroRNA-mediated systemic down-regulation of copper protein expression in response to low copper availability in Arabidopsis." Journal of Biological Chemistry **283**(23): 15932-15945.

Ahsan, M. U., A. Hayward, M. Alam, J. H. Bandaralage, B. Topp, C. A. Beveridge and N. Mitter (2019). "Scion control of miRNA abundance and tree maturity in grafted avocado." BMC plant biology **19**: 1-11.

Albacete, A., C. Martínez-Andújar, F. Pérez-Alfocea, J. Lozano and M. J. Asins (2015). "Rootstock-mediated variation in tomato vegetative growth under low potassium or phosphorous supplies." Acta horticulturae(1086): 147-152.

Almeida, K. H. and R. W. Sobol (2007). "A unified view of base excision repair: lesion-dependent protein complexes regulated by post-translational modification." DNA repair **6**(6): 695-711.

Aloni, B., R. Cohen, L. Karni, H. Aktas and M. Edelstein (2010). "Hormonal signaling in rootstock–scion interactions." Scientia Horticulturae **127**(2): 119-126.

Aloni, B., L. Karni, G. Deventurero, Z. Levin, R. Cohen, N. Katzir, M. Lotan-Pompan, M. Edelstein, H. Aktas and E. Turhan (2008). "Physiological and biochemical changes at the rootstock-scion interface in graft combinations between Cucurbita rootstocks and a melon scion." The Journal of Horticultural Science and Biotechnology **83**(6): 777-783.

Altschul, S. F., W. Gish, W. Miller, E. W. Myers and D. J. Lipman (1990). "Basic local alignment search tool." Journal of molecular biology **215**(3): 403-410.

Alvarez, S., J. Q. Goodger, E. L. Marsh, S. Chen, V. S. Asirvatham and D. P. Schachtman (2006). "Characterization of the maize xylem sap proteome." Journal of proteome research **5**(4): 963-972.

Álvarez-Hernández, J. C., J. Z. Castellanos-Ramos, C. L. Aguirre-Mancilla, M. V. Huitrón-Ramírez and F. Camacho-Ferre (2015). "Influence of rootstocks on fusarium wilt, nematode infestation, yield and fruit quality in watermelon production." Ciência e Agrotecnologia **39**: 323-330.

Anders, S., P. T. Pyl and W. Huber (2015). "HTSeq—a Python framework to work with high-throughput sequencing data." bioinformatics **31**(2): 166-169.

Arefin, S. A., N. Zeba, A. H. Solaiman, M. T. Naznin, M. O. K. Azad, M. Tabassum and C. H. Park (2019). "Evaluation of compatibility, growth characteristics, and yield of tomato grafted on potato ('Pomato')." Horticulturae **5**(2): 37.

Argles, G. (1937). "A review of the literature on stock-scion incompatibility in fruit trees, with particular reference to pome and stone fruits."

Asins, M. J., V. Raga, D. Roca, A. Belver and E. A. Carbonell (2015). "Genetic dissection of tomato rootstock effects on scion traits under moderate salinity." Theoretical and Applied Genetics **128**: 667-679.

Atkins, D., R. Hull, B. Wells, K. Roberts, P. Moore and R. Beachy (1991). "The tobacco mosaic virus 30K movement protein in transgenic tobacco plants is localized to plasmodesmata." Journal of General Virology **72**(1): 209-211.

Avramidou, E., A. Kapazoglou, F. A. Aravanopoulos, A. Xanthopoulou, I. Ganopoulos, A. Tsaballa, P. Madesis, A. G. Doulis and A. Tsaftaris (2015). "Global DNA methylation changes in Cucurbitaceae inter-species grafting." Crop Breeding and Applied Biotechnology **15**: 112-116.

Axtell, M. J. (2013). "ShortStack: comprehensive annotation and quantification of small RNA genes." Rna **19**(6): 740-751.

Bai, C., L. Liu and B. W. Wood (2013). "Nickel affects xylem Sap RNase a and converts RNase A to a urease." BMC plant biology **13**(1): 1-9.

Bai, S., A. Kasai, K. Yamada, T. Li and T. Harada (2011). "A mobile signal transported over a long distance induces systemic transcriptional gene silencing in a grafted partner." Journal of experimental botany **62**(13): 4561-4570.

Bailey, T. L., J. Johnson, C. E. Grant and W. S. Noble (2015). "The MEME suite." Nucleic acids research **43**(W1): W39-W49.

Banerjee, A. K., M. Chatterjee, Y. Yu, S.-G. Suh, W. A. Miller and D. J. Hannapel (2006). "Dynamics of a mobile RNA of potato involved in a long-distance signaling pathway." The Plant Cell **18**(12): 3443-3457.

Barchi, L., M. T. Rabanus-Wallace, J. Prohens, L. Toppino, S. Padmarasu, E. Portis, G. L. Rotino, N. Stein, S. Lanteri and G. Giuliano (2021). "Improved genome assembly and pan-genome provide key insights into eggplant domestication and breeding." The Plant Journal **107**(2): 579-596.

Barends, S., J. Rudinger-Thirion, C. Florentz, R. Giegé, C. W. Pleij and B. Kraal (2004). "tRNA-like structure regulates translation of Brome mosaic virus RNA." Journal of virology **78**(8): 4003-4010.

Basile, B. and T. M. DeJong (2018). "Control of fruit tree vigor induced by dwarfing rootstocks." Horticultural Reviews **46**: 39-97.

Batovska, D. I., I. T. Todorova, D. V. Nedelcheva, S. P. Parushev, A. I. Atanassov, T. D. Hvarleva, G. J. Djakova, V. S. Bankova and S. S. Popov (2008). "Preliminary study on biomarkers for the fungal resistance in Vitis vinifera leaves." Journal of Plant Physiology **165**(8): 791-795.

Baumberger, N. and D. Baulcombe (2005). "Arabidopsis ARGONAUTE1 is an RNA Slicer that selectively recruits microRNAs and short interfering RNAs." Proceedings of the National Academy of Sciences **102**(33): 11928-11933.

Bayer, P. E., A. A. Golicz, A. Scheben, J. Batley and D. Edwards (2020). "Plant pan-genomes are the new reference." Nature plants **6**(8): 914-920.

Beernink, B. M., R. R. Lappe, M. Bredow and S. A. Whitham (2022). "Impacts of RNA mobility signals on virus induced somatic and germline gene editing." Frontiers in Genome Editing **4**: 925088.

Bewick, A. J. and R. J. Schmitz (2017). "Gene body DNA methylation in plants." Current opinion in plant biology **36**: 103-110.

Bhogale, S., A. S. Mahajan, B. Natarajan, M. Rajabhoj, H. V. Thulasiram and A. K. Banerjee (2014). "MicroRNA156: a potential graft-transmissible microRNA that modulates plant architecture and tuberization in Solanum tuberosum ssp. andigena." Plant physiology **164**(2): 1011-1027.

Bie ZhiLong, B. Z., M. A. Nawaz, H. Y. Huang Yuan, L. J. Lee JungMyung and G. Colla (2017). Introduction to vegetable grafting. Vegetable grafting: principles and practices, CABI Wallingford UK**:** 1-21.

Black, L., D. Wu, J. Wang, T. Kalb, D. Abbass and J. Chen (2003). "Grafting tomatoes for production in the hot-wet season." Asian Vegetable Research & Development Center. AVRDC Publication **3**(2): 551-555.

Blanco-Míguez, A., F. Beghini, F. Cumbo, L. J. McIver, K. N. Thompson, M. Zolfo, P. Manghi, L. Dubois, K. D. Huang and A. M. Thomas (2023). "Extending and improving metagenomic taxonomic profiling with uncharacterized species using MetaPhlAn 4." Nature Biotechnology **41**(11): 1633-1644.

Bletsos, F., C. Thanassoulopoulos and D. Roupakias (2003). "Effect of grafting on growth, yield, and Verticillium wilt of eggplant." HortScience **38**(2): 183-186.

Boerjan, W., J. Ralph and M. Baucher (2003). "Lignin biosynthesis." Annual review of plant biology **54**(1): 519-546.

Boex-Fontvieille, E., M. Davanture, M. Jossier, M. Zivy, M. Hodges and G. Tcherkez (2014). "Photosynthetic activity influences cellulose biosynthesis and phosphorylation of proteins involved therein in Arabidopsis leaves." Journal of experimental botany **65**(17): 4997-5010.

Bolger, A. M., M. Lohse and B. Usadel (2014). "Trimmomatic: a flexible trimmer for Illumina sequence data." Bioinformatics **30**(15): 2114-2120.

Bombarely, A., H. G. Rosli, J. Vrebalov, P. Moffett, L. A. Mueller and G. B. Martin (2012). "A draft genome sequence of Nicotiana benthamiana to enhance molecular plant-microbe biology research." Molecular Plant-Microbe Interactions **25**(12): 1523-1530.

Borges, F. and R. A. Martienssen (2015). "The expanding world of small RNAs in plants." Nature reviews Molecular cell biology **16**(12): 727-741.

Boualem, A., P. Laporte, M. Jovanovic, C. Laffont, J. Plet, J. P. Combier, A. Niebel, M. Crespi and F. Frugier (2008). "MicroRNA166 controls root and nodule development in Medicago truncatula." The Plant Journal **54**(5): 876-887.

Boudsocq, M., M. R. Willmann, M. McCormack, H. Lee, L. Shan, P. He, J. Bush, S.-H. Cheng and J. Sheen (2010). "Differential innate immune signalling via Ca2+ sensor protein kinases." Nature **464**(7287): 418-422.

Brandoli, C., C. Petri, M. Egea-Cortines and J. Weiss (2020). "Gigantea: uncovering new functions in flower development." Genes **11**(10): 1142.

Brant, E. J. and H. Budak (2018). "Plant small non-coding RNAs and their roles in biotic stresses." Frontiers in Plant Science **9**: 1038.

Brisson, N., P. Gate, D. Gouache, G. Charmet, F.-X. Oury and F. Huard (2010). "Why are wheat yields stagnating in Europe? A comprehensive data analysis for France." Field crops research **119**(1): 201-212.

Brosnan, C. A. and O. Voinnet (2011). "Cell-to-cell and long-distance siRNA movement in plants: mechanisms and biological implications." Current opinion in plant biology **14**(5): 580-587.

Buhtz, A., J. Pieritz, F. Springer and J. Kehr (2010). "Phloem small RNAs, nutrient stress responses, and systemic mobility." BMC plant biology **10**: 1-13.

Buhtz, A., F. Springer, L. Chappell, D. C. Baulcombe and J. Kehr (2008). "Identification and characterization of small RNAs from the phloem of Brassica napus." The Plant Journal **53**(5): 739-749.

Busch, F. A., R. F. Sage and G. D. Farquhar (2018). "Plants increase CO2 uptake by assimilating nitrogen via the photorespiratory pathway." Nature plants **4**(1): 46-54.

Calatayud, Á., A. San Bautista, B. Pascual, J. V. Maroto and S. López-Galarza (2013). "Use of chlorophyll fluorescence imaging as diagnostic technique to predict compatibility in melon graft." Scientia horticulturae **149**: 13-18.

Calderan-Rodrigues, M. J. and C. Caldana (2024). "Impact of the TOR pathway on plant growth via cell wall remodeling." Journal of Plant Physiology: 154202.

Calderwood, A., S. Kopriva and R. J. Morris (2016). "Transcript abundance explains mRNA mobility data in Arabidopsis thaliana." The Plant Cell **28**(3): 610-615.

Camacho, C., G. Coulouris, V. Avagyan, N. Ma, J. Papadopoulos, K. Bealer and T. L. Madden (2009). "BLAST+: architecture and applications." BMC bioinformatics **10**: 1-9.

Canher, B., F. Lanssens, A. Zhang, A. Bisht, S. Mazumdar, J. Heyman, S. Wolf, C. W. Melnyk and L. De Veylder (2022). "The regeneration factors ERF114 and ERF115 regulate auxin-mediated lateral root development in response to mechanical cues." Molecular Plant **15**(10): 1543-1557.

Cantero-Navarro, E., R. Romero-Aranda, R. Fernández-Muñoz, C. Martínez-Andújar, F. Pérez-Alfocea and A. Albacete (2016). "Improving agronomic water use efficiency in tomato by rootstock-mediated hormonal regulation of leaf biomass." Plant Science **251**: 90-100.

Cao, D., Z. Ju, C. Gao, X. Mei, D. Fu, H. Zhu, Y. Luo and B. Zhu (2014). "Genome-wide identification of cytosine-5 DNA methyltransferases and demethylases in Solanum lycopersicum." Gene **550**(2): 230-237.

Cao, L., N. Yu, J. Li, Z. Qi, D. Wang and L. Chen (2016). "Heritability and reversibility of DNA methylation induced by in vitro grafting between Brassica juncea and B. oleracea." Scientific Reports **6**(1): 27233.

Capistrán-Barradas, A., P. Moreno-Casasola and O. Defeo (2006). "Postdispersal fruit and seed removal by the crab gecarcinus lateralis in a coastal forest in veracruz, Mexico 1." Biotropica: The Journal of Biology and Conservation **38**(2): 203-209.

Carrió-Seguí, À., O. Ruiz-Rivero, L. Villamayor-Belinchón, S. Puig, A. Perea-García and L. Peñarrubia (2019). "The altered expression of microRNA408 influences the Arabidopsis response to iron deficiency." Frontiers in plant science **10**: 324.

Cassman, K. G. (1999). "Ecological intensification of cereal production systems: yield potential, soil quality, and precision agriculture." Proceedings of the National Academy of Sciences **96**(11): 5952-5959.

Catoni, M., A. Lucioli, P. Doblas-Ibáñez, G. P. Accotto and A. M. Vaira (2013). "From immunity to susceptibility: virus resistance induced in tomato by a silenced transgene is lost as TGS overcomes PTGS." The Plant Journal **75**(6): 941-953.

Catoni, M. and N. R. Zabet (2021). Analysis of plant DNA methylation profiles using R. Plant Transposable Elements: Methods and Protocols, Springer**:** 219-238.

Cerruti, E., C. Gisbert, H.-G. Drost, D. Valentino, E. Portis, L. Barchi, J. Prohens, S. Lanteri, C. Comino and M. Catoni (2021). "Grafting vigour is associated with DNA de-methylation in eggplant." Horticulture Research **8**.

Chan, P. P. and T. M. Lowe (2019). tRNAscan-SE: searching for tRNA genes in genomic sequences, Springer.

Chen, H.-M., L.-T. Chen, K. Patel, Y.-H. Li, D. C. Baulcombe and S.-H. Wu (2010). "22-Nucleotide RNAs trigger secondary siRNA biogenesis in plants." Proceedings of the National Academy of Sciences **107**(34): 15269-15274.

Chen, S. (2023). "Ultrafast one-pass FASTQ data preprocessing, quality control, and deduplication using fastp." Imeta **2**(2): e107.

Cheng, S. L. H., H. Xu, J. H. T. Ng and N.-H. Chua (2023). "Systemic movement of long non-coding RNA ELENA1 attenuates leaf senescence under nitrogen deficiency." Nature Plants **9**(10): 1598-1606.

Cheng, Z., X. Zhang, W. Yao, Y. Gao, K. Zhao, Q. Guo, B. Zhou and T. Jiang (2021). "Genome-wide identification and expression analysis of the xyloglucan

endotransglucosylase/hydrolase gene family in poplar." BMC genomics **22**: 1-13.

Choi, J., D. B. Lyons, M. Y. Kim, J. D. Moore and D. Zilberman (2020). "DNA methylation and histone H1 jointly repress transposable elements and aberrant intragenic transcripts." Molecular Cell **77**(2): 310-323. e317.

Choi, S. J., Z. Lee, S. Kim, E. Jeong and J. S. Shim (2023). "Modulation of lignin biosynthesis for drought tolerance in plants." Frontiers in Plant Science **14**: 1116426.

Clancy, S. and W. Brown (2008). "Translation: DNA to mRNA to protein." Nature Education **1**(1): 101.

Cohen, R., M. Edelstein and H. Aktas (2010). "The use of plant grafting and plant growth regulators for enhancing abiotic stress tolerance in vegetable transplants." Scientia Horticulturae **127**: 119-126.

Cohen, R., S. Pivonia, Y. Burger, M. Edelstein, A. Gamliel and J. Katan (2000). "Toward integrated management of Monosporascus wilt of melons in Israel." Plant Disease **84**(5): 496-505.

Cokus, S. J., S. Feng, X. Zhang, Z. Chen, B. Merriman, C. D. Haudenschild, S. Pradhan, S. F. Nelson, M. Pellegrini and S. E. Jacobsen (2008). "Shotgun bisulphite sequencing of the Arabidopsis genome reveals DNA methylation patterning." Nature **452**(7184): 215-219.

Colla, G., F. Pérez-Alfocea and D. Schwarz (2017). Vegetable grafting: Principles and practices, CABI.

Colla, G., Y. Rouphael, M. Cardarelli, A. Salerno and E. Rea (2010). "The effectiveness of grafting to improve alkalinity tolerance in watermelon." Environmental and Experimental Botany **68**(3): 283-291.

Colla, G., C. M. C. Suárez, M. Cardarelli and Y. Rouphael (2010). "Improving nitrogen use efficiency in melon by grafting." HortScience **45**(4): 559-565.

Collum, T. D., A. L. Stone, D. J. Sherman, E. E. Rogers, C. Dardick and J. N. Culver (2020). "Translatome profiling of Plum pox virus–infected leaves in European plum reveals temporal and spatial coordination of defense responses in phloem tissues." Molecular plant-microbe interactions **33**(1): 66-77.

Cookson, S. J., M. J. Clemente Moreno, C. Hevin, L. Z. Nyamba Mendome, S. Delrot, C. Trossat-Magnin and N. Ollat (2013). "Graft union formation in grapevine induces transcriptional changes related to cell wall modification, wounding, hormone signalling, and secondary metabolism." Journal of experimental botany **64**(10): 2997-3008.

Cookson, S. J. and N. Ollat (2013). "Grafting with rootstocks induces extensive transcriptional re-programming in the shoot apical meristem of grapevine." BMC plant biology **13**: 1-14.

Crofts, A. J., H. Washida, T. W. Okita, M. Ogawa, T. Kumamaru and H. Satoh (2004). "Targeting of proteins to endoplasmic reticulum-derived compartments in plants. The importance of RNA localization." Plant physiology **136**(3): 3414-3419.

Cuerda-Gil, D. and R. K. Slotkin (2016). "Non-canonical RNA-directed DNA methylation." Nature plants **2**(11): 1-8.

Cuevas-Velazquez, C. L. and J. R. Dinneny (2018). "Organization out of disorder: liquid–liquid phase separation in plants." Current opinion in plant biology **45**: 68-74.

Cuperus, J. T., A. Carbonell, N. Fahlgren, H. Garcia-Ruiz, R. T. Burke, A. Takeda, C. M. Sullivan, S. D. Gilbert, T. A. Montgomery and J. C. Carrington (2010). "Unique functionality of 22-nt miRNAs in triggering RDR6-dependent siRNA biogenesis from target transcripts in Arabidopsis." Nature structural & molecular biology **17**(8): 997-1003.

Dai, C. and H. W. Xue (2010). "Rice early flowering 1, a CKI, phosphorylates DELLA protein SLR1 to negatively regulate gibberellin signalling." The EMBO Journal **29**(11): 1916-1927.

Dai, X., Z. Zhuang and P. X. Zhao (2018). "psRNATarget: a plant small RNA target analysis server (2017 release)." Nucleic acids research **46**(W1): W49-W54.

Dallimore, W. (1917). "Natural grafting of branches and roots." Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew) **1917**(9/10): 303-306.

Danecek, P. (2021). "Bon eld JK, Liddle J, Marshall J, Ohan V, Pollard MO, et al." Twelve years of SAMtools and BCFtools. Gigascience **10**(2): 1-4.

Davis, A. R., P. Perkins-Veazie, Y. Sakata, S. Lopez-Galarza, J. V. Maroto, S.-G. Lee, Y.-C. Huh, Z. Sun, A. Miguel and S. R. King (2008). "Cucurbit grafting." Critical reviews in plant Sciences **27**(1): 50-74.

Davoudi, M., M. Song, M. Zhang, J. Chen and Q. Lou (2022). "Long-distance control of the scion by the rootstock under drought stress as revealed by transcriptome sequencing and mobile mRNA identification." Horticulture Research **9**: uhab033.

De Schepper, V., T. De Swaef, I. Bauweraerts and K. Steppe (2013). "Phloem transport: a review of mechanisms and controls." Journal of experimental botany **64**(16): 4839-4850.

de Stigter, H. d. (1966). "Parallelism between the transport of 14C-photosynthates and the flowering response in grafted Silene armeria L."

Deeken, R., P. Ache, I. Kajahn, J. Klinkenberg, G. Bringmann and R. Hedrich (2008). "Identification of Arabidopsis thaliana phloem RNAs provides a search criterion for phloem-based transcripts hidden in complex datasets of microarray experiments." The Plant Journal **55**(5): 746-759.

Dermit, M., M. Dodel and F. K. Mardakheh (2017). "Methods for monitoring and measurement of protein translation in time and space." Molecular BioSystems **13**(12): 2477-2488.

Deshpande, D., K. Chhugani, Y. Chang, A. Karlsberg, C. Loeffler, J. Zhang, A. Muszyńska, V. Munteanu, H. Yang and J. Rotman (2023). "RNA-seq data science: From raw data to effective interpretation." Frontiers in Genetics **14**: 997383.

Devers, E. A., C. A. Brosnan, A. Sarazin, D. Albertini, A. C. Amsler, F. Brioudes, P. E. Jullien, P. Lim, G. Schott and O. Voinnet (2020). "Movement and differential consumption of short interfering RNA duplexes underlie mobile RNA interference." Nature Plants **6**(7): 789-799.

Devers, E. A., C. A. Brosnan, A. Sarazin, G. Schott, P. Lim, S. Lehesranta, Y. Helariutta and O. Voinnet (2023). "In planta dynamics, transport biases, and endogenous functions of mobile siRNAs in Arabidopsis." The Plant Journal **115**(5): 1377-1393.

Dhall, R. (2015). "Breeding for biotic stresses resistance in vegetable crops: a review." J. Crop Sci. Tech **4**: 13-27.

Dimmer, E., L. Roden, D. Cai, C. Kingsnorth and E. Mutasa-Göttgens (2004). "Transgenic analysis of sugar beet xyloglucan endo-transglucosylase/hydrolase Bv-XTH1 and Bv-XTH2 promoters reveals overlapping tissue-specific and wound-inducible expression profiles." Plant Biotechnology Journal **2**(2): 127-139.

Ding, B. and A. Itaya (2007). "Viroid: a useful model for studying the basic principles of infection and RNA biology." Molecular plant-microbe interactions **20**(1): 7-20.

Dixon, R. A., M. Srinivasa Reddy and L. Gallego-Giraldo (2014). "Monolignol biosynthesis and its genetic manipulation: the good, the bad, and the ugly." Recent advances in polyphenol research: 1-38.

Djidonou, D., A. H. Simonne, K. E. Koch, J. K. Brecht and X. Zhao (2016). "Nutritional quality of field-grown tomato fruit as affected by grafting with interspecific hybrid rootstocks." HortScience **51**(12): 1618-1624.

Dobin, A., C. A. Davis, F. Schlesinger, J. Drenkow, C. Zaleski, S. Jha, P. Batut, M. Chaisson and T. R. Gingeras (2013). "STAR: ultrafast universal RNA-seq aligner." Bioinformatics **29**(1): 15-21.

Doering-Saad, C., H. J. Newbury, J. S. Bale and J. Pritchard (2002). "Use of aphid stylectomy and RT-PCR for the detection of transporter mRNAs in sieve elements." Journal of Experimental Botany **53**(369): 631-637.

Dong, Q., B. Hu and C. Zhang (2022). "microRNAs and their roles in plant development." Frontiers in Plant Science **13**: 824240.

Du, J., L. M. Johnson, M. Groth, S. Feng, C. J. Hale, S. Li, A. A. Vashisht, J. Gallego-Bartolome, J. A. Wohlschlegel and D. J. Patel (2014). "Mechanism of DNA methylation-directed histone methylation by KRYPTONITE." Molecular cell **55**(3): 495-504.

Du, J., X. Zhong, Y. V. Bernatavichute, H. Stroud, S. Feng, E. Caro, A. A. Vashisht, J. Terragni, H. G. Chin and A. Tu (2012). "Dual binding of chromomethylase domains to H3K9me2-containing nucleosomes directs DNA methylation in plants." Cell **151**(1): 167-180.

Duan, X., W. Zhang, J. Huang, L. Hao, S. Wang, A. Wang, D. Meng, Q. Zhang, Q. Chen and T. Li (2016). "PbWoxT1 mRNA from pear (Pyrus betulaefolia) undergoes long-distance transport assisted by a polypyrimidine tract binding protein." New Phytologist **210**(2): 511-524.

Edelstein, M., Y. Burger, C. Horev, A. Porat, A. Meir and R. Cohen (2004). "Assessing the effect of genetic and anatomic variation of Cucurbita rootstocks on vigour, survival and yield of grafted melons." The Journal of Horticultural Science and Biotechnology **79**(3): 370-374.

Edelstein, M., Z. Plaut and M. Ben-Hur (2011). "Sodium and chloride exclusion and retention by non-grafted and grafted melon and Cucurbita plants." Journal of Experimental Botany **62**(1): 177-184.

Edwards, D., J. Batley and R. J. Snowdon (2013). "Accessing complex crop genomes with next-generation sequencing." Theoretical and Applied Genetics **126**: 1-11.

Elkind, Y., R. Edwards, M. Mavandad, S. A. Hedrick, O. Ribak, R. A. Dixon and C. J. Lamb (1990). "Abnormal plant development and down-regulation of phenylpropanoid biosynthesis in transgenic tobacco containing a heterologous phenylalanine ammonia-lyase gene." Proceedings of the National Academy of Sciences **87**(22): 9057-9061.

Ellison, E. E., U. Nagalakshmi, M. E. Gamo, P.-j. Huang, S. Dinesh-Kumar and D. F. Voytas (2020). "Multiplexed heritable gene editing using RNA viruses and mobile single guide RNAs." Nature plants **6**(6): 620-624.

Emmerson, R. A. (2023). The physiological and epigenetic effects of dynamic light acclimation in Arabidopsis thaliana, University of Essex.

Erdmann, R. M. and C. L. Picard (2020). "RNA-directed DNA methylation." PLoS genetics **16**(10): e1009034.

Evans, L. (1997). "Adapting and improving crops: the endless task." Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences **352**(1356): 901-906.

Fallik, E., S. Alkalai-Tuvia, D. Chalupowicz, Y. Zutahy, M. Zaaroor, M. Beniches and A. Gamliel (2016). "Effects of rootstock and soil disinfection on quality of grafted watermelon fruit (Citrullus lanatus L.): a two-year study." Israel Journal of Plant Sciences **63**(1): 38-44.

Fan, J., R. Yang, X. Li, W. Zhao, F. Zhao and S. Wang (2015). "The processes of graft union formation in tomato." Horticulture, Environment, and Biotechnology **56**: 569-574.

Fan, L., C. Zhang, B. Gao, Y. Zhang, E. Stewart, J. Jez, K. Nakajima and X. Chen (2022). "Microtubules promote the non-cell autonomous action of microRNAs by inhibiting their cytoplasmic loading onto ARGONAUTE1 in Arabidopsis." Developmental cell **57**(8): 995-1008. e1005.

Fang, X., L. Wang, R. Ishikawa, Y. Li, M. Fiedler, F. Liu, G. Calder, B. Rowan, D. Weigel and P. Li (2019). "Arabidopsis FLL2 promotes liquid–liquid phase separation of polyadenylation complexes." Nature **569**(7755): 265-269.

Fechter, P., J. Rudinger-Thirion, C. Florentz and R. Giege (2001). "Novel features in the tRNA-like world of plant viral RNAs." Cellular and Molecular Life Sciences CMLS **58**: 1547-1561.

Fernandez-Calvino, L., C. Faulkner, J. Walshaw, G. Saalbach, E. Bayer, Y. Benitez-Alfonso and A. Maule (2011). "Arabidopsis plasmodesmal proteome." PloS one **6**(4): e18880.

Fernández-García, N., V. Martínez, A. Cerdá and M. Carvajal (2002). "Water and nutrient uptake of grafted tomato plants grown under saline conditions." Journal of Plant Physiology **159**(8): 899-905.

Fernandez-Pozo, N., N. Menda, J. D. Edwards, S. Saha, I. Y. Tecle, S. R. Strickler, A. Bombarely, T. Fisher-York, A. Pujar and H. Foerster (2015). "The Sol Genomics Network (SGN)—from genotype to phenotype to breeding." Nucleic acids research **43**(D1): D1036-D1041.

Fernández-García, N., V. Martínez and M. Carvajal (2004). "Effect of salinity on growth, mineral composition, and water relations of grafted tomato plants." Journal of Plant Nutrition and Soil Science **167**(5): 616-622.

Finger, R. (2010). "Evidence of slowing yield growth–the example of Swiss cereal yields." Food Policy **35**(2): 175-182.

Flaishman, M. A., K. Loginovsky, S. Golobowich and S. Lev-Yadun (2008). "Arabidopsis thaliana as a model system for graft union development in homografts and heterografts." Journal of Plant Growth Regulation **27**: 231-239.

Flores, F. B., P. Sanchez-Bel, M. T. Estañ, M. M. Martinez-Rodriguez, E. Moyano, B. Morales, J. F. Campos, J. O. Garcia-Abellán, M. I. Egea and N. Fernández-Garcia (2010). "The effectiveness of grafting to improve tomato fruit quality." Scientia horticulturae **125**(3): 211-217.

Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray and P. C. West (2011). "Solutions for a cultivated planet." Nature **478**(7369): 337-342.

Foo, E., C. G. Turnbull and C. A. Beveridge (2001). "Long-distance signaling and the control of branching in the rms1 mutant of pea." Plant Physiology **126**(1): 203-209.

Food and A. Organization (2013). FAOSTAT, Food and Agriculture Organization of the United Nations, FAO Rome, Italy.

Foster, T. M., T. J. Lough, S. J. Emerson, R. H. Lee, J. L. Bowman, R. L. Forster and W. J. Lucas (2002). "A surveillance system regulates selective entry of RNA into the shoot apex." The Plant Cell **14**(7): 1497-1508.

Foster, T. M., P. A. McAtee, C. N. Waite, H. L. Boldingh and T. K. McGhie (2017). "Apple dwarfing rootstocks exhibit an imbalance in carbohydrate allocation and reduced cell growth and metabolism." Horticulture research **4**.

Franco-Zorrilla, J. M., A. Valli, M. Todesco, I. Mateos, M. I. Puga, I. Rubio-Somoza, A. Leyva, D. Weigel, J. A. García and J. Paz-Ares (2007). "Target mimicry provides a new mechanism for regulation of microRNA activity." Nature genetics **39**(8): 1033-1037.

Frazee, A., A. Jaffe, R. Kirchner and J. Leek (2024). "polyester: Simulate RNA-seq reads." (R package version 1.39.0.).

French (2007). "The grapevine genome sequence suggests ancestral hexaploidization in major angiosperm phyla." nature **449**(7161): 463-467.

Fu, M., Z. Xu, H. Ma, Y. Hao, J. Tian, Y. Wang, X. Zhang, X. Xu, Z. Han and T. Wu (2024). "Characteristics of long-distance mobile mRNAs from shoot to root in grafted plant species." Horticultural Plant Journal **10**(1): 25-37.

Fuentes, I., S. Stegemann, H. Golczyk, D. Karcher and R. Bock (2014). "Horizontal genome transfer as an asexual path to the formation of new species." Nature **511**(7508): 232-235.

Fullana-Pericàs, M., M. À. Conesa, F. Pérez-Alfocea and J. Galmés (2020). "The influence of grafting on crops' photosynthetic performance." Plant science **295**: 110250.

Gaion, L. A., L. T. Braz and R. F. Carvalho (2018). "Grafting in vegetable crops: A great technique for agriculture." International Journal of Vegetable Science **24**(1): 85-102.

Galatti, F. d. S., A. J. Franco, L. A. Ito, H. d. O. Charlo, L. A. Gaion and L. T. Braz (2013). "Rootstocks resistant to Meloidogyne incognita and compatibility of grafting in net melon." Revista Ceres **60**: 432-436.

Gao, L., Q. Lv, L. Wang, S. Han, J. Wang, Y. Chen, W. Zhu, X. Zhang, F. Bao and Y. Hu (2024). "Abscisic acid–mediated autoregulation of the MYB41-BRAHMA module enhances drought tolerance in Arabidopsis." Plant Physiology **196**(2): 1608-1626.

Gao, Y., B. Feng, C. Gao, H. Zhang, F. Wen, L. Tao, G. Fu and J. Xiong (2022). "The evolution and functional roles of miR408 and its targets in plants." International Journal of Molecular Sciences **23**(1): 530.

Garcia-Lozano, M., S. K. Dutta, P. Natarajan, Y. R. Tomason, C. Lopez, R. Katam, A. Levi, P. Nimmakayala and U. K. Reddy (2020). "Transcriptome changes in reciprocal grafts involving watermelon and bottle gourd reveal molecular mechanisms involved in increase of the fruit size, rind toughness and soluble solids." Plant molecular biology **102**: 213-223.

Gaupels, F., A. Buhtz, T. Knauer, S. Deshmukh, F. Waller, A. J. Van Bel, K.-H. Kogel and J. Kehr (2008). "Adaptation of aphid stylectomy for analyses of proteins and mRNAs in barley phloem sap." Journal of Experimental Botany **59**(12): 3297-3306.

Gautier, A. T., C. Chambaud, L. Brocard, N. Ollat, G. A. Gambetta, S. Delrot and S. J. Cookson (2019). "Merging genotypes: graft union formation and scion–rootstock interactions." Journal of Experimental Botany **70**(3): 747-755.

Ge, S. X., D. Jung and R. Yao (2020). "ShinyGO: a graphical gene-set enrichment tool for animals and plants." Bioinformatics **36**(8): 2628-2629.

Geiger, D., S. Scherzer, P. Mumm, I. Marten, P. Ache, S. Matschi, A. Liese, C. Wellmann, K. Al-Rasheid and E. Grill (2010). "Guard cell anion channel SLAC1 is regulated by CDPK protein kinases with distinct Ca2+ affinities." Proceedings of the National Academy of Sciences **107**(17): 8023-8028.

Geiger, D., S. Scherzer, P. Mumm, A. Stange, I. Marten, H. Bauer, P. Ache, S. Matschi, A. Liese and K. A. Al-Rasheid (2009). "Activity of guard cell anion channel SLAC1 is controlled by drought-stress signaling kinase-phosphatase pair." Proceedings of the National Academy of Sciences **106**(50): 21425-21430.

Ghanem, M. E., A. Albacete, A. C. Smigocki, I. Frébort, H. Pospíšilová, C. Martínez-Andújar, M. Acosta, J. Sánchez-Bravo, S. Lutts and I. C. Dodd (2011). "Root-synthesized cytokinins improve shoot growth and fruit yield in salinized tomato (Solanum lycopersicum L.) plants." Journal of experimental botany **62**(1): 125-140.

Ghate, T. H., P. Sharma, K. R. Kondhare, D. J. Hannapel and A. K. Banerjee (2017). "The mobile RNAs, StBEL11 and StBEL29, suppress growth of tubers in potato." Plant molecular biology **93**: 563-578.

Girollet, N., B. Rubio, C. Lopez-Roques, S. Valière, N. Ollat and P.-F. Bert (2019). "De novo phased assembly of the Vitis riparia grape genome." Scientific Data **6**(1): 127.

Gisbert, C., J. Prohens and F. Nuez (2011). "Performance of eggplant grafted onto cultivated, wild, and hybrid materials of eggplant and tomato."

Gisbert, C., J. Prohens, M. D. Raigón, J. R. Stommel and F. Nuez (2011). "Eggplant relatives as sources of variation for developing new rootstocks:

Effects of grafting on eggplant yield and fruit apparent quality and composition." Scientia horticulturae **128**(1): 14-22.

Goda, H., S. Sawa, T. Asami, S. Fujioka, Y. Shimada and S. Yoshida (2004). "Comprehensive comparison of auxin-regulated and brassinosteroid-regulated genes in Arabidopsis." Plant physiology **134**(4): 1555-1573.

Godfray, H. C. J., J. R. Beddington, I. R. Crute, L. Haddad, D. Lawrence, J. F. Muir, J. Pretty, S. Robinson, S. M. Thomas and C. Toulmin (2010). "Food security: the challenge of feeding 9 billion people." science **327**(5967): 812-818.

Goldschmidt, E. E. (2014). "Plant grafting: new mechanisms, evolutionary implications." Frontiers in plant Science **5**: 727.

Golecki, B., A. Schulz, U. Carstens-Behrens and R. Kollmann (1998). "Evidence for graft transmission of structural phloem proteins or their precursors in heterografts of Cucurbitaceae." Planta **206**: 630-640.

Golecki, B., A. Schulz and G. A. Thompson (1999). "Translocation of structural P proteins in the phloem." The Plant Cell **11**(1): 127-140.

Gómez, G. and V. Pallás (2004). "A long-distance translocatable phloem protein from cucumber forms a ribonucleoprotein complex in vivo with Hop stunt viroid RNA." Journal of virology **78**(18): 10104-10110.

Goodstein, D. M., S. Shu, R. Howson, R. Neupane, R. D. Hayes, J. Fazo, T. Mitros, W. Dirks, U. Hellsten and N. Putnam (2012). "Phytozome: a comparative platform for green plant genomics." Nucleic acids research **40**(D1): D1178-D1186.

Gratão, P. L., C. C. Monteiro, T. Tezotto, R. F. Carvalho, L. R. Alves, L. P. Peters and R. A. Azevedo (2015). "Cadmium stress antioxidant responses and root-to-shoot communication in grafted tomato plants." Biometals **28**(5): 803-816.

Green, R. E., S. J. Cornell, J. P. Scharlemann and A. Balmford (2005). "Farming and the fate of wild nature." science **307**(5709): 550-555.

Gregorio Jorge, J., M. A. Villalobos-López, K. L. Chavarría-Alvarado, S. Ríos-Meléndez, M. López-Meyer and A. Arroyo-Becerra (2020). "Genome-wide transcriptional changes triggered by water deficit on a drought-tolerant common bean cultivar." BMC plant biology **20**: 1-20.

Grieneisen, M. L., B. J. Aegerter, C. Scott Stoddard and M. Zhang (2018). "Yield and fruit quality of grafted tomatoes, and their potential for soil fumigant use reduction. A meta-analysis." Agronomy for Sustainable Development **38**: 1-16.

Gu, Z., R. Eils and M. Schlesner (2016). "Complex heatmaps reveal patterns and correlations in multidimensional genomic data." Bioinformatics **32**(18): 2847-2849.

Guan, D., B. Yan, C. Thieme, J. Hua, H. Zhu, K. R. Boheler, Z. Zhao, F. Kragler, Y. Xia and S. Zhang (2016). "PlaMoM: a comprehensive database compiles plant mobile macromolecules." Nucleic acids research: gkw988.

Gurdon, C., Z. Svab, Y. Feng, D. Kumar and P. Maliga (2016). "Cell-to-cell movement of mitochondria in plants." Proceedings of the National Academy of Sciences **113**(12): 3395-3400.

Gutermuth, T., R. Lassig, M.-T. Portes, T. Maierhofer, T. Romeis, J.-W. Borst, R. Hedrich, J. A. Feijó and K. R. Konrad (2013). "Pollen tube growth regulation by free anions depends on the interaction between the anion channel SLAH3 and calcium-dependent protein kinases CPK2 and CPK20." The Plant Cell **25**(11): 4525-4543.

Habibi, F., T. Liu, K. Folta and A. Sarkhosh (2022). "Physiological, biochemical, and molecular aspects of grafting in fruit trees." Horticulture Research **9**.

Ham, B.-K., J. L. Brandom, B. Xoconostle-Cazares, V. Ringgold, T. J. Lough and W. J. Lucas (2009). "A polypyrimidine tract binding protein, pumpkin RBP50, forms the basis of a phloem-mobile ribonucleoprotein complex." The Plant Cell **21**(1): 197-215.

Ham, B. K., G. Li, W. Jia, J. A. Leary and W. J. Lucas (2014). "Systemic delivery of si RNA in pumpkin by a plant PHLOEM SMALL RNA-BINDING PROTEIN 1–ribonucleoprotein complex." The Plant Journal **80**(4): 683-694.

Hamdi, M. M., N. Boughalleb, N. Tarchoun and L. Belbahri (2009). "Evaluation of grafting effect on tomato crop yield and Fusarium crown and root rot disease." Journal of Applied Horticulture **11**(2): 107-110.

Hamilton, A., O. Voinnet, L. Chappell and D. Baulcombe (2002). "Two classes of short interfering RNA in RNA silencing." The EMBO journal **21**(17): 4671-4679.

Hamilton, A. J. and D. C. Baulcombe (1999). "A species of small antisense RNA in posttranscriptional gene silencing in plants." Science **286**(5441): 950-952.

Harada, T., Y. Torii, S. Morita, R. Onodera, Y. Hara, R. Yokoyama, K. Nishitani and S. Satoh (2011). "Cloning, characterization, and expression of xyloglucan endotransglucosylase/hydrolase and expansin genes associated with petal growth and development during carnation flower opening." Journal of Experimental Botany **62**(2): 815-823.

Harrison, D. and P. Burgess (1962). "USE OF ROOTSTOCK RESISTANCE FOR CONTROLLING FUSARIIUM WILT OF TOMATOES." Plant Pathology **11**(1).

Haywood, V., T. S. Yu, N. C. Huang and W. J. Lucas (2005). "Phloem long-distance trafficking of GIBBERELLIC ACID-INSENSITIVE RNA regulates leaf development." The Plant Journal **42**(1): 49-68.

He, Y., Z. Zhu, J. Yang, X. Ni and B. Zhu (2009). "Grafting increases the salt tolerance of tomato by improvement of photosynthesis and enhancement of antioxidant enzymes activity." Environmental and Experimental Botany **66**(2): 270-278.

Heeney, M. and M. H. Frank (2023). "The mRNA mobileome: challenges and opportunities for deciphering signals from the noise." The Plant Cell **35**(6): 1817-1833.

Henderson, I. R. and S. E. Jacobsen (2007). "Epigenetic inheritance in plants." Nature **447**(7143): 418-424.

Hertle, A. P., B. Haberl and R. Bock (2021). "Horizontal genome transfer by cell-to-cell travel of whole organelles." Science Advances **7**(1): eabd8215.

Hipper, C., V. Brault, V. Ziegler-Graff and F. Revers (2013). "Viral and cellular factors involved in phloem transport of plant viruses." Frontiers in plant science **4**: 154.

Hofacker, I. L. (2003). "Vienna RNA secondary structure server." Nucleic acids research **31**(13): 3429-3431.

Honma, S. (1977). "Grafting eggplants." Scientia Horticulturae **7**(3): 207-211.

Hosmani, P. S., M. Flores-Gonzalez, H. van de Geest, F. Maumus, L. V. Bakker, E. Schijlen, J. van Haarst, J. Cordewener, G. Sanchez-Perez and S. Peters (2019). "An improved de novo assembly and annotation of the tomato reference genome using single-molecule sequencing, Hi-C proximity ligation and optical maps." biorxiv: 767764.

Hu, C., B. K. Ham, H. M. El-shabrawi, D. Alexander, D. Zhang, J. Ryals and W. J. Lucas (2016). "Proteomics and metabolomics analyses reveal the cucurbit sieve tube system as a complex metabolic space." The Plant Journal **87**(5): 442-454.

Huang, H., R. Liu, Q. Niu, K. Tang, B. Zhang, H. Zhang, K. Chen, J.-K. Zhu and Z. Lang (2019). "Global increase in DNA methylation during orange fruit development and ripening." Proceedings of the National Academy of Sciences **116**(4): 1430-1436.

Huang, Y., Z. Bie, S. He, B. Hua, A. Zhen and Z. Liu (2010). "Improving cucumber tolerance to major nutrients induced salinity by grafting onto Cucurbita ficifolia." Environmental and Experimental Botany **69**(1): 32-38.

Huang, Y., Z. Bie, Z. Liu, A. Zhen and X. Jiao (2011). "Improving cucumber photosynthetic capacity under NaCl stress by grafting onto two salt-tolerant pumpkin rootstocks." Biologia plantarum **55**: 285-290.

Huang, Y., Q. Kong, F. Chen and Z. Bie (2014). The history, current status and future prospects of vegetable grafting in China. I International Symposium on Vegetable Grafting 1086.

Huang, Y., J. Li, B. Hua, Z. Liu, M. Fan and Z. Bie (2013). "Grafting onto different rootstocks as a means to improve watermelon tolerance to low potassium stress." Scientia Horticulturae **149**: 80-85.

Hudzik, C., Y. Hou, W. Ma and M. J. Axtell (2020). "Exchange of small regulatory RNAs between plants and their pests." Plant physiology **182**(1): 51-62.

Hussain, S., N. Iqbal, P. Ting, M. N. Khan, W.-g. LIU and W.-y. YANG (2019). "Weak stem under shade reveals the lignin reduction behavior." Journal of Integrative Agriculture **18**(3): 496-505.

Ikeuchi, M., A. Iwase, T. Ito, H. Tanaka, D. S. Favero, A. Kawamura, S. Sakamoto, M. Wakazaki, T. Tameshige and H. Fujii (2022). "Wound-inducible WUSCHEL-RELATED HOMEOBOX 13 is required for callus growth and organ reconnection." Plant Physiology **188**(1): 425-441.

Imaizumi, T., H. G. Tran, T. E. Swartz, W. R. Briggs and S. A. Kay (2003). "FKF1 is essential for photoperiodic-specific light signalling in Arabidopsis." Nature **426**(6964): 302-306.

Imlau, A., E. Truernit and N. Sauer (1999). "Cell-to-cell and long-distance trafficking of the green fluorescent protein in the phloem and symplastic unloading of the protein into sink tissues." The Plant Cell **11**(3): 309-322.

Itaya, A., F. Ma, Y. Qi, Y. Matsuda, Y. Zhu, G. Liang and B. Ding (2002). "Plasmodesma-mediated selective protein traffic between "symplasmically isolated" cells probed by a viral movement protein." The Plant Cell **14**(9): 2071-2083.

Ito, L. A., H. C. d. O. Charlo, R. Castoldi, L. T. Braz and M. Camargo (2009). "Rootstocks seletion to grummy stem blight resistance and their effect on the yield of melon'Bonus nº 2'." Revista Brasileira de Fruticultura **31**: 262-267.

Iwase, A., N. Mitsuda, T. Koyama, K. Hiratsu, M. Kojima, T. Arai, Y. Inoue, M. Seki, H. Sakakibara and K. Sugimoto (2011). "The AP2/ERF transcription factor WIND1 controls cell dedifferentiation in Arabidopsis." Current Biology **21**(6): 508-514.

Jeffery, W. R., C. R. Tomlinson and R. D. Brodeur (1983). "Localization of actin messenger RNA during early ascidian development." Developmental biology **99**(2): 408-417.

Jeynes-Cupper, K. and M. Catoni (2023). "Long distance signalling and epigenetic changes in crop grafting." Frontiers in Plant Science **14**: 1121704.

Jeynes-Cupper, K. and M. Catoni (2023). "mobileRNA: Investigate the RNA mobilome & population-scale changes." Bioconductor.

Jeynes-Cupper, K. and M. Catoni (2024). "mobileRNA: a tool for efficient analysis of mobile RNA molecules in multiple genomes." bioRxiv: 2024.2008. 2019.608270.

Jiang, Y., S. S. Neti, I. Sitarik, P. Pradhan, P. To, Y. Xia, S. D. Fried, S. J. Booker and E. P. O'Brien (2023). "How synonymous mutations alter enzyme structure and function over long timescales." Nature Chemistry **15**(3): 308-318.

Jiang, Z., G. Xu, Y. Jing, W. Tang and R. Lin (2016). "Phytochrome B and REVEILLE1/2-mediated signalling controls seed dormancy and germination in Arabidopsis." Nature communications **7**(1): 12377.

Jiao, W.-B. and K. Schneeberger (2019). "Chromosome-level assemblies of multiple Arabidopsis thaliana accessions reveal hotspots of genomic rearrangements." bioRxiv **738880**.

Jiao, W.-B. and K. Schneeberger (2020). "Chromosome-level assemblies of multiple Arabidopsis genomes reveal hotspots of rearrangements with altered evolutionary dynamics." Nature communications **11**(1): 989.

Johkan, M., K. Mitukuri, S. Yamasaki, G. Mori and M. Oda (2009). "Causes of defoliation and low survival rate of grafted sweet pepper plants." Scientia Horticulturae **119**(2): 103-107.

Johnson, S., D. Inglis and C. Miles (2014). "Grafting effects on eggplant growth, yield, and verticillium wilt incidence." International Journal of Vegetable Science **20**(1): 3-20.

Jorgensen, R. A., R. G. Atkinson, R. L. Forster and W. J. Lucas (1998). "An RNA-based information superhighway in plants." Science **279**(5356): 1486-1487.

Kacjan Maršić, N., M. Mikulic-Petkovsek and F. Stampar (2014). "Grafting influences phenolic profile and carpometric traits of fruits of greenhouse-grown eggplant (Solanum melongena L.)." Journal of agricultural and food chemistry **62**(43): 10504-10514.

Kamthan, A., A. Chaudhuri, M. Kamthan and A. Datta (2015). "Small RNAs in plants: recent development and application for crop improvement." Frontiers in plant science **6**: 208.

Kaniyassery, A., S. A. Thorat, K. R. Kiran, T. S. Murali and A. Muthusamy (2023). "Fungal diseases of eggplant (Solanum melongena L.) and components of the disease triangle: a review." Journal of Crop Improvement **37**(4): 543-594.

Kasai, A., S. Bai, H. Hojo and T. Harada (2016). "Epigenome editing of potato by grafting using transgenic tobacco as siRNA donor." PLoS One **11**(8): e0161729.

Kasai, A., A. Kanehira and T. Harada (2010). "miR172 can move long distances in Nicotiana benthamiana." The Open Plant Science Journal **4**(1).

Kasschau, K. D., N. Fahlgren, E. J. Chapman, C. M. Sullivan, J. S. Cumbie, S. A. Givan and J. C. Carrington (2007). "Genome-wide profiling and analysis of Arabidopsis siRNAs." PLoS biology **5**(3): e57.

Kawaguchi, M., A. Taji, D. Backhouse and M. Oda (2008). "Anatomy and physiology of graft incompatibility in solanaceous plants." The Journal of Horticultural Science and Biotechnology **83**(5): 581-588.

Keck, F. and A. Mahon (2020). "Handling biological sequences in R with the bioseq package." Methods in Ecology & Evolution **11**(12).

Kehr, J. and F. Kragler (2018). "Long distance RNA movement." New Phytologist **218**(1): 29-40.

Kehr, J., R. J. Morris and F. Kragler (2022). "Long-distance transported RNAs: from identity to function." Annual review of plant biology **73**(1): 457-474.

Kehr, J., R. J. Morris and F. Kragler (2022). "Long-distance transported RNAs: from identity to function." Annual review of plant biology **73**: 457-474.

Kempers, R. and A. J. van Bel (1997). "Symplasmic connections between sieve element and companion cell in the stem phloem of Vicia faba L. have a molecular exclusion limit of at least 10 kDa." Planta **201**: 195-201.

Khankahdani, H. H., E. Zakeri, G. Saeedi and G. Shakerdargah (2012). "Evaluation of different rootstocks and grafting techniques on graft union percent, yield and yield components of watermelon cv.'Crimson Sweet'." World Appl. Sci. J **18**(5): 645-651.

Kim, D., B. Langmead and S. L. Salzberg (2015). "HISAT: a fast spliced aligner with low memory requirements." Nature methods **12**(4): 357-360.

Kim, D., J. M. Paggi, C. Park, C. Bennett and S. L. Salzberg (2019). "Graph-based genome alignment and genotyping with HISAT2 and HISAT-genotype." Nature biotechnology **37**(8): 907-915.

Kim, G., M. L. LeBlanc, E. K. Wafula, C. W. DePamphilis and J. H. Westwood (2014). "Genomic-scale exchange of mRNA between a parasitic plant and its hosts." Science **345**(6198): 808-811.

Kim, M., W. Canio, S. Kessler and N. Sinha (2001). "Developmental changes due to long-distance movement of a homeobox fusion transcript in tomato." Science **293**(5528): 287-289.

King, S. R., A. R. Davis, X. Zhang and K. Crosby (2010). "Genetics, breeding and selection of rootstocks for Solanaceae and Cucurbitaceae." Scientia horticulturae **127**(2): 106-111.

Kitagawa, M., T. M. Tran and D. Jackson (2023). "Traveling with purpose: cell-to-cell transport of plant mRNAs." Trends in Cell Biology.

Kitagawa, M., P. Wu, R. Balkunde, P. Cunniff and D. Jackson (2022). "An RNA exosome subunit mediates cell-to-cell trafficking of a homeobox mRNA via plasmodesmata." Science **375**(6577): 177-182.

Knoblauch, M., W. S. Peters, K. Bell, T. J. Ross-Elliott and K. J. Oparka (2018). "Sieve-element differentiation and phloem sap contamination." Current opinion in plant biology **43**: 43-49.

Kong, D., H.-C. Hu, E. Okuma, Y. Lee, H. S. Lee, S. Munemasa, D. Cho, C. Ju, L. Pedoeim and B. Rodriguez (2016). "L-Met activates Arabidopsis GLR Ca2+ channels upstream of ROS production and regulates stomatal movement." Cell Reports **17**(10): 2553-2561.

Kong, X., M. Yang, B. H. Le, W. He and Y. Hou (2022). "The master role of siRNAs in plant immunity." Molecular Plant Pathology **23**(10): 1565-1574.

Kornberg, R. D. (1999). "Eukaryotic transcriptional control." Trends in cell biology **9**(12): M46-M49.

Kornblihtt, A. R., I. E. Schor, M. Alló, G. Dujardin, E. Petrillo and M. J. Muñoz (2013). "Alternative splicing: a pivotal step between eukaryotic transcription and translation." Nature reviews Molecular cell biology **14**(3): 153-165.

Krueger F, J. F., Ewels P, Afyounian E, Schuster-Boeckler B (2021). " FelixKrueger/TrimGalore: v0.6.7 - DOI via Zenodo (0.6.7). Zenodo.".

Kühn, C., V. R. Franceschi, A. Schulz, R. Lemoine and W. B. Frommer (1997). "Macromolecular trafficking indicated by localization and turnover of sucrose transporters in enucleate sieve elements." Science **275**(5304): 1298-1300.

Kühn, C., W. Quick, A. Schulz, J. Riesmeier, U. Sonnewald and W. Frommer (1996). "Companion cell-specific inhibition of the potato sucrose transporter SUT1." Plant, Cell & Environment **19**(10): 1115-1123.

Kumar, P., L. Lucini, Y. Rouphael, M. Cardarelli, R. M. Kalunke and G. Colla (2015). "Insight into the role of grafting and arbuscular mycorrhiza on cadmium stress tolerance in tomato." Frontiers in Plant Science **6**: 149154.

Kumar, P., Y. Rouphael, M. Cardarelli and G. Colla (2015). "Effect of nickel and grafting combination on yield, fruit quality, antioxidative enzyme activities, lipid peroxidation, and mineral composition of tomato." Journal of Plant Nutrition and Soil Science **178**(6): 848-860.

Kumar, S. and T. Mohapatra (2021). "Dynamics of DNA methylation and its functions in plant growth and development." Frontiers in Plant Science **12**: 596236.

Kumari, A., J. Kumar, A. Kumar, A. Chaudhury and S. P. Singh (2015). "Grafting triggers differential responses between scion and rootstock." PLoS One **10**(4): e0124438.

Kundariya, H., X. Yang, K. Morton, R. Sanchez, M. J. Axtell, S. F. Hutton, M. Fromm and S. A. Mackenzie (2020). "MSH1-induced heritable enhanced growth vigor through grafting is associated with the RdDM pathway in plants." Nature communications **11**(1): 5343.

Kurotani, K.-i., C. Huang, K. Okayasu, T. Suzuki, Y. Ichihashi, K. Shirasu, T. Higashiyama, M. Niwa and M. Notaguchi (2022). "Discovery of the interfamily grafting capacity of Petunia, a floricultural species." Horticulture research **9**: uhab056.

Kushwah, S., A. Banasiak, N. Nishikubo, M. Derba-Maceluch, M. Majda, S. Endo, V. Kumar, L. Gomez, A. Gorzsas and S. McQueen-Mason (2020). "Arabidopsis XTH4 and XTH9 contribute to wood cell expansion and secondary wall formation." Plant Physiology **182**(4): 1946-1965.

Kyriacou, M. C., G. A. Soteriou, Y. Rouphael, A. S. Siomos and D. Gerasopoulos (2016). "Configuration of watermelon fruit quality in response to rootstock-mediated harvest maturity and postharvest storage." Journal of the Science of Food and Agriculture **96**(7): 2400-2409.

Lähnemann, D., J. Köster, E. Szczurek, D. J. McCarthy, S. C. Hicks, M. D. Robinson, C. A. Vallejos, K. R. Campbell, N. Beerenwinkel and A. Mahfouz (2020). "Eleven grand challenges in single-cell data science." Genome biology **21**: 1-35.

Lamesch, P., T. Z. Berardini, D. Li, D. Swarbreck, C. Wilks, R. Sasidharan, R. Muller, K. Dreher, D. L. Alexander and M. Garcia-Hernandez (2012). "The Arabidopsis Information Resource (TAIR): improved gene annotation and new tools." Nucleic acids research **40**(D1): D1202-D1210.

Langmead, B. and S. L. Salzberg (2012). "Fast gapped-read alignment with Bowtie 2." Nature methods **9**(4): 357-359.

Langmead, B., C. Trapnell, M. Pop and S. L. Salzberg (2009). "Ultrafast and memory-efficient alignment of short DNA sequences to the human genome." Genome biology **10**: 1-10.

Laslett, D. and B. Canback (2004). "ARAGORN, a program to detect tRNA genes and tmRNA genes in nucleotide sequences." Nucleic acids research **32**(1): 11-16.

Law, J. A. and S. E. Jacobsen (2010). "Establishing, maintaining and modifying DNA methylation patterns in plants and animals." Nature Reviews Genetics **11**(3): 204-220.

Lawrence, M., W. Huber, H. Pagès, P. Aboyoun, M. Carlson, R. Gentleman, M. T. Morgan and V. J. Carey (2013). "Software for computing and annotating genomic ranges." PLoS computational biology **9**(8): e1003118.

Lécuyer, E., H. Yoshida and H. M. Krause (2009). "Global implications of mRNA localization pathways in cellular organization." Current opinion in cell biology **21**(3): 409-415.

Lécuyer, E., H. Yoshida, N. Parthasarathy, C. Alm, T. Babak, T. Cerovina, T. R. Hughes, P. Tomancak and H. M. Krause (2007). "Global analysis of mRNA localization reveals a prominent role in organizing cellular architecture and function." Cell **131**(1): 174-187.

Lee, J.-M. (1994). "Cultivation of grafted vegetables I. Current status, grafting methods, and benefits." HortScience **29**(4): 235-239.

Lee, J.-M., C. Kubota, S. Tsao, Z. Bie, P. H. Echevarria, L. Morra and M. Oda (2010). "Current status of vegetable grafting: Diffusion, grafting techniques, automation." Scientia Horticulturae **127**(2): 93-105.

Lee, J.-Y. and W. Cui (2009). "Non-cell autonomous RNA trafficking and long-distance signaling." Journal of Plant Biology **52**: 10-18.

Lewsey, M. G., T. J. Hardcastle, C. W. Melnyk, A. Molnar, A. Valli, M. A. Urich, J. R. Nery, D. C. Baulcombe and J. R. Ecker (2016). "Mobile small RNAs regulate genome-wide DNA methylation." Proceedings of the National Academy of Sciences **113**(6): E801-E810.

Li, H., F. Wang, X. J. Chen, K. Shi, X. J. Xia, M. J. Considine, J. Q. Yu and Y. H. Zhou (2014). "The sub/supra-optimal temperature-induced inhibition of photosynthesis and oxidative damage in cucumber leaves are alleviated by grafting onto figleaf gourd/luffa rootstocks." Physiologia Plantarum **152**(3): 571-584.

Li, N., Q. He, J. Wang, B. Wang, J. Zhao, S. Huang, T. Yang, Y. Tang, S. Yang and P. Aisimutuola (2023). "Super-pangenome analyses highlight genomic diversity and structural variation across wild and cultivated tomato species." Nature Genetics **55**(5): 852-860.

Li, S., X. Wang, W. Xu, T. Liu, C. Cai, L. Chen, C. B. Clark and J. Ma (2021). "Unidirectional movement of small RNAs from shoots to roots in interspecific heterografts." Nature Plants **7**(1): 50-59.

Li, X. (2018). "Next-generation sequencing sheds new light on small RNAs in plant reproductive development." Current Issues in Molecular Biology **27**(1): 143-170.

Li, X., F. Liu, Y. Huang, Q. Kong, Z. Wan, X. Li and Z. Bie (2015). "Growth and physiology of grafted watermelon seedlings as affected by different light sources." Acta Hortic **1086**: 59-64.

Li, X., X. Wang, Y. Zhang, A. Zhang and C.-X. You (2022). "Regulation of fleshy fruit ripening: from transcription factors to epigenetic modifications." Horticulture Research **9**: uhac013.

Li, X. J., X. J. Chen, X. Guo, L. L. Yin, G. J. Ahammed, C. J. Xu, K. S. Chen, C. C. Liu, X. J. Xia and K. Shi (2016). "DWARF overexpression induces alteration in phytohormone homeostasis, development, architecture and carotenoid accumulation in tomato." Plant Biotechnology Journal **14**(3): 1021-1033.

Li, Y., S. Kumar and W. Qian (2018). "Active DNA demethylation: mechanism and role in plant development." Plant cell reports **37**: 77-85.

Li, Y. and D. Zhao (2021). "Transcriptome analysis of scions grafted to potato rootstock for improving late blight resistance." BMC Plant Biology **21**(1): 272.

Liang, D., R. G. White and P. M. Waterhouse (2012). "Gene silencing in Arabidopsis spreads from the root to the shoot, through a gating barrier, by template-dependent, nonvascular, cell-to-cell movement." Plant physiology **159**(3): 984-1000.

Lifschitz, E., T. Eviatar, A. Rozman, A. Shalit, A. Goldshmidt, Z. Amsellem, J. P. Alvarez and Y. Eshed (2006). "The tomato FT ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli." Proceedings of the National Academy of Sciences **103**(16): 6398-6403.

Lin, M. and P. Huybers (2012). "Reckoning wheat yield trends." Environmental Research Letters **7**(2): 024016.

Lin, S.-I., S.-F. Chiang, W.-Y. Lin, J.-W. Chen, C.-Y. Tseng, P.-C. Wu and T.-J. Chiou (2008). "Regulatory network of microRNA399 and PHO2 by systemic signaling." Plant physiology **147**(2): 732-746.

Liu, B., J. Li, A. Tsykin, L. Liu, A. B. Gaur and G. J. Goodall (2009). "Exploring complex miRNA-mRNA interactions with Bayesian networks by splitting-averaging strategy." BMC bioinformatics **10**(1): 1-19.

Liu, B. and J. F. Wendel (2003). "Epigenetic phenomena and the evolution of plant allopolyploids." Molecular phylogenetics and evolution **29**(3): 365-379.

Liu, C., Y. Jia, L. He, H. Li, J. Song, L. Ji and C. Wang (2024). "Integrated transcriptome and DNA methylome analysis reveal the biological base of increased resistance to gray leaf spot and growth inhibition in interspecific grafted tomato scions." BMC Plant Biology **24**(1): 130.

Liu, G., W. Yang, X. Zhang, T. Peng, Y. Zou, T. Zhang, H. Wang, X. Liu and L. Z. Tao (2019). "Cystathionine beta-lyase is crucial for embryo patterning and the maintenance of root stem cell niche in Arabidopsis." The Plant Journal **99**(3): 536-555.

Liu, L. and X. Chen (2018). "Intercellular and systemic trafficking of RNAs in plants." Nature plants **4**(11): 869-878.

Liu, N., J. Yang, X. Fu, L. Zhang, K. Tang, K. M. Guy, Z. Hu, S. Guo, Y. Xu and M. Zhang (2016). "Genome-wide identification and comparative analysis of grafting-responsive mRNA in watermelon grafted onto bottle gourd and squash rootstocks by high-throughput sequencing." Molecular Genetics and Genomics **291**: 621-633.

Liu, R., Y.-H. Xu, S.-C. Jiang, K. Lu, Y.-F. Lu, X.-J. Feng, Z. Wu, S. Liang, Y.-T. Yu and X.-F. Wang (2013). "Light-harvesting chlorophyll a/b-binding proteins, positively involved in abscisic acid signalling, require a transcription repressor, WRKY40, to balance their function." Journal of experimental botany **64**(18): 5443-5456.

Liu, S., H. Li, X. Lv, G. J. Ahammed, X. Xia, J. Zhou, K. Shi, T. Asami, J. Yu and Y. Zhou (2016). "Grafting cucumber onto luffa improves drought tolerance by increasing ABA biosynthesis and sensitivity." Scientific Reports **6**(1): 20212.

Liu, S.-J., Y.-H. Huang, C.-J. He, F. Cheng and Y.-W. Zhang (2016). "Cloning, bioinformatics and transcriptional analysis of caffeoyl-coenzyme A 3-O-methyltransferase in switchgrass under abiotic stress." Journal of integrative agriculture **15**(3): 636-649.

Liu, W., C. Xiang, X. Li, T. Wang, X. Lu, Z. Liu, L. Gao and W. Zhang (2020). "Identification of long-distance transmissible mRNA between scion and rootstock in cucurbit seedling heterografts." International journal of molecular sciences **21**(15): 5253.

Liu, W., Z. H. Xu, D. Luo and H. W. Xue (2003). "Roles of OsCKI1, a rice casein kinase I, in root development and plant hormone sensitivity." The Plant Journal **36**(2): 189-202.

Liu, X., C. Tan, X. Cheng, X. Zhao, T. Li and J. Jiang (2020). "miR168 targets Argonaute1A mediated miRNAs regulation pathways in response to potassium deficiency stress in tomato." BMC plant biology **20**: 1-17.

Liu, X.-Y., J. Li, M.-M. Liu, Q. Yao and J.-Z. Chen (2017). "Transcriptome profiling to understand the effect of citrus rootstocks on the growth of 'Shatangju'mandarin." PLoS One **12**(1): e0169897.

Liu, Z., Z. Bie, Y. Huang, A. Zhen, B. Lei and H. Zhang (2012). "Grafting onto Cucurbita moschata rootstock alleviates salt stress in cucumber plants by delaying photoinhibition." Photosynthetica **50**(1): 152-160.

Liu, Z., Z. Bie, Y. Huang, A. Zhen, M. Niu and B. Lei (2013). "Rootstocks improve cucumber photosynthesis through nitrogen metabolism regulation under salt stress." Acta physiologiae plantarum **35**: 2259-2267.

Liu, Z., X. Wu, H. Liu, M. Zhang and W. Liao (2022). "DNA methylation in tomato fruit ripening." Physiologia Plantarum **174**(1): e13627.

Liu, Z.-W., C.-R. Shao, C.-J. Zhang, J.-X. Zhou, S.-W. Zhang, L. Li, S. Chen, H.-W. Huang, T. Cai and X.-J. He (2014). "The SET domain proteins SUVH2 and SUVH9 are required for Pol V occupancy at RNA-directed DNA methylation loci." PLoS genetics **10**(1): e1003948.

Long, S. P., A. Marshall-Colon and X.-G. Zhu (2015). "Meeting the global food demand of the future by engineering crop photosynthesis and yield potential." Cell **161**(1): 56-66.

Lopez-Gomollon, S., S. Y. Müller and D. C. Baulcombe (2022). "Interspecific hybridization in tomato influences endogenous viral sRNAs and alters gene expression." Genome Biology **23**(1): 120.

López-Marín, J., A. Gálvez, F. M. del Amor, A. Albacete, J. A. Fernández, C. Egea-Gilabert and F. Pérez-Alfocea (2017). "Selecting vegetative/generative/dwarfing rootstocks for improving fruit yield and quality in water stressed sweet peppers." Scientia Horticulturae **214**: 9-17.

Lorenz, R., S. H. Bernhart, C. Höner zu Siederdissen, H. Tafer, C. Flamm, P. F. Stadler and I. L. Hofacker (2011). "ViennaRNA Package 2.0." Algorithms for molecular biology **6**: 1-14.

Louws, F. J., C. L. Rivard and C. Kubota (2010). "Grafting fruiting vegetables to manage soilborne pathogens, foliar pathogens, arthropods and weeds." Scientia horticulturae **127**(2): 127-146.

Love, M. I., W. Huber and S. Anders (2014). "Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2." Genome biology **15**: 1-21.

Lu, C., K. Kulkarni, F. F. Souret, R. MuthuValliappan, S. S. Tej, R. S. Poethig, I. R. Henderson, S. E. Jacobsen, W. Wang and P. J. Green (2006). "MicroRNAs and other small RNAs enriched in the Arabidopsis RNA-dependent RNA polymerase-2 mutant." Genome research **16**(10): 1276-1288.

Lucas, W. J. (1995). "Plasmodesmata: intercellular channels for macromolecular transport in plants." Current Opinion in Cell Biology **7**(5): 673-680.

Lucas, W. J., B.-C. Yoo and F. Kragler (2001). "RNA as a long-distance information macromolecule in plants." Nature Reviews Molecular Cell Biology **2**(11): 849-857.

Luo, K.-R., N.-C. Huang, Y.-H. Chang and T.-S. Yu (2022). "Arabidopsis cyclophilins direct plasmodesmata-targeting of mobile mRNA via organelle hitchhiking."

Luo, K.-R., N.-C. Huang and T.-S. Yu (2018). "Selective targeting of mobile mRNAs to plasmodesmata for cell-to-cell movement." Plant physiology **177**(2): 604-614.

Macke, T. J., D. J. Ecker, R. R. Gutell, D. Gautheret, D. A. Case and R. Sampath (2001). "RNAMotif, an RNA secondary structure definition and search algorithm." Nucleic acids research **29**(22): 4724-4735.

Magome, H., S. Yamaguchi, A. Hanada, Y. Kamiya and K. Oda (2004). "dwarf and delayed-flowering 1, a novel Arabidopsis mutant deficient in gibberellin biosynthesis because of overexpression of a putative AP2 transcription factor." The Plant Journal **37**(5): 720-729.

Mahajan, A., S. Bhogale, I. H. Kang, D. J. Hannapel and A. K. Banerjee (2012). "The mRNA of a Knotted1-like transcription factor of potato is phloem mobile." Plant molecular biology **79**: 595-608.

Marí-Ordóñez, A., A. Marchais, M. Etcheverry, A. Martin, V. Colot and O. Voinnet (2013). "Reconstructing de novo silencing of an active plant retrotransposon." Nature genetics **45**(9): 1029-1039.

Martin, A., H. l. n. Adam, M. Díaz-Mendoza, M. Zurczak, N. D. González-Schain and P. Suárez-López (2009). "Graft-transmissible induction of potato tuberization by the microRNA miR172." Development **136**(17): 2873-2881.

Martínez-Ballesta, M. C., C. Alcaraz-López, B. Muries, C. Mota-Cadenas and M. Carvajal (2010). "Physiological aspects of rootstock–scion interactions." Scientia Horticulturae **127**(2): 112-118.

Martinho, C. and S. Lopez-Gomollon (2023). "Detection of MicroRNAs by Northern Blot." Methods Mol Biol **2630**: 47-66.

MASUDA, M. and K. GOMI (1984). "Mineral absorption and oxygen consumption in grafted and non-grafted cucumbers." Journal of the Japanese Society for Horticultural Science **52**(4): 414-419.

Mata-Pérez, C., B. Sánchez-Calvo, J. C. Begara-Morales, F. Luque, J. Jiménez-Ruiz, M. N. Padilla, J. Fierro-Risco, R. Valderrama, A. Fernández-Ocaña and F. J. Corpas (2015). "Transcriptomic profiling of linolenic acid-responsive genes in ROS signaling from RNA-seq data in Arabidopsis." Frontiers in Plant Science **6**: 122.

Matschi, S., S. Werner, W. X. Schulze, J. Legen, H. H. Hilger and T. Romeis (2013). "Function of calcium-dependent protein kinase CPK 28 of Arabidopsis thaliana in plant stem elongation and vascular development." The Plant Journal **73**(6): 883-896.

Matson, P. A. and P. M. Vitousek (2006). "Agricultural intensification: will land spared from farming be land spared for nature?".

Matsuoka, K., E. Sugawara, R. Aoki, K. Takuma, M. Terao-Morita, S. Satoh and M. Asahina (2016). "Differential cellular control by cotyledon-derived phytohormones involved in graft reunion of Arabidopsis hypocotyls." Plant and Cell Physiology **57**(12): 2620-2631.

Matzke, M. A. and R. A. Mosher (2014). "RNA-directed DNA methylation: an epigenetic pathway of increasing complexity." Nature Reviews Genetics **15**(6): 394-408.

Maurya, D., A. K. Pandey, V. Kumar, S. Dubey and V. Prakash (2019). "Grafting techniques in vegetable crops: A review." International Journal of Chemical Studies **7**(2): 1664-1672.

McClain, A. M. and T. D. Sharkey (2019). "Triose phosphate utilization and beyond: from photosynthesis to end product synthesis." Journal of Experimental Botany **70**(6): 1755-1766.

McCue, A. D., K. Panda, S. Nuthikattu, S. G. Choudury, E. N. Thomas and R. K. Slotkin (2015). "ARGONAUTE 6 bridges transposable element m RNA-derived si RNA s to the establishment of DNA methylation." The EMBO journal **34**(1): 20-35.

McKendry, P. (2002). "Energy production from biomass (part 1): overview of biomass." Bioresource technology **83**(1): 37-46.

Medicine, N. L. o. (1988). "National Center for Biotechnology Information (NCBI)." Bethesda (MD). Available from.

Mehak, G., N. A. Akram, M. Ashraf, P. Kaushik, M. A. El-Sheikh and P. Ahmad (2021). "Methionine-induced regulation of growth, secondary metabolites and oxidative defense system in sunflower (Helianthus annuus L.) plants subjected to water deficit stress." Plos one **16**(12): e0259585.

Melnyk, C. W. (2017). "Plant grafting: insights into tissue regeneration." Regeneration **4**(1): 3-14.

Melnyk, C. W., A. Gabel, T. J. Hardcastle, S. Robinson, S. Miyashima, I. Grosse and E. M. Meyerowitz (2018). "Transcriptome dynamics at Arabidopsis graft

junctions reveal an intertissue recognition mechanism that activates vascular regeneration." Proceedings of the National Academy of Sciences **115**(10): E2447-E2456.

Melnyk, C. W. and E. M. Meyerowitz (2015). "Plant grafting." Current Biology **25**(5): R183-R188.

Melnyk, C. W., A. Molnar and D. C. Baulcombe (2011). "Intercellular and systemic movement of RNA silencing signals." The EMBO journal **30**(17): 3553-3563.

Mendel, K. (1936). "The anatomy and histology of the bud-union in citrus."

Mercé, C., P. E. Bayer, C. Tay Fernandez, J. Batley and D. Edwards (2020). "Induced methylation in plants as a crop improvement tool: progress and perspectives." Agronomy **10**(10): 1484.

Messeguer, R., M. W. Ganal, J. C. Steffens and S. D. Tanksley (1991). "Characterization of the level, target sites and inheritance of cytosine methylation in tomato nuclear DNA." Plant Molecular Biology **16**: 753-770.

Meyer, K. D. and S. R. Jaffrey (2014). "The dynamic epitranscriptome: N 6-methyladenosine and gene expression control." Nature reviews Molecular cell biology **15**(5): 313-326.

Miedes, E. and E. P. Lorences (2009). "Xyloglucan endotransglucosylase/hydrolases (XTHs) during tomato fruit growth and ripening." Journal of plant physiology **166**(5): 489-498.

Miguel, A., J. Maroto, A. San Bautista, C. Baixauli, V. Cebolla, B. Pascual, S. Lopez and J. Guardiola (2004). "The grafting of triploid watermelon is an advantageous alternative to soil fumigation by methyl bromide for control of Fusarium wilt." Scientia Horticulturae **103**(1): 9-17.

Miles, C., J. Wimer and D. Inglis (2014). Grafting eggplant and tomato for Verticillium wilt resistance. I International Symposium on Vegetable Grafting 1086.

Miskovic, A., O. Ilic, J. Bacanovic, V. Vujasinovic and B. Kukic (2016). "Effect of eggplant rootstock on yield and quality parameters of grafted tomato." Acta Scientiarum Polonorum. Hortorum Cultus **15**(6).

Mohamed, F., K. Abd El-Hamed, M. Elwan and M. Hussien (2014). "Evaluation of different grafting methods and rootstocks in watermelon grown in Egypt." Scientia Horticulturae **168**: 145-150.

Molnar, A., C. W. Melnyk, A. Bassett, T. J. Hardcastle, R. Dunn and D. C. Baulcombe (2010). "Small silencing RNAs in plants are mobile and direct epigenetic modification in recipient cells." science **328**(5980): 872-875.

Moncada, A., A. Miceli, F. Vetrano, V. Mineo, D. Planeta and F. D'Anna (2013). "Effect of grafting on yield and quality of eggplant (Solanum melongena L.)." Scientia Horticulturae **149**: 108-114.

Montoya, T., T. Nomura, T. Yokota, K. Farrar, K. Harrison, J. G. Jones, T. Kaneta, Y. Kamiya, M. Szekeres and G. J. Bishop (2005). "Patterns of Dwarf expression and brassinosteroid accumulation in tomato reveal the importance of brassinosteroid synthesis during fruit development." The Plant Journal **42**(2): 262-269.

Moore, R. (1984). "A model for graft compatibility-incompatibility in higher plants." American Journal of Botany **71**(5): 752-758.

Morrell, P. L., E. S. Buckler and J. Ross-Ibarra (2012). "Crop genomics: advances and applications." Nature Reviews Genetics **13**(2): 85-96.

Morris, R. J. (2018). "On the selectivity, specificity and signalling potential of the long-distance movement of messenger RNA." Current Opinion in Plant Biology **43**: 1-7.

Mosse, B. (1962). "Graft-incompatibility in fruit trees."

Mudge, K., J. Janick, S. Scofield and E. E. Goldschmidt (2009). "A history of grafting." Horticultural reviews **35**: 437-493.

Münch, E. (1930). "Die stoffbewegungen in der pflanze (Gustav Fischer, jena)." Curr. Opin. Plant Biol **43**: 36-42.

Munsky, B., G. Neuert and A. Van Oudenaarden (2012). "Using gene expression noise to understand gene regulation." Science **336**(6078): 183-187.

Myers, C., S. M. Romanowsky, Y. D. Barron, S. Garg, C. L. Azuse, A. Curran, R. M. Davis, J. Hatton, A. C. Harmon and J. F. Harper (2009). "Calcium-dependent protein kinases regulate polarized tip growth in pollen tubes." The Plant Journal **59**(4): 528-539.

Nakamichi, N., M. Kusano, A. Fukushima, M. Kita, S. Ito, T. Yamashino, K. Saito, H. Sakakibara and T. Mizuno (2009). "Transcript profiling of an Arabidopsis PSEUDO RESPONSE REGULATOR arrhythmic triple mutant reveals a role for the circadian clock in cold stress response." Plant and Cell Physiology **50**(3): 447-462.

Nakamura, T., R. Yokoyama, E. Tomita and K. Nishitani (2003). "Two azuki bean XTH genes, VaXTH1 and VaXTH2, with similar tissue-specific expression profiles, are differently regulated by auxin." Plant and cell physiology **44**(1): 16-24.

Nam, N. N., H. D. K. Do, K. T. Loan Trinh and N. Y. Lee (2023). "Metagenomics: An effective approach for exploring microbial diversity and functions." Foods **12**(11): 2140.

Nanda, A. K. and C. W. Melnyk (2018). "The role of plant hormones during grafting." Journal of plant research **131**(1): 49-58.

Naqvi, A. R., M. Sarwat, S. Hasan and N. Roychodhury (2012). "Biogenesis, functions and fate of plant microRNAs." Journal of cellular physiology **227**(9): 3163-3168.

Nawaz, M. A., L. Wang, Y. Jiao, C. Chen, L. Zhao, M. Mei, Y. Yu, Z. Bie and Y. Huang (2017). "Pumpkin rootstock improves nitrogen use efficiency of watermelon scion by enhancing nutrient uptake, cytokinin content, and expression of nitrate reductase genes." Plant growth regulation **82**: 233-246.

Neocleous, D. (2015). "Grafting and silicon improve photosynthesis and nitrate absorption in melon (Cucumis melo L.) plants." Journal of Agricultural Science and Technology **17**(7): 1815-1824.

Neves, D. M., L. A. d. H. Almeida, D. D. S. Santana-Vieira, L. Freschi, C. F. Ferreira, W. d. S. Soares Filho, M. G. C. Costa, F. Micheli, M. A. Coelho Filho and A. d. S. Gesteira (2017). "Recurrent water deficit causes epigenetic and hormonal changes in citrus plants." Scientific reports **7**(1): 13684.

Nilsen, E. T., J. Freeman, R. Grene and J. Tokuhisa (2014). "A rootstock provides water conservation for a grafted commercial tomato (Solanum lycopersicum L.) line in response to mild-drought conditions: a focus on vegetative growth and photosynthetic parameters." PLoS One **9**(12): e115380.

Nisini, P. T., G. Colla, E. Granati, O. Temperini, P. Crino and F. Saccardo (2002). "Rootstock resistance to fusarium wilt and effect on fruit yield and quality of two muskmelon cultivars." Scientia Horticulturae **93**(3-4): 281-288.

Notaguchi, M., Y. Daimon, M. Abe and T. Araki (2009). "Graft-transmissible action of Arabidopsis FLOWERING LOCUS T protein to promote flowering." Plant Signaling & Behavior **4**(2): 123-125.

Notaguchi, M., T. Higashiyama and T. Suzuki (2015). "Identification of mRNAs that move over long distances using an RNA-Seq analysis of Arabidopsis/Nicotiana benthamiana heterografts." Plant and Cell Physiology **56**(2): 311-321.

Notaguchi, M., K.-i. Kurotani, Y. Sato, R. Tabata, Y. Kawakatsu, K. Okayasu, Y. Sawai, R. Okada, M. Asahina and Y. Ichihashi (2020). "Cell-cell adhesion in plant grafting is facilitated by β-1, 4-glucanases." Science **369**(6504): 698-702.

Notaguchi, M., S. Wolf and W. J. Lucas (2012). "Phloem-Mobile Aux/IAA Transcripts Target to the Root Tip and Modify Root Architecture F." Journal of integrative plant biology **54**(10): 760-772.

Ntatsi, G., D. Savvas, U. Druege and D. Schwarz (2013). "Contribution of phytohormones in alleviating the impact of sub-optimal temperature stress on grafted tomato." Scientia horticulturae **149**: 28-38.

Ntatsi, G., D. Savvas, V. Papasotiropoulos, A. Katsileros, R. M. Zrenner, D. K. Hincha, E. Zuther and D. Schwarz (2017). "Rootstock sub-optimal temperature tolerance determines transcriptomic responses after long-term root cooling in rootstocks and scions of grafted tomato plants." Frontiers in Plant Science **8**: 911.

Nuthikattu, S., A. D. McCue, K. Panda, D. Fultz, C. DeFraia, E. N. Thomas and R. K. Slotkin (2013). "The initiation of epigenetic silencing of active transposable elements is triggered by RDR6 and 21-22 nucleotide small interfering RNAs." Plant physiology **162**(1): 116-131.

O'Malley, R. C., S.-s. C. Huang, L. Song, M. G. Lewsey, A. Bartlett, J. R. Nery, M. Galli, A. Gallavotti and J. R. Ecker (2016). "Cistrome and epicistrome features shape the regulatory DNA landscape." Cell **165**(5): 1280-1292.

Omid, A., T. Keilin, A. Glass, D. Leshkowitz and S. Wolf (2007). "Characterization of phloem-sap transcription profile in melon plants." Journal of experimental botany **58**(13): 3645-3656.

Oparka, K., D. Prior, S. S. Cruz, H. Padgett and R. Beachy (1997). "Gating of epidermal plasmodesmata is restricted to the leading edge of expanding infection sites of tobacco mosaic virus (TMV)." The Plant Journal **12**(4): 781-789.

Orsini, F., R. Sanoubar, G. B. Oztekin, N. Kappel, M. Tepecik, C. Quacquarelli, Y. Tuzel, S. Bona and G. Gianquinto (2013). "Improved stomatal regulation and ion partitioning boosts salt tolerance in grafted melon." Functional Plant Biology **40**(6): 628-636.

Ostendorp, A., S. Ostendorp, Y. Zhou, Z. Chaudron, L. Wolffram, K. Rombi, L. von Pein, S. Falke, C. M. Jeffries and D. I. Svergun (2022). "Intrinsically disordered plant protein PARCL colocalizes with RNA in phase-separated condensates whose formation can be regulated by mutating the PLD." Journal of Biological Chemistry **298**(12).

Ostendorp, A., S. Pahlow, L. Krüßel, P. Hanhart, M. Y. Garbe, J. Deke, P. Giavalisco and J. Kehr (2017). "Functional analysis of Brassica napus phloem protein and ribonucleoprotein complexes." New Phytologist **214**(3): 1188-1197.

Oumouloud, A., M. Arnedo-Andrés, R. González-Torres and J. Alvarez (2010). "Inheritance of resistance to Fusarium oxysporum f. sp. melonis races 0 and 2 in melon accession Tortuga." Euphytica **176**: 183-189.

Oumouloud, A., M. El-Otmani, H. Chikh-Rouhou, A. G. Claver, R. G. Torres, R. Perl-Treves and J. Alvarez (2013). "Breeding melon for resistance to Fusarium wilt: recent developments." Euphytica **192**: 155-169.

Owusu, S., C. Kwoseh, J. Starr and F. Davies (2016). "Grafting for management of root-knot nematodes, Meloidogyne incognita, in tomato (Solanum lycopersicum L.)." Nematropica **46**(1): 14-21.

Paajanen, P., M. Tomkins, F. Hoerbst, R. Veevers, M. Heeney, H. R. Thomas, F. Apelt, E. Saplaoura, S. Gupta and M. Frank (2024). "Re-analysis of mobile mRNA datasets highlights challenges in the detection of mobile transcripts from short-read RNA-Seq data." bioRxiv: 2024.2007. 2025.604588.

Pan, J., D. Huang, Z. Guo, Z. Kuang, H. Zhang, X. Xie, Z. Ma, S. Gao, M. T. Lerdau and C. Chu (2018). "Overexpression of microRNA408 enhances

photosynthesis, growth, and seed yield in diverse plants." Journal of Integrative Plant Biology **60**(4): 323-340.

Pant, B. D., A. Buhtz, J. Kehr and W. R. Scheible (2008). "MicroRNA399 is a long-distance signal for the regulation of plant phosphate homeostasis." The Plant Journal **53**(5): 731-738.

Pardo-Alonso, J.-L., Á. Carreño-Ortega, C.-C. Martínez-Gaitán and Á.-J. Callejón-Ferre (2018). "Combined influence of cutting angle and diameter differences between seedlings on the grafting success of tomato using the splicing technique." Agronomy **9**(1): 5.

Parent, J.-S., A. E. Martinez de Alba and H. Vaucheret (2012). "The origin and effect of small RNA signaling in plants." Frontiers in plant science **3**: 179.

Park, S.-Y., K. Shimizu, J. Brown, K. Aoki and J. H. Westwood (2021). "Mobile host mRNAs are translated to protein in the associated parasitic plant Cuscuta campestris." Plants **11**(1): 93.

Parry, M. (1981). "Trials of dwarfing quince rootstocks with Comice and Conference pears." Journal of Horticultural Science **56**(2): 139-143.

Parthasarathi, T., J. E. Ephrath and N. Lazarovitch (2021). "Grafting of tomato (Solanum lycopersicum L.) onto potato (Solanum tuberosum L.) to improve salinity tolerance." Scientia Horticulturae **282**: 110050.

Peltonen-Sainio, P., L. Jauhiainen and I. P. Laurila (2009). "Cereal yield trends in northern European conditions: Changes in yield potential and its realisation." Field Crops Research **110**(1): 85-90.

Peng, J., P. Carol, D. E. Richards, K. E. King, R. J. Cowling, G. P. Murphy and N. P. Harberd (1997). "The Arabidopsis GAI gene defines a signaling pathway that negatively regulates gibberellin responses." Genes & development **11**(23): 3194-3205.

Peng, J., D. E. Richards, N. M. Hartley, G. P. Murphy, K. M. Devos, J. E. Flintham, J. Beales, L. J. Fish, A. J. Worland and F. Pelica (1999). "'Green revolution'genes encode mutant gibberellin response modulators." nature **400**(6741): 256-261.

Phalan, B., A. Balmford, R. E. Green and J. P. Scharlemann (2011). "Minimising the harm to biodiversity of producing more food globally." Food Policy **36**: S62-S71.

Phani, V., M. T. Gowda and T. K. Dutta (2023). "Grafting vegetable crops to manage plant-parasitic nematodes: a review." Journal of Pest Science: 1-22.

Pingali, P. L. (2012). "Green revolution: impacts, limits, and the path ahead." Proceedings of the national academy of sciences **109**(31): 12302-12308.

Pirrello, J., F. Jaimes-Miranda, M. T. Sanchez-Ballesta, B. Tournier, Q. Khalil-Ahmad, F. Regad, A. Latche, J. C. Pech and M. Bouzayen (2006). "Sl-ERF2, a

tomato ethylene response factor involved in ethylene response and seed germination." Plant and Cell Physiology **47**(9): 1195-1205.

Pockrandt, C., M. Alzamel, C. S. Iliopoulos and K. Reinert (2020). "GenMap: ultra-fast computation of genome mappability." Bioinformatics **36**(12): 3687-3692.

Polizzi, G., V. Guarnaccia, A. Vitale, M. Marra, M. Rocco, S. Arena, A. Scaloni, F. Giuffrida, C. Cassaniti and C. Leonardi (2014). Scion/rootstock interaction and tolerance expression of tomato to FORL. I International Symposium on Vegetable Grafting 1086.

Pontier, D., C. Picart, F. Roudier, D. Garcia, S. Lahmy, J. Azevedo, E. Alart, M. Laudié, W. M. Karlowski and R. Cooke (2012). "NERD, a plant-specific GW protein, defines an additional RNAi-dependent chromatin-based pathway in Arabidopsis." Molecular cell **48**(1): 121-132.

Pouget, R. (1990). "Histoire de la lutte contre le phylloxéra de la vigne en France." Histoire de la lutte contre le phylloxera de la vigne en France: 1-168.

Pulgar, G., G. Villora, D. Moreno and L. Romero (2000). "Improving the mineral nutrition in grafted watermelon plants: Nitrogen metabolism." Biologia Plantarum **43**: 607-609.

Putri, G. H., S. Anders, P. T. Pyl, J. E. Pimanda and F. Zanini (2022). "Analysing high-throughput sequencing data in Python with HTSeq 2.0." Bioinformatics **38**(10): 2943-2945.

Qi, Y., X. He, X.-J. Wang, O. Kohany, J. Jurka and G. J. Hannon (2006). "Distinct catalytic and non-catalytic roles of ARGONAUTE4 in RNA-directed DNA methylation." Nature **443**(7114): 1008-1012.

Qi, Y., T. Peélissier, A. Itaya, E. Hunt, M. Wassenegger and B. Ding (2004). "Direct role of a viroid RNA motif in mediating directional RNA trafficking across a specific cellular boundary." The Plant Cell **16**(7): 1741-1752.

Quinlan, A. R. and I. M. Hall (2010). "BEDTools: a flexible suite of utilities for comparing genomic features." Bioinformatics **26**(6): 841-842.

Ramírez, F., D. P. Ryan, B. Grüning, V. Bhardwaj, F. Kilpert, A. S. Richter, S. Heyne, F. Dündar and T. Manke (2016). "deepTools2: a next generation web server for deep-sequencing data analysis." Nucleic acids research **44**(Web Server issue): W160.

Ramírez-Jiménez, J. A., P. E. R. Marchiori and O. d. J. Córdoba-Gaona (2021). "Grafting effect on photosynthetic activity and yield of tomato under a plastic house in Colombia." Revista Facultad Nacional de Agronomía Medellín **74**(3): 9621-9629.

Rauluseviciute, I., R. Riudavets-Puig, R. Blanc-Mathieu, J. A. Castro-Mondragon, K. Ferenc, V. Kumar, R. B. Lemma, J. Lucas, J. Chèneby and D. Baranasic (2024). "JASPAR 2024: 20th anniversary of the open-access database

of transcription factor binding profiles." Nucleic Acids Research **52**(D1): D174-D182.

Ray, D. K., N. D. Mueller, P. C. West and J. A. Foley (2013). "Yield trends are insufficient to double global crop production by 2050." PloS one **8**(6): e66428.

Ray, D. K., N. Ramankutty, N. D. Mueller, P. C. West and J. A. Foley (2012). "Recent patterns of crop yield growth and stagnation." Nature communications **3**(1): 1293.

Reddy, A. S., Y. Marquez, M. Kalyna and A. Barta (2013). "Complexity of the alternative splicing landscape in plants." The Plant Cell **25**(10): 3657-3683.

Reeves, G., A. Tripathi, P. Singh, M. R. Jones, A. K. Nanda, C. Musseau, M. Craze, S. Bowden, J. F. Walker and A. R. Bentley (2022). "Monocotyledonous plants graft at the embryonic root–shoot interface." Nature **602**(7896): 280-286.

Regulski, M., Z. Lu, J. Kendall, M. T. Donoghue, J. Reinders, V. Llaca, S. Deschamps, A. Smith, D. Levy and W. R. McCombie (2013). "The maize methylome influences mRNA splice sites and reveals widespread paramutation-like switches guided by small RNA." Genome research **23**(10): 1651-1662.

Ren, Y., Q. Xu, L. Wang, S. Guo, S. Shu, N. Lu and J. Sun (2018). "Involvement of metabolic, physiological and hormonal responses in the graft-compatible process of cucumber/pumpkin combinations was revealed through the integrative analysis of mRNA and miRNA expression." Plant physiology and biochemistry **129**: 368-380.

Riga, P., L. Benedicto, L. García-Flores, D. Villaño, S. Medina and Á. Gil-Izquierdo (2016). "Rootstock effect on serotonin and nutritional quality of tomatoes produced under low temperature and light conditions." Journal of Food Composition and Analysis **46**: 50-59.

Rippa, V., C. Cirulli, B. Di Palo, N. Doti, A. Amoresano and A. Duilio (2010). "The ribosomal protein L2 interacts with the RNA polymerase α subunit and acts as a transcription modulator in Escherichia coli." Journal of bacteriology **192**(7): 1882-1889.

Rivero, R., J. Ruiz and L. Romero (2005). "Iron metabolism in tomato and watermelon plants: influence of grafting." Journal of plant nutrition **27**(12): 2221-2234.

Rosas-Diaz, T., D. Zhang, P. Fan, L. Wang, X. Ding, Y. Jiang, T. Jimenez-Gongora, L. Medina-Puche, X. Zhao and Z. Feng (2018). "A virus-targeted plant receptor-like kinase promotes cell-to-cell spread of RNAi." Proceedings of the National Academy of Sciences **115**(6): 1388-1393.

Rouphael, Y., M. Cardarelli, G. Colla and E. Rea (2008). "Yield, mineral composition, water relations, and water use efficiency of grafted mini-watermelon plants under deficit irrigation." HortScience **43**(3): 730-736.

Rouphael, Y., D. Schwarz, A. Krumbein and G. Colla (2010). "Impact of grafting on product quality of fruit vegetables." Scientia horticulturae **127**(2): 172-179.

Ru, L., S. Osorio, L. Wang, A. R. Fernie, J. W. Patrick and Y.-L. Ruan (2017). "Transcriptomic and metabolomics responses to elevated cell wall invertase activity during tomato fruit set." Journal of Experimental Botany **68**(15): 4263-4279.

Rubio, B., L. Stammitti, S. J. Cookson, E. Teyssier and P. Gallusci (2022). "Small RNA populations reflect the complex dialogue established between heterograft partners in grapevine." Horticulture research **9**: uhab067.

Ruiz, J. and L. Romero (1999). "Nitrogen efficiency and metabolism in grafted melon plants." Scientia Horticulturae **81**(2): 113-123.

Ruiz-Ferrer, V. and O. Voinnet (2009). "Roles of plant small RNAs in biotic stress responses." Annual review of plant biology **60**: 485-510.

Ruiz-Medrano, R., B. Xoconostle-Cázares and W. J. Lucas (1999). "Phloem long-distance transport of CmNACP mRNA: implications for supracellular regulation in plants." Development **126**(20): 4405-4419.

Sabatino, L., G. Iapichino, A. Maggio, E. D'anna, M. Bruno and F. D'Anna (2016). "Grafting affects yield and phenolic profile of Solanum melongena L. landraces." Journal of integrative agriculture **15**(5): 1017-1024.

Sala, K., J. Karcz, A. Rypień and E. U. Kurczyńska (2019). "Unmethyl-esterified homogalacturonan and extensins seal Arabidopsis graft union." BMC plant biology **19**: 1-16.

Salar, N., R. Salehi and M. Delshad (2014). Effect of grafting and nitrogen application on yield and fruit quality of grafted and non-grafted melon. I International Symposium on Vegetable Grafting 1086.

Salehi, R., A. Kashi, J.-M. Lee, M. Babalar, M. Delshad, S.-G. Lee and Y.-C. Huh (2010). "Leaf gas exchanges and mineral ion composition in xylem sap of iranian melon affected by rootstocks and training methods." HortScience **45**(5): 766-770.

San Bautista, A., A. Calatayud, S. G. Nebauer, B. Pascual, J. V. Maroto and S. López-Galarza (2011). "Effects of simple and double grafting melon plants on mineral absorption, photosynthesis, biomass and yield." Scientia Horticulturae **130**(3): 575-580.

Sanan-Mishra, N., A. Abdul Kader Jailani, B. Mandal and S. K. Mukherjee (2021). "Secondary siRNAs in plants: biosynthesis, various functions, and applications in virology." Frontiers in Plant Science **12**: 610283.

Sanchez, A. and I. Golding (2013). "Genetic determinants and cellular constraints in noisy gene expression." Science **342**(6163): 1188-1193.

Sasaki, T., M. Chino, H. Hayashi and T. Fujiwara (1998). "Detection of several mRNA species in rice phloem sap." Plant and Cell Physiology **39**(8): 895-897.

Savvas, D., G. Colla, Y. Rouphael and D. Schwarz (2010). "Amelioration of heavy metal and nutrient stress in fruit vegetables by grafting." Scientia horticulturae **127**(2): 156-161.

Savvas, D., G. Ntatsi and P. Barouchas (2013). "Impact of grafting and rootstock genotype on cation uptake by cucumber (Cucumis sativus L.) exposed to Cd or Ni stress." Scientia Horticulturae **149**: 86-96.

Savvas, D., G. B. Öztekin, M. Tepecik, A. Ropokis, Y. Tüzel, G. Ntatsi and D. Schwarz (2017). "Impact of grafting and rootstock on nutrient-to-water uptake ratios during the first month after planting of hydroponically grown tomato." The Journal of Horticultural Science and Biotechnology **92**(3): 294-302.

Sawa, M., D. A. Nusinow, S. A. Kay and T. Imaizumi (2007). "FKF1 and GIGANTEA complex formation is required for day-length measurement in Arabidopsis." Science **318**(5848): 261-265.

Schmutz, J., S. B. Cannon, J. Schlueter, J. Ma, T. Mitros, W. Nelson, D. L. Hyten, Q. Song, J. J. Thelen and J. Cheng (2010). "Genome sequence of the palaeopolyploid soybean." nature **463**(7278): 178-183.

Schmutz, J., P. E. McClean, S. Mamidi, G. A. Wu, S. B. Cannon, J. Grimwood, J. Jenkins, S. Shu, Q. Song and C. Chavarro (2014). "A reference genome for common bean and genome-wide analysis of dual domestications." Nature genetics **46**(7): 707-713.

Schneeberger, K., S. Ossowski, F. Ott, J. D. Klein, X. Wang, C. Lanz, L. M. Smith, J. Cao, J. Fitz and N. Warthmann (2011). "Reference-guided assembly of four diverse Arabidopsis thaliana genomes." Proceedings of the National Academy of Sciences **108**(25): 10249-10254.

Schöning, U. and R. Kollmann (1997). "Phloem translocation in regenerating in vitro-heterografts of different compatibility." Journal of experimental botany **48**(2): 289-295.

Sederoff, R. R., J. J. MacKay, J. Ralph and R. D. Hatfield (1999). "Unexpected variation in lignin." Current Opinion in Plant Biology **2**(2): 145-152.

SEMİZ, G. D. and D. L. Suarez (2015). "Tomato salt tolerance: impact of grafting and water compositionon yield and ion relations." Turkish Journal of Agriculture and Forestry **39**(6): 876-886.

Shahid, S. and M. J. Axtell (2014). "Identification and annotation of small RNA genes using ShortStack." Methods **67**(1): 20-27.

Shahid, S., G. Kim, N. R. Johnson, E. Wafula, F. Wang, C. Coruh, V. Bernal-Galeano, T. Phifer, C. W. Depamphilis and J. H. Westwood (2018). "MicroRNAs from the parasitic plant Cuscuta campestris target host messenger RNAs." Nature **553**(7686): 82-85.

Shinbori, F., N. Kota and A. Yoshino (1981). "Studies on the maturation-physiology and the quality of watermelon, 2: Influence of rootstocks on the

growth properties and the quality in grafting culture." Bulletin of the Chiba ken Agricultural Experiment Station.

Simon, S. A. and B. C. Meyers (2011). "Small RNA-mediated epigenetic modifications in plants." Current opinion in plant biology **14**(2): 148-155.

Singh, A., V. Gautam, S. Singh, S. Sarkar Das, S. Verma, V. Mishra, S. Mukherjee and A. K. Sarkar (2018). "Plant small RNAs: advancement in the understanding of biogenesis and role in plant development." Planta **248**: 545-558.

Singh, H., P. Kumar, S. Chaudhari and M. Edelstein (2017). "Tomato grafting: a global perspective." HortScience **52**(10): 1328-1336.

Singh, H., P. Kumar, A. Kumar, M. C. Kyriacou, G. Colla and Y. Rouphael (2020). "Grafting tomato as a tool to improve salt tolerance." Agronomy **10**(2): 263.

Singh, K. B., R. C. Foley and L. Oñate-Sánchez (2002). "Transcription factors in plant defense and stress responses." Current opinion in plant biology **5**(5): 430-436.

Skopelitis, D. S., K. Hill, S. Klesen, C. F. Marco, P. von Born, D. H. Chitwood and M. C. Timmermans (2018). "Gating of miRNA movement at defined cell-cell interfaces governs their impact as positional signals." Nature communications **9**(1): 3107.

Slavov, G., G. Allison and M. Bosch (2013). "Advances in the genetic dissection of plant cell walls: tools and resources available in Miscanthus." Frontiers in plant science **4**: 217.

Solanke, A. U., M. K. Sharma, A. K. Tyagi and A. K. Sharma (2009). "Characterization and phylogenetic analysis of environmental stress-responsive SAP gene family encoding A20/AN1 zinc finger proteins in tomato." Molecular Genetics and Genomics **282**: 153-164.

Song, Q., T. Zhang, D. M. Stelly and Z. J. Chen (2017). "Epigenomic and functional analyses reveal roles of epialleles in the loss of photoperiod sensitivity during domestication of allotetraploid cottons." Genome biology **18**: 1-14.

Soteriou, G., M. Kyriacou, A. Siomos and D. Gerasopoulos (2014). "Evolution of watermelon fruit physicochemical and phytochemical composition during ripening as affected by grafting." Food chemistry **165**: 282-289.

Spanò, R., M. Ferrara, D. Gallitelli and T. Mascia (2020). "The role of grafting in the resistance of tomato to viruses." Plants **9**(8): 1042.

Spanò, R., M. Ferrara, C. Montemurro, G. Mulè, D. Gallitelli and T. Mascia (2020). "Grafting alters tomato transcriptome and enhances tolerance to an airborne virus infection." Scientific Reports **10**(1): 2538.

Spanò, R., D. Gallitelli and T. Mascia (2017). "Grafting to manage infections of top stunting and necrogenic strains of cucumber mosaic virus in tomato." Annals of Applied Biology **171**(3): 393-404.

Spanò, R., T. Mascia, R. Kormelink and D. Gallitelli (2015). "Grafting on a non-transgenic tolerant tomato variety confers resistance to the infection of a Sw5-breaking strain of tomato spotted wilt virus via RNA silencing." PLoS One **10**(10): e0141319.

Spanova, M., D. Zweytick, K. Lohner, L. Klug, E. Leitner, A. Hermetter and G. Daum (2012). "Influence of squalene on lipid particle/droplet and membrane organization in the yeast Saccharomyces cerevisiae." Biochimica et Biophysica Acta (BBA)-Molecular and Cell Biology of Lipids **1821**(4): 647-653.

Spielmeyer, W., M. H. Ellis and P. M. Chandler (2002). "Semidwarf (sd-1),"green revolution" rice, contains a defective gibberellin 20-oxidase gene." Proceedings of the National Academy of Sciences **99**(13): 9043-9048.

Stadler, R., K. M. Wright, C. Lauterbach, G. Amon, M. Gahrtz, A. Feuerstein, K. J. Oparka and N. Sauer (2005). "Expression of GFP-fusions in Arabidopsis companion cells reveals non-specific protein trafficking into sieve elements and identifies a novel post-phloem domain in roots." The Plant Journal **41**(2): 319-331.

Stahl, Y. and C. Faulkner (2016). "Receptor complex mediated regulation of symplastic traffic." Trends in plant science **21**(5): 450-459.

Stegemann, S. and R. Bock (2009). "Exchange of genetic material between cells in plant tissue grafts." science **324**(5927): 649-651.

Stegemann, S., M. Keuthe, S. Greiner and R. Bock (2012). "Horizontal transfer of chloroplast genomes between plant species." Proceedings of the National Academy of Sciences **109**(7): 2434-2438.

Stroud, H., T. Do, J. Du, X. Zhong, S. Feng, L. Johnson, D. J. Patel and S. E. Jacobsen (2014). "Non-CG methylation patterns shape the epigenetic landscape in Arabidopsis." Nature structural & molecular biology **21**(1): 64-72.

Stroud, H., M. V. Greenberg, S. Feng, Y. V. Bernatavichute and S. E. Jacobsen (2013). "Comprehensive analysis of silencing mutants reveals complex regulation of the Arabidopsis methylome." Cell **152**(1): 352-364.

Suchoff, D. H., P. Perkins-Veazie, H. W. Sederoff, J. R. Schultheis, M. D. Kleinhenz, F. J. Louws and C. C. Gunter (2018). "Grafting the indeterminate tomato cultivar moneymaker onto multifort rootstock improves cold tolerance." HortScience **53**(11): 1610-1617.

Sun, Y., L. Shang, Q.-H. Zhu, L. Fan and L. Guo (2022). "Twenty years of plant genome sequencing: achievements and challenges." Trends in Plant Science **27**(4): 391-401.

Szklarczyk, D., R. Kirsch, M. Koutrouli, K. Nastou, F. Mehryary, R. Hachilif, A. L. Gable, T. Fang, N. T. Doncheva and S. Pyysalo (2023). "The STRING database in 2023: protein–protein association networks and functional enrichment analyses for any sequenced genome of interest." Nucleic acids research **51**(D1): D638-D646.

Takeda, R., C. L. Zirbel, N. B. Leontis, Y. Wang and B. Ding (2018). "Allelic RNA Motifs in Regulating Systemic Trafficking of Potato Spindle Tuber Viroid." Viruses **10**(4): 160.

Tamura, F. (2012). "Recent advances in research on Japanese pear rootstocks." Journal of the Japanese Society for Horticultural Science **81**(1): 1-10.

Tan, S.-T., C. Dai, H.-T. Liu and H.-W. Xue (2013). "Arabidopsis casein kinase1 proteins CK1. 3 and CK1. 4 phosphorylate cryptochrome2 to regulate blue light signaling." The Plant Cell **25**(7): 2618-2632.

Tanksley, S., M. Ganal, J. Prince, M. De Vicente, M. Bonierbale, P. Broun, T. Fulton, J. Giovannoni, S. Grandillo and G. Martin (1992). "High density molecular linkage maps of the tomato and potato genomes." Genetics **132**(4): 1141-1160.

Thieme, C. J., M. Rojas-Triana, E. Stecyk, C. Schudoma, W. Zhang, L. Yang, M. Miñambres, D. Walther, W. X. Schulze and J. Paz-Ares (2015). "Endogenous Arabidopsis messenger RNAs transported to distant tissues." Nature Plants **1**(4): 1-9.

Thomas, H., L. Van den Broeck, R. Spurney, R. Sozzani and M. Frank (2022). "Gene regulatory networks for compatible versus incompatible grafts identify a role for SlWOX4 during junction formation." The Plant Cell **34**(1): 535-556.

Thomas, H. R., A. Gevorgyan and M. H. Frank (2023). "Anatomical and biophysical basis for graft incompatibility within the Solanaceae." Journal of Experimental Botany **74**(15): 4461-4470.

Thomas, H. R., A. Gevorgyan, A. Hermanson, S. Yanders, L. Erndwein, M. Norman-Ariztia, E. E. Sparks and M. H. Frank (2024). "Graft incompatibility between pepper and tomato can be attributed to genetic incompatibility between diverged immune systems." bioRxiv.

Thompson, A. J., M. Pico, H. Yetişir, R. Cohen and P. J. Bebeli (2017). Rootstock breeding: current practices and future technologies. Vegetable grafting: principles and practices, CABI Wallingford UK**:** 70-93.

Thompson, J. E. and S. C. Fry (2001). "Restructuring of wall-bound xyloglucan by transglycosylation in living plant cells." The Plant Journal **26**(1): 23-34.

Tirot, L., D. M. Bonnet and P. E. Jullien (2022). "DNA methyltransferase 3 (MET3) is regulated by Polycomb group complex during Arabidopsis endosperm development." Plant reproduction **35**(2): 141-151.

To, T. K., H. Saze and T. Kakutani (2015). "Focus on chromatin/epigenetics: DNA methylation within transcribed regions." Plant Physiology **168**(4): 1219.

Tomato Genome Consortium, x. (2012). "The tomato genome sequence provides insights into fleshy fruit evolution." Nature **485**(7400): 635.

Tomkins, M., F. Hoerbst, S. Gupta, F. Apelt, J. Kehr, F. Kragler and R. J. Morris (2022). "Exact Bayesian inference for the detection of graft-mobile transcripts from sequencing data." Journal of the Royal Society Interface **19**(197): 20220644.

Tournier, B., M. Tabler and K. Kalantidis (2006). "Phloem flow strongly influences the systemic spread of silencing in GFP Nicotiana benthamiana plants." The Plant Journal **47**(3): 383-394.

Tran, R. K., J. G. Henikoff, D. Zilberman, R. F. Ditt, S. E. Jacobsen and S. Henikoff (2005). "DNA methylation profiling identifies CG methylation clusters in Arabidopsis genes." Current Biology **15**(2): 154-159.

Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer and A. Whitbread (2012). "Global food security, biodiversity conservation and the future of agricultural intensification." Biological conservation **151**(1): 53-59.

Tsiantis, M. (2001). "Control of shoot cell fate: beyond homeoboxes." The Plant Cell **13**(4): 733-738.

Tsutsui, H. and M. Notaguchi (2017). "The use of grafting to study systemic signaling in plants." Plant and Cell Physiology **58**(8): 1291-1301.

Tukey, H. (1978). "Dwarfing rootstocks for pear." Dwarfed fruit trees. Cornell Univ. Press, Ithaca: 182-189.

Turgeon, R. and S. Wolf (2009). "Phloem transport: cellular pathways and molecular trafficking." Annual review of plant biology **60**: 207-221.

Turlapati, P. V., K.-W. Kim, L. B. Davin and N. G. Lewis (2011). "The laccase multigene family in Arabidopsis thaliana: towards addressing the mystery of their gene function (s)." Planta **233**: 439-470.

Turnbull, C. G., J. P. Booker and H. O. Leyser (2002). "Micrografting techniques for testing long-distance signalling in Arabidopsis." The Plant Journal **32**(2): 255-262.

Tuttle, M. A. and A. R. Gotlieb (1985). "Graft union histology and distribution of tomato ringspot virus in infected McIntosh/Malling Merton 106 apple trees." Phytopathology **75**(3): 347-351.

Tutucci, E., N. M. Livingston, R. H. Singer and B. Wu (2018). "Imaging mRNA in vivo, from birth to death." Annual review of biophysics **47**: 85-106.

Van der Auwera, G. A. and B. D. O'Connor (2020). Genomics in the cloud: using Docker, GATK, and WDL in Terra, O'Reilly Media.

Vatén, A., J. Dettmer, S. Wu, Y.-D. Stierhof, S. Miyashima, S. R. Yadav, C. J. Roberts, A. Campilho, V. Bulone and R. Lichtenberger (2011). "Callose biosynthesis regulates symplastic trafficking during root development." Developmental cell **21**(6): 1144-1155.

Vaucheret, H. and O. Voinnet (2024). "The plant siRNA landscape." The Plant Cell **36**(2): 246-275.

Velasco-Alvarado, M. d. J., R. Castro-Brindis, A. Castillo-González, E. Avitia-Garcia, J. Sahagun-Castellanos and R. Lobato-Ortiz (2016). "Mineral composition, biomass and fruit yield in grafted tomato (Solanum lycopersicum L.)." Interciencia **41**(10): 703-708.

Velez-Ramirez, A. I., W. van Ieperen, D. Vreugdenhil and F. F. Millenaar (2015). "Continuous-light tolerance in tomato is graft-transferable." Planta **241**: 285-290.

Velkov, N. and G. Pevicharova (2016). "Effects of cucumber grafting on yield and fruit sensory characteristics." Zemdirbyste-Agriculture **103**(4).

Venema, J. H., B. E. Dijk, J. M. Bax, P. R. van Hasselt and J. T. M. Elzenga (2008). "Grafting tomato (Solanum lycopersicum) onto the rootstock of a high-altitude accession of Solanum habrochaites improves suboptimal-temperature tolerance." Environmental and Experimental Botany **63**(1-3): 359-367.

Villocino Jr, S. and M. Quevedo (2015). "Effects of grafting on flowering, fruiting and fruit quality of'Sweet 16'watermelon (Citrullus lanatus Thunb.)." Acta horticulturae(1088): 469-472.

Voiniciuc, C., K. A. Engle, M. Günl, S. Dieluweit, M. H.-W. Schmidt, J.-Y. Yang, K. W. Moremen, D. Mohnen and B. Usadel (2018). "Identification of key enzymes for pectin synthesis in seed mucilage." Plant Physiology **178**(3): 1045-1064.

Voutsela, S., G. Yarsi, S. A. Petropoulos and E. M. Khan (2012). "The effect of grafting of five different rootstocks on plant growth and yield of tomato plants cultivated outdoors and indoors under salinity stress." Afr. J. Agric. Res **7**(41): 5553-5557.

Walker, R. P., Z.-H. Chen and F. Famiani (2021). "Gluconeogenesis in plants: a key interface between organic acid/amino acid/lipid and sugar metabolism." Molecules **26**(17): 5129.

Wang, D., Q. Lu, X. Wang, H. Ling and N. Huang (2023). "Elucidating the role of SlXTH5 in tomato fruit softening." Horticultural Plant Journal **9**(4): 777-788.

Wang, H.-C. and D. A. Hickey (2007). "Rapid divergence of codon usage patterns within the rice genome." BMC evolutionary biology **7**: 1-10.

Wang, K., H. Guo and Y. Yin (2024). "AP2/ERF transcription factors and their functions in Arabidopsis responses to abiotic stresses." Environmental and Experimental Botany: 105763.

Wang, S.-S., Z.-Z. Liu, C. Sun, Q.-H. Shi, Y.-X. Yao, C.-X. You and Y.-J. Hao (2012). "Functional characterization of the apple MhGAI1 gene through ectopic expression and grafting experiments in tomatoes." Journal of plant physiology **169**(3): 303-310.

Wang, T., X. Li, X. Zhang, Q. Wang, W. Liu, X. Lu, S. Gao, Z. Liu, M. Liu and L. Gao (2021). "RNA motifs and modification involve in RNA long-distance transport in plants." Frontiers in Cell and Developmental Biology **9**: 651278.

Wang, X. C., J. Wu, M. L. Guan, C. H. Zhao, P. Geng and Q. Zhao (2020). "Arabidopsis MYB4 plays dual roles in flavonoid biosynthesis." The Plant Journal **101**(3): 637-652.

Wang, Y., Y. Hao, Y. Guo, H. Shou and J. Du (2022). "PagDET2 promotes cambium cell division and xylem differentiation in poplar stem." Frontiers in Plant Science **13**: 923530.

Wang, Y., L. Wang, N. Xing, X. Wu, X. Wu, B. Wang, Z. Lu, P. Xu, Y. Tao and G. Li (2020). "A universal pipeline for mobile mRNA detection and insights into heterografting advantages under chilling stress." Horticulture research **7**.

Warschefsky, E. J., L. L. Klein, M. H. Frank, D. H. Chitwood, J. P. Londo, E. J. von Wettberg and A. J. Miller (2016). "Rootstocks: diversity, domestication, and impacts on shoot phenotypes." Trends in plant science **21**(5): 418-437.

Waterhouse, P. M., M.-B. Wang and T. Lough (2001). "Gene silencing as an adaptive defence against viruses." Nature **411**(6839): 834-842.

Webber, H. J. (1948). "Rootstocks: their character and reactions." The citrus industry **2**: 69-168.

Weis, B. L., E. Schleiff and W. Zerges (2013). "Protein targeting to subcellular organelles via MRNA localization." Biochimica et Biophysica Acta (BBA)-Molecular Cell Research **1833**(2): 260-273.

Wertheim, S. (2000). Rootstocks for European pear: a review. VIII International Symposium on Pear 596.

Wolf, S., W. J. Lucas, C. M. Deom and R. N. Beachy (1989). "Movement protein of tobacco mosaic virus modifies plasmodesmatal size exclusion limit." Science **246**(4928): 377-379.

Woo, H. R., T. A. Dittmer and E. J. Richards (2008). "Three SRA-domain methylcytosine-binding proteins cooperate to maintain global CpG methylation and epigenetic silencing in Arabidopsis." PLoS genetics **4**(8): e1000156.

Wu, F., N. T. Eannetta, Y. Xu and S. D. Tanksley (2009). "A detailed synteny map of the eggplant genome based on conserved ortholog set II (COSII) markers." Theoretical and Applied Genetics **118**: 927-935.

Wu, F., L. A. Mueller, D. Crouzillat, V. Pétiard and S. D. Tanksley (2006). "Combining bioinformatics and phylogenetics to identify large sets of single-

copy orthologous genes (COSII) for comparative, evolutionary and systematic studies: a test case in the euasterid plant clade." Genetics **174**(3): 1407-1420.

Wu, F. and S. D. Tanksley (2010). "Chromosomal evolution in the plant family Solanaceae." BMC genomics **11**: 1-11.

Wu, R., X. Wang, Y. Lin, Y. Ma, G. Liu, X. Yu, S. Zhong and B. Liu (2013). "Inter-species grafting caused extensive and heritable alterations of DNA methylation in Solanaceae plants." PLoS One **8**(4): e61995.

Wutscher, H. K. (1979). "Citrus rootstocks." Horticultural reviews **1**: 237-269.

Wyngaard, S. R. and M. Kissinger (2022). "Tomatoes from the desert: Environmental footprints and sustainability potential in a changing world." Frontiers in Sustainable Food Systems **6**: 994920.

Xia, C., Y. Zheng, J. Huang, X. Zhou, R. Li, M. Zha, S. Wang, Z. Huang, H. Lan and R. Turgeon (2018). "Elucidation of the mechanisms of long-distance mRNA movement in a Nicotiana benthamiana/tomato heterograft system." Plant physiology **177**(2): 745-758.

Xiao, R., C. Zhang, X. Guo, H. Li and H. Lu (2021). "MYB transcription factors and its regulation in secondary cell wall formation and lignin biosynthesis during xylem development." International Journal of Molecular Sciences **22**(7): 3560.

Xiao, Z., X. Zhang, D. J. Gregg and J. N. Saddler (2004). Effects of sugar inhibition on cellulases and β-glucosidase during enzymatic hydrolysis of softwood substrates. Proceedings of the twenty-fifth symposium on biotechnology for fuels and chemicals held May 4–7, 2003, in Breckenridge, CO, Springer.

Xiong, M., C. Liu, L. Guo, J. Wang, X. Wu, L. Li, Z. Bie and Y. Huang (2021). "Compatibility evaluation and anatomical observation of melon grafted onto eight Cucurbitaceae species." Frontiers in Plant Science **12**: 762889.

Xoconostle-Cázares, B., Y. Xiang, R. Ruiz-Medrano, H.-L. Wang, J. Monzer, B.-C. Yoo, K. McFarland, V. R. Franceschi and W. J. Lucas (1999). "Plant paralog to viral movement protein that potentiates transport of mRNA into the phloem." Science **283**(5398): 94-98.

Xu, Y., S.-r. Guo, H. Li, H.-z. Sun, N. Lu, S. Shu and J. Sun (2017). "Resistance of cucumber grafting rootstock pumpkin cultivars to chilling and salinity stresses." Horticultural Science & Technology **35**(2): 220-231.

Xu, Y., A. Szekely, S. Ostendorp, S. Gupta, M. Tomkins, L. Yang, F. Apelt, Y. Zhao, E. Mavrothalassiti and L. Wansing (2024). "Systemic mRNA transport depends on m5C methylation, nuclear mRNA export factors and developmental phase changes." bioRxiv: 2024.2005. 2030.596576.

Xue, C., Y. Zhao and L. Li (2020). "Advances in RNA cytosine-5 methylation: detection, regulatory mechanisms, biological functions and links to cancer." Biomarker Research **8**: 1-13.

Yadav, V., Z. Wang, C. Wei, A. Amo, B. Ahmed, X. Yang and X. Zhang (2020). "Phenylpropanoid pathway engineering: An emerging approach towards plant defense." Pathogens **9**(4): 312.

Yan, Y. and B.-K. Ham (2022). "The mobile small RNAs: Important messengers for long-distance communication in plants." Frontiers in Plant Science **13**: 928729.

Yang, L., Y. Chen, X. Liu, S. Zhang and Q. Han (2023). "Genome-wide identification and expression analysis of xyloglucan endotransglucosylase/hydrolase genes family in Salicaceae during grafting." BMC genomics **24**(1): 676.

Yang, L., F. Machin, S. Wang, E. Saplaoura and F. Kragler (2023). "Heritable transgene-free genome editing in plants by grafting of wild-type shoots to transgenic donor rootstocks." Nature Biotechnology: 1-10.

Yang, L., V. Perrera, E. Saplaoura, F. Apelt, M. Bahin, A. Kramdi, J. Olas, B. Mueller-Roeber, E. Sokolowska and W. Zhang (2019). "m5C methylation guides systemic transport of messenger RNA over graft junctions in plants." Current Biology **29**(15): 2465-2476. e2465.

Yang, X., R. Sanchez, H. Kundariya, T. Maher, I. Dopp, R. Schwegel, K. Virdi, M. J. Axtell and S. A. Mackenzie (2020). "Segregation of an MSH1 RNAi transgene produces heritable non-genetic memory in association with methylome reprogramming." Nature Communications **11**(1): 2214.

Yang, Y., L. Mao, Y. Jittayasothorn, Y. Kang, C. Jiao, Z. Fei and G.-Y. Zhong (2015). "Messenger RNA exchange between scions and rootstocks in grafted grapevines." BMC Plant Biology **15**(1): 1-14.

Yin, L., W. Zhao, C. Shu, X. Li, J. Fan and S. Wang (2014). Role of protective enzymes in tomato rootstocks to resist root knot nematodes. I International Symposium on Vegetable Grafting 1086.

Yip Delormel, T. and M. Boudsocq (2019). "Properties and functions of calcium-dependent protein kinases and their relatives in Arabidopsis thaliana." New Phytologist **224**(2): 585-604.

Yokotani, N., R. Nakano, S. Imanishi, M. Nagata, A. Inaba and Y. Kubo (2009). "Ripening-associated ethylene biosynthesis in tomato fruit is autocatalytically and developmentally regulated." Journal of experimental botany **60**(12): 3433-3442.

Yoo, B.-C., F. Kragler, E. Varkonyi-Gasic, V. Haywood, S. Archer-Evans, Y. M. Lee, T. J. Lough and W. J. Lucas (2004). "A systemic small RNA signaling system in plants." The Plant Cell **16**(8): 1979-2000.

Žanić, K., G. Vuletin Selak and S. Goreta Ban (2018). "
Bemisia tabaci MED population density as affected by rootstock-modified leaf anatomy and amino acid profiles in hydroponically grown tomato." Frontiers in plant science **9**: 319970.

Zeevaart, J. A. (2006). "Florigen coming of age after 70 years." The Plant Cell **18**(8): 1783-1789.

Zemach, A., M. Y. Kim, P.-H. Hsieh, D. Coleman-Derr, L. Eshed-Williams, K. Thao, S. L. Harmer and D. Zilberman (2013). "The Arabidopsis nucleosome remodeler DDM1 allows DNA methyltransferases to access H1-containing heterochromatin." Cell **153**(1): 193-205.

Zhai, J., D.-H. Jeong, E. De Paoli, S. Park, B. D. Rosen, Y. Li, A. J. González, Z. Yan, S. L. Kitto and M. A. Grusak (2011). "MicroRNAs as master regulators of the plant NB-LRR defense gene family via the production of phased, trans-acting siRNAs." Genes & development **25**(23): 2540-2553.

Zhan, J. and B. C. Meyers (2023). "Plant small RNAs: their biogenesis, regulatory roles, and functions." Annual Review of Plant Biology **74**(1): 21-51.

Zhang, A., K. Matsuoka, A. Kareem, M. Robert, P. Roszak, B. Blob, A. Bisht, L. De Veylder, C. Voiniciuc and M. Asahina (2022). "Cell-wall damage activates DOF transcription factors to promote wound healing and tissue regeneration in Arabidopsis thaliana." Current Biology **32**(9): 1883-1894. e1887.

Zhang, B., W. Li, J. Zhang, L. Wang and J. Wu (2019). "Roles of small RNAs in virus-plant interactions." Viruses **11**(9): 827.

Zhang, G. and H. Guo (2019). "Effects of tomato and potato heterografting on photosynthesis, quality and yield of grafted parents." Horticulture, Environment, and Biotechnology **60**: 9-18.

Zhang, G., F. Zhao, L. Chen, Y. Pan, L. Sun, N. Bao, T. Zhang, C.-X. Cui, Z. Qiu and Y. Zhang (2019). "Jasmonate-mediated wound signalling promotes plant regeneration." Nature plants **5**(5): 491-497.

Zhang, H., Z. Lang and J.-K. Zhu (2018). "Dynamics and function of DNA methylation in plants." Nature reviews Molecular cell biology **19**(8): 489-506.

Zhang, S., L. Sun and F. Kragler (2009). "The phloem-delivered RNA pool contains small noncoding RNAs and interferes with translation." Plant physiology **150**(1): 378-387.

Zhang, S., J. Yang, H. Li, V. L. Chiang and Y. Fu (2021). "Cooperative regulation of flavonoid and lignin biosynthesis in plants." Critical Reviews in Plant Sciences **40**(2): 109-126.

Zhang, W., L. Kang, M. Yang, Y. Zhou, J. Wang, Z. Liu and S. Yuan (2016). "Purification, characterization and function analysis of an extracellular β-glucosidase from elongating stipe cell walls in Coprinopsis cinerea." FEMS Microbiology Letters **363**(9): fnw078.

Zhang, W., G. Kollwig, E. Stecyk, F. Apelt, R. Dirks and F. Kragler (2014). "Graft-transmissible movement of inverted-repeat-induced si RNA signals into flowers." The Plant Journal **80**(1): 106-121.

Zhang, W., C. J. Thieme, G. Kollwig, F. Apelt, L. Yang, N. Winter, N. Andresen, D. Walther and F. Kragler (2016). "tRNA-related sequences trigger systemic mRNA transport in plants." The Plant Cell **28**(6): 1237-1249.

Zhang, W. J., Y. Zhou, Y. Zhang, Y. H. Su and T. Xu (2023). "Protein phosphorylation: A molecular switch in plant signaling." Cell Reports **42**(7).

Zhang, X., Y. Liu, A. Ayaz, H. Zhao and S. Lü (2022). "The plant fatty acyl reductases." International Journal of Molecular Sciences **23**(24): 16156.

Zhang, Y. Y., M. Fischer, V. Colot and O. Bossdorf (2013). "Epigenetic variation creates potential for evolution of plant phenotypic plasticity." New Phytologist **197**(1): 314-322.

Zhang, Z., B. Cao, N. Li, Z. Chen and K. Xu (2019). "Comparative transcriptome analysis of the regulation of ABA signaling genes in different rootstock grafted tomato seedlings under drought stress." Environmental and Experimental Botany **166**: 103814.

Zhang, Z., Y. Zheng, B.-K. Ham, J. Chen, A. Yoshida, L. V. Kochian, Z. Fei and W. J. Lucas (2016). "Vascular-mediated signalling involved in early phosphate stress response in plants." Nature Plants **2**(4): 1-9.

Zhao, M., B. C. Meyers, C. Cai, W. Xu and J. Ma (2015). "Evolutionary patterns and coevolutionary consequences of MIRNA genes and microRNA targets triggered by multiple mechanisms of genomic duplications in soybean." The Plant Cell **27**(3): 546-562.

Zhao, P., Q. Li, J. Li, L. Wang and Z. Ren (2014). "Genome-wide identification and characterization of R2R3MYB family in Solanum lycopersicum." Molecular Genetics and Genomics **289**: 1183-1207.

Zhen, A., Z. Bie, Y. Huang, Z. Liu and B. Lei (2011). "Effects of salt-tolerant rootstock grafting on ultrastructure, photosynthetic capacity, and H 2 O 2-scavenging system in chloroplasts of cucumber seedlings under NaCl stress." Acta Physiologiae Plantarum **33**: 2311-2319.

Zhen, A., Z. Liu, B. Lei, Q. Kong, Z. Bie, Y. Huang and L. Chen (2014). Effects of ISO-osmotic NA+, Cl-and NACL stress on the plant growth and physiological parameters of grafted cucumber. I International Symposium on Vegetable Grafting 1086.

Zhong, X., A. J. Archual, A. A. Amin and B. Ding (2008). "A Genomic Map of Viroid RNA Motifs Critical for Replication and Systemic Trafficking." The Plant Cell **20**(1): 35-47.

Zhong, X., X. Tao, J. Stombaugh, N. Leontis and B. Ding (2007). "Tertiary structure and function of an RNA motif required for plant vascular entry to initiate systemic trafficking." The EMBO Journal **26**(16): 3836-3846.

Zhou, X., Y. Wu, S. Chen, Y. Chen, W. Zhang, X. Sun and Y. Zhao (2014). "Using Cucurbita rootstocks to reduce fusarium wilt incidence and increase fruit yield and carotenoid content in oriental melons." HortScience **49**(11): 1365-1369.

Zhou, X. n., Y. Zheng, Z. Cai, X. Wang, Y. Liu, A. Yu, X. Chen, J. Liu, Y. Zhang and A. Wang (2021). "Identification and functional analysis of tomato TPR gene family." International Journal of Molecular Sciences **22**(2): 758.

Zilberman, D., M. Gehring, R. K. Tran, T. Ballinger and S. Henikoff (2007). "Genome-wide analysis of Arabidopsis thaliana DNA methylation uncovers an interdependence between methylation and transcription." Nature genetics **39**(1): 61-69.

Zink, F. and W. Gubler (1985). "Inheritance of resistance in muskmelon to Fusarium wilt." Journal of the American Society for Horticultural Science **110**(5): 600-604.

Zink, F. and C. Thomas (1990). "Genetics of resistance to Fusarium oxysporum f. sp. melonis races 0, 1, and 2 in muskmelon line MR-1." Phytopathology **80**(11): 1230-1232.