

From branch to forest to globe.

How do tree strategies regarding wood growth and turnover affect forest responses to increased carbon dioxide levels?

By

Klaske van Wijngaarden (BSc, MSc)

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Birmingham Institute of Forest Research

School of Geography

University of Birmingham

&

Hawkesbury Institute for the Environment

Western Sydney University

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Statement of Authentication

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I hereby declare that I have not submitted this material, either in full or in part, for a degree at this or any other institution.

This thesis is submitted towards the completion of a Dual Award Higher Degree Research program offered jointly and examined by both the institutions, Western Sydney University and the University of Birmingham.

A handwritten signature in blue ink, consisting of a stylized, cursive script that is difficult to decipher. The signature is written in a fluid, continuous stroke.

Statement of Contributions

Chapter 2

Klaske van Wijngaarden developed the experimental design; performed data collection, analysis and interpretation; wrote chapter; all under guidance of supervisory panel. Kim Calders provided input on scan position pattern and steps to process point clouds. Peter Miles, Kris Hart, Andrea Rabbai, Manon Rumeau, Lisa Degenhardt and 5 student volunteers contributed to data collection on selected field days.

Chapter 3

Klaske van Wijngaarden developed the experimental design; performed data collection, analysis and interpretation; wrote chapter; all under guidance of supervisory panel. Peter Miles, Kris Hart, Andrea Rabbai contributed to data collection on selected field days. Belinda Medlyn provided input for analytical validation for probability simulation.

Chapter 4

Klaske van Wijngaarden developed the experimental design; performed data collection, analysis and interpretation; wrote chapter; all under guidance of supervisory panel. Peter Miles, Kris Hart, Andrea Rabbai, Vinod Kumar, Craig McNamara and a casual worker contributed to data collection on selected field days. David Ellsworth provided input bark trap design and Craig Barton assisted in bark trap construction.

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List of abbreviations

aCO₂ = ambient Carbon Dioxide (levels)

AGB = Above-Ground Biomass

C = Carbon

CWD = Coarse Woody Debris

DBH = Diameter at Breast Height

DGMV = Dynamic Global Vegetation Model

eCO₂ = elevated Carbon Dioxide (levels)

FACE = Free Air Carbon Enrichment

FC = Fallen Canopy

GPP = Gross Primary Production

LAI = Leaf Area Index

LMA = Leaf Mass Area

MSA = Multi Station Alignment

NPP = Net Primary Production

QSM = Quantitative Structure Model

TLS = Terrestrial Laser Scanning

Abstract

Forests make a vital contribution to the terrestrial carbon (C) sink, by assimilating more C from the atmosphere than is respired back, utilising the available C in both short-lived and long-lived biomass. The role of rising CO₂ levels in the atmosphere for the Earth's radiative balance and climate change has intensified research into the long-term stability of the forest C sink. While CO₂ fertilisation enhances growth in young trees, it is also hypothesised to accelerate tree mortality, with canopy dieback and subsequent branchfall acting as precursors as stand age advances. To improve understanding of the role of smaller woody material (branches, barks and twigs) in these dynamics, this thesis examines the effects of elevated carbon dioxide (eCO₂) levels on wood distribution within the canopy of mature oak-dominated woodland. It compares woody turnover, defined as the fraction of total woody biomass in the canopy lost through branch and twig litterfall over time, in two mature forests exposed to eCO₂. This research was conducted across oak woodland and phosphorus-limited eucalypt forests using terrestrial laser scanning (TLS), allometric scaling, transect intercept sampling, and traps to measure litterfall. The oak woodland and the eucalypt forests were exposed to eCO₂ in Free Air Carbon Enrichment (FACE) facilities, running for four and ten years, respectively.

Chapter 2 explores the impact of eCO₂ on the distribution of branch biomass within the canopy of oak (*Quercus robur*) trees of the BIFoR Free-Air Carbon Dioxide Enrichment (FACE) Experiment in the United Kingdom. It was hypothesised that alleviating C limitation on growth would present itself in increased light foraging. The branch biomass in the canopy was quantified by a single time point Terrestrial Laser Scanning campaign at the start of 2022. Results indicate a significant increase in upper canopy volume, branch volume, and fine branch density in the upper canopy in response to four years of eCO₂ exposure preceding these measurements. This supports the hypothesis that additional C availability, resulting from recently published photosynthetic enhancement, is partly directed towards further optimising light capture by trees. This chapter underscores the importance of considering small woody material in predicting mature forest responses to changing atmospheric conditions. Chapter 3 delves into branch and twig litterfall dynamics in an oak-dominated forest under eCO₂. The expectation was that the branch and twig litterfall would increase with previously published observations in increased stem growth and observed branch density in Chapter 2.

Despite an observed increase in leaf litterfall, there was no increase in twig, small and larger branchfall evident. Using the branchfall observation to calculate the percentage of branch biomass in the canopy lost over time also showed no significant enhancement in woody turnover after four years of treatment. This finding highlights the complex dynamics of forest ecosystems and the need for ongoing research into woody material turnover after longer exposure to eCO₂. Chapter 4 examines branchfall and litterfall in two mature forest stands exposed to eCO₂, which exhibit diverse responses of stem growth to eCO₂ treatment. It was theorised that the mature forests would be in a steady state and branch turnover would follow previously observed or not observed growth response to eCO₂. In addition, the eCO₂ response of understory and dominant species wood turnover was expected to differ due to varying growth-mortality trade-offs. Moreover, effect size was expected to scale with exposure time, with eCO₂ effect size most prominent in small-sized branch turnover. Branchfall at BIFoR was monitored over 12 months between 2022 and 2023 and was compared to observations on branchfall in the eucalyptus FACE (EucFACE) experiment in Australia between 2023 and 2024. Contrary to expectations, increased branch or twig litter fall was not observed in the oak forest despite increased stem growth under eCO₂. In contrast, the eucalypt forest exhibited positive effect sizes for branch and litterfall across multiple size classes under eCO₂ despite the lack of a treatment effect on stem growth. This did not disprove the hypothesis that the effects of eCO₂ on wood turnover may be more pronounced over longer exposure periods.

Overall, this thesis reveals complex responses of mature forests to eCO₂, with implications for understanding forest dynamics, future carbon sequestration, and the potential for increased carbon capture through light foraging strategies. The findings suggest for the two experimental forest sites examined that increases in wood biomass due to eCO₂ do not directly translate into increased woody turnover or that such effects may be delayed longer than the ~5-10-year duration of these experiments. However, in one of the two studies (EucFACE in Australia), woody turnover increased even though stem biomass increase had not occurred after ~10 years of eCO₂ exposure. A notable finding was that branches larger than 3 cm in diameter constituted a sizeable proportion of total turnover production under eCO₂ and ambient conditions, particularly in the eucalyptus Forest. Branches this size are rarely quantified and constitute a ‘blind spot’ in most forest ecosystem experiments. Taken together, the results of this thesis point to a significant role of wood growth and woody turnover of the smallest size classes in the responses of mature forest ecosystems to elevated CO₂ levels. This emphasises the need to reassess predictions of carbon sequestration benefits of forests under future climate scenarios.

Chapter 1

General Introduction

1.1 Background

Human emissions have substantially increased the rise of CO₂ concentrations in the atmosphere. Efforts to understand the carbon (C) cycle in terrestrial vegetation have accordingly increased, as have attempts to identify how the capacity of plants to assimilate C from the atmosphere during photosynthesis and subsequent usage in biomass might change considering these rising CO₂ levels. Respiration by plants and other organisms that use their biomass as an energy source returns CO₂ into the atmosphere. Currently, the global balance of photosynthesis, where plants absorb CO₂, exceeds that of respiration, where CO₂ is emitted, resulting in a net carbon sink. The size of this terrestrial C sink is quantified annually through the Global Carbon Budget synthesis and was estimated to be $3.5 \pm 0.9 \text{ GtC yr}^{-1}$ in 2021, which is a large portion of the $10.1 \pm 0.5 \text{ GtC yr}^{-1}$ in fossil fuel emissions predicted in the same year (Friedlingstein et al., 2022).

Dynamic global vegetation models (DGVMs) calculate the size of the land carbon sink and its geographical distribution across the world's biomes. Utilising a process-based approach, these models employ mathematical interpretations of various biological system processes to capture the essential dynamics of these systems and use observations to initialise and validate the outcomes (Sitch et al., 2015; Li et al., 2022). Despite uncertainties in the magnitude of elevated CO₂ (eCO₂) impact on the global terrestrial ecosystems, studies show that on a plant level, responses to eCO₂ include increased photosynthesis and reduced stomatal conductivity. In turn, this has caused increased C assimilation, lessened water loss through evaporation, increased C availability, and reduced water usage needs (Ainsworth & Long, 2005; Pritchard et al., 1999). This is called the CO₂-fertilization effect (CFE), which can also generate a positive feedback loop when the increased C available is directed to more metabolic tissues, further optimising growth conditions and C assimilation (Walker et al., 2019). On average, plant leaf area increase under is 24% under eCO₂, with young trees showing a 14% increase (Pritchard et al., 1999).

DGVMs bring forth estimates that CO₂-fertilization occurs in forests, but whether the effect will occur globally, persist over time, and what the magnitude of the effect will be in mature trees remains uncertain. This is a notable knowledge gap, as mature and old-growth forests are

particularly interesting for long-term sequestration in the terrestrial C sink (Wijas et al., 2024). The difference between C-rich compounds that trees capture during photosynthesis (Gross primary production, GPP) and the fraction that is respired back into the atmosphere by trees (Net Primary Production, NPP) can be directed into short-lived biomass pools (leaves, fine roots, or exudates) or used to build long-lived biomass pools (stem, branches, coarse roots). Longer residence times delay the return of C to the atmosphere through decomposition and therefore long-lived biomass compartments can lock C in ecosystems for centuries to come. Yet, it remains unclear if the CO₂-fertilisation effect occurs in mature forests or if the increased NPP_{wood} under increasing CO₂ concentrations occurs in woody compartments of all sizes. In DGVMs, these compartments are often pooled together in the same NPP flux of how much is added to the accumulated biomass already present (standing crop) and given a constant residence time in the canopy (Yu et al., 2023). Field experiment data is used to underpin the calculation of NPP, however, show the limitation of this generalisation. As branches are a more dynamic tree component that is shed at more regular intervals compared to stem compartments yet are less dynamic than leaves or reproductive tissues. While at least some of the additional C available with rising CO₂ levels is estimated to be used for increased woody NPP (Walker et al., 2019), it could be followed by faster lifecycle completion, increasing tree mortality and subsequently advancing the pace at which C returned into the atmosphere (Brienen et al., 2020; Green & Keenan, 2022; Körner, 2017). The CFE response of branches and fine woody tissue in both productivity and mortality in mature forests remains unknown.

Despite these gaps in knowledge, policymakers consider the (continued) existence of the forest C sink when creating government mitigation strategies to counteract the negative impact of CO₂ emissions and other greenhouse gases, as agreed under the Paris Agreement (2015). We must increase our understanding of CO₂ fertilisation in forests and its influence on C-sequestration across different stand ages, dominant species, and climate zones.

The following section presents a basic introduction to tree growth under eCO₂, followed by a general review of the current knowledge on mature forest responses to increased CO₂ levels in terms of growth and mortality.

1.2 Literature review

1.2.1 Growth trade-offs for tree form and function

The allocation of C, obtained from photosynthesis and not lost through respiration, towards NPP_{wood} instead of NPP_{leaf} , NPP_{root} or $NPP_{\text{reproductive tissues}}$ represent a strategic trade-off influenced by the current environmental context and past evolutionary pressures. Within allocation towards NPP_{wood} , another trade-off exists between increasing tree height or trunk diameter growth. This trade-off may be driven by the need for plumbing to transfer photosynthate throughout the plant (phloem) and to get soil water and nutrients to the site of photosynthesis (xylem). In the case of source limitation of light, investing in smaller branches to support optimal leaf distribution in the canopy is prioritised (Arseniou et al., 2021) while investing in branch diameter growth to support mechanical resilience to internal stress (gravity) or external stress (drag force caused by wind) will support overall fitness (King & Loucks, 1978). The study of tree growth in terms of form and function has a central focus in plant science, leading to the development of various models describing tree allometry. Allometry can be defined as the study of relationship between size and attributes in living organisms. These models all provide a framework for understanding how trees allocation biomass across different structural components but differ in their underlying assumptions and methodological approaches.

In the 1500s, Leonardo da Vinci what is now known as the area preservation rule, described how each generation of the branch will, summed up with their sibling branches, keep the same area as the previous generation. This early principle of tree structure laid the groundwork for later models of tree allometry; however, it has also been contested by models that propose alternative scaling relationships, differing in their underlying physical and geometrical assumptions. The Pipe Model Theory (PMT) refers to a similar assumption about preservation; a unit number of leaves is associated with a downward continuation of non-photosynthetic tissue at a constant cross-sectional area (Shinozaki et al., 1964 via McCulloh & Sperry, 2005). The PMT framework aimed to establish what determines tree form and which rules drive biomass allocation to the foliar versus stem compartments in plants (Lehnebach et al., 2018). The general model for organism structure by West, Brown, and Enquist (1997) (WBE) encapsulates compelling evidence that quarter-power scaling laws arising from network geometry may underpin hydraulic architecture in plants. In contrast, the importance of the trade-off with mechanical strength is hitherto understudied. Research that has scrutinised the topic (Coomes, 2006), has focused mainly on the significant simplifications the authors made

to support these scaling aspects. Conduit tapering references the vascular tissue in trees that, according to the WBE model, will grow narrower with length so that the three may compensate for increased length, thus keeping hydraulic resistance from faulting. King & Louks (1978) made a case focussing on ecological strategy. They use the costs of mechanical strength needed for tree support to explore optimal tree form design. Landing on $3/2$ power laws for branch diameters meant no change in shape as trees got bigger. The hydraulic mechanism of cohesion-tension theory explaining water ascent is now widely accepted. Fractal dimension can be used to estimate the area of the crown's volume and to understand the performance of the trees. McCulloh and Sperry (2005) looked at multiple structure patterns relating to tree (hydraulic) architecture to evaluate WBE theory and surface preservation (Da Vinci's rule) and confirm the robustness of theories like the PMT model.

Debate continues regarding the best way to capture the key components of tree form and constrain allocation models within the wood C pool, as intricate trade-offs driven by fitness considerations influence the distribution of C among the various wood compartments. Collectively these studies underline the challenges researchers have faced in understanding and predicting tree form and projected tree growth patterns up to the smallest size of branches, and ultimately still face in present efforts to constrain models that inform on the difference between the absorption of the increasingly available C into different tissues and total retention of C in global ecosystems (e.g. Net Ecosystem Productivity, NEP). During this ongoing debate, incorporating field experiments and in situ observations remains a key component in increasing accuracy in the C budget modelling process (Norby et al., 2011; Medlyn et al., 2015).

1.2.2 Vegetation growth response to eCO₂

Determining if the NEP is a net C increase or net loss depends on the balance of two major fluxes; inputs gained from the photosynthesis and subsequent growth of vegetation and outputs through a variety of different process, i.e. autotrophic respiration or litterfall decomposition and subsequent CO₂ release. To study the impact of rising CO₂ concentrations on vegetation growth and the CO₂-fertilisation effect in particular, several experimental approaches have been used. These approaches range from individual plants treated with eCO₂ in controlled environments, such as growth chambers and whole tree chambers (Ainsworth & Long, 2005; Pritchard et al., 1999), to complete stands or ecosystem plots in natural, open-air conditions. Collectively the investigations using individual plants, grown in controlled, small-scale environments provide well documented evidence of higher rates of photosynthesis, during which the higher eCO₂ concentration also increase binding of CO₂ to the enzyme RuBisCO in

favour to O₂ for the same amount of energy derived from the sunlight, resulting in increased light-use-efficiency (Drake et al., 1997, Ainsworth & Long, 2005). When looking at woody plants, the benefits of increased photosynthesis rate, productivity and improved water status are in line with earlier meta-analysis, however, the papers included in the review a < 1 year exposure time median and tend to be young saplings still in exponential growth phase (Mndele et al., 2020). Another indirect effect of eCO₂ is reducing stomatal conductance and improve water use efficiency. The increased CO₂ availability in the environment makes that stomata on the leaf surfaces need to stay open for a shorter period to take up the same amount of C during carboxylation, reducing the time water evaporates and O₂ is emitted during the photosynthesis progress (photorespiration). This leads to increasing water-use-efficiency with a higher total C uptake per water vapor lost.

The response of plants to an increasing supply of CO₂ is also modified by the availability of other resources, i.e. nutrient limitations, soil water availability and light. Common nutrient limitations in terrestrial ecosystems are Nitrogen (N) (Reich et al., 2006) (and to a lesser extent Phosphorus (P) (Ellsworth et al., 2017), which are essential in supporting photosynthesis and other mechanisms, but not always available in enough quantities to sustain growth processes. Some simulations suggest that forest growth under eCO₂ will outpace the soil nutrient supply and therefor reduce the CFE back to baseline (Fenzi et al., 2008). DMVG models predict a decline in CFE, but when compared to long-term satellite data, they underestimate the magnitude of the decline in CO₂ uptake response to a 100-ppm CO₂ increase. Partly due to inaccurately incorporating progressive nutrient limitations and sensitivity to water availability (Wang et al., 2020). Ultimately impact of eCO₂ with nutrient limitation of growth varies between species, across timescales and is best researched in a field experiment where all these factors and prolonged exposure come into play.

Investigation into the interaction of eCO₂ with other growth limiting factors on the input flux such as light limitation has been mostly restricted to controlled environments experiments. Photosynthesis is ultimately driven by light and the interplay of light intensity and eCO₂ in controlled environments has been done in agricultural experimental studies, where in hop the leaves in sub-optimal light conditions showed the highest benefit (up to 18% enhanced carbon gain) from short-term eCO₂ exposure treatments compared to net photosynthesis in light saturated leaves under eCO₂ (Bauerle 2021). Shaded conditions showing more pronounced eCO₂ treatment effects on growth, as plant can utilise CO₂ more efficiently under low light conditions (Körner 2004). In the case of light limitation in trees, shading due to understory-

overstory competition or obstruction for canopy expansion due to reaching canopies of neighbouring trees be expected. While controlled environments have offered valuable insights, there are unanswered questions due to their limited capacity to capture the complex interactions of increased CO₂ supply with multiple processes and impacting each other at the same time. Experimental field measurements that can observe eCO₂ impact on tree growth and interactions with nutrient, light resource or space competition on the ecosystem level.

1.2.3 Field experiments to capture tree and forest growth response to eCO₂.

Free Air Carbon dioxide Enrichment (FACE) experiments were built to research the impact of eCO₂ at the ecosystem level and have been applied to complete forest stands in several studies (Norby & Zak, 2011). The earliest iterations of these large-scale *in situ* research sites, referred to as first-generation, have shown that the strength and persistence of the CFE on C input flux fraction of NEP are varied in terms of exposure duration (Lichter et al., 2008; Palmroth et al., 2024), vegetation type (Ainsworth & Long, 2005), geographic location and environment (McGrath & Lobell, 2013). More recent studies also show this varied CFE outcome in forests, with C input not always followed by sustained productivity increase. At ORNL FACE, a young even aged sweet gum plantation, canopy structure did not show an enhancement of canopy structure change, or tree stand development. But within-canopy distribution of LMA (leaf mass per area), leaf thickness, and leaf density were, although non-significantly, weakly increased throughout the canopy vertical profile (Norby et al., 2022). After 4 years of eCO₂ exposure at WEB-FACE the C assimilation was found enhanced over time but showed no increase in stem growth, leaving a clear gap in evidence as to where this additional C goes (Klein et al., 2016). The first-generation FACE experiments were conducted in younger mesic-temperate forests, causing the eCO₂ impact on mature, boreal and dryland forests to remain unexplored, while it is these forests are particularly important for long-term C storage. Due to the large standing crop, along with increasing amounts of deadwood on the forest floor (Burrascano et al., 2013)

The large variation in tree responses in first generation FACE experiments that were collected and analysed (Ainsworth & Long, 2005) did provide opportunity to directly inform the second-generation FACE facilities. These are designed to tackle the evidence gap on the missing C flux, by increasing the biogeographic coverage of FACE experiments as a group, particularly applied to forests (Norby et al., 2016). And by researching forest ecosystems that are presumed to be in a quasi-steady state, with older trees, by making this generalised assumption on balanced growth-mortality responses over time, the individual C fluxes can be disentangled

from the exponential growth phase responses that first generation FACE experiments encounter. Investigating the impact of eCO₂ on forest ecosystems remains, of course, challenging. Trees, especially mature ones that have accumulated a lot of biomass over time, have a large stature and branches are not always easily accessible. Additionally, tree life cycles can span multiple human generations, and it is well known that the productivity and carbon balance of forests change systematically as the stand develops (Hyvönen et al., 2007). With the 2nd generation FACE experiments, more developed stands can be researched, focusing on mature woodlands instead of young plantation forests.

Currently, three mature forest FACE experiments run globally. Hawkesbury Institute for the Environment's EucFACE is in the Southern Hemisphere and has the longest running time. It has exposed a mature native Australian eucalyptus forest to eCO₂ since 2012. The Birmingham Institute for Forest Research (BIFoR)'s FACE experiment is in a mature temperate broadleaf woodland and has been fumigating since 2017. English oak (*Quercus robur*) dominates the mixed-broadleaf woodland and is representative of a large portion of the forested area in the Northern Hemisphere. The most recently built second-generation FACE experiment is Amazon FACE, situated in the highly diverse Amazon rainforest in Brazil, South America. The experiment has started with pre-treatment measurements in 2022. EucFACE has been running for over ten years, with BIFoR FACE and AmazonFACE aiming to reach at least the same exposure times to capture as much of the lifespan of the target trees as possible. In the EucFACE eucalyptus forest, a photosynthesis enhancement of 19% was observed. However, this was not reflected in increased tree stem growth in the first four years of CO₂ fumigation (Jiang et al., 2020b). This was due to phosphorus limitation (Crous et al., 2015; Ellsworth et al., 2017). Results from BIFoR FACE have shown a 33% enhancement of Gross Primary Production (GPP) under eCO₂ (Gardner et al., 2022) and recent work has shown evidence of enhanced stem growth (Norby et al., 2024).

1.2.4 Longevity of trees and tree compartments under eCO₂

The second major flux is one determines the output of C in the NEP equation, encompassing vegetation mortality, tissues transitioning from one C pool to another and finally the decomposition of vegetation. Conceptualizing all C output processes to accurately reflect ecosystem-level is challenging due to the variation in how long C in different tissues is held sequestered within the ecosystem. Particularly the stem and branch tissues of trees are essential when projecting NEP for global carbon budgets, as the longevity of the long-lived wood will ultimately drive the long-term C sequestration in forests (Körner, 2017). More accurate data is

still required on woody C, on a more detailed scale than the currently used whole tree mortality, to address uncertainty regarding global carbon budgets (Sierra et al., 2017). Removal of non-photosynthesizing and non-reproductive tissue from the canopy can be part of the tree's function in the form of shedding, driven by endogenous processes affecting the rate of senescence and decoration (bark removal). Alternatively, the abscission of branches and twigs can be caused by exogenous disturbances such as wind (Pook et al., 1997), snow, ice, disease (Campbell et al., 2019; Sturtevant et al., 1997), or drought (Choat et al., 2018).

Litterfall is the largest pathway of nutrient transfer between vegetation, microbes and soils (Finzi et al., 2008) and thus an important internal ecosystem flux of C along with other nutrients. Once tissues detach from the canopy structure and arrive at the forest floor, detritivores decompose the tissues as substrate down to organic matter. During decompositions CO_2 is also returned back into the atmosphere as the final C output flux for ecosystem NEP. To investigate the missing C flux under eCO_2 in mature forests effectively, the different mechanisms before the final C output flux back into the atmosphere and their interaction with eCO_2 are important to consider. Understanding how eCO_2 influences the timing and magnitude of internal fluxes through branch and litterfall does not only impact the substrate availability for decomposition but also influences the canopy productivity by photosynthetic capacity. In other words, the branch and litterfall mechanisms that come after the initial C input flux through photosynthesis, but before the last C output flux of decomposition are bi-directional.

Evidence on these mechanisms under eCO_2 , especially on forest stand scale, is limited compared to research done on CFE on productivity. In DGVMs the C output is generally associated with complete tree mortality. Increase in tree mortality can be caused by increased climate variability, such as shifting boundaries for habitable regions, extreme weather events, insect plagues or combination of the above (Brienen et al., 2020). On ecosystem scales the increased productivity under eCO_2 is expected to impact ecosystem C output flux through tree mortality by boosting competition between trees and result in higher tree mortality rates (tree deaths per unit area). The CFE may cause forests to become more dynamic and have faster tree turnover rates (change in trees per unit). This would reduce standing C stock over time if increased tree recruitment (new growth of trees per unit) and mortality of fast growing, early successional stage trees outcompete the late successional stage species. Higher productivity and wood growth in faster growers will not increase long-term C storage (Körner 2004), which shows that accurate turnover rates can predict long-term C sequestration in above-ground biomass (AGB) better than NPP alone (Malhi et al., 2015; Yu et al., 2023).

1.2.5 Challenges in defining and assessing woody turnover in models and field experiments

Turnover time is commonly defined as the ratio of total C stock to input or output flux, with the flux sized fraction of gain or loss being proportional to the C stock, turnover rate reflecting the fraction of total stock being lost or gained per unit of time (Sierra et al., 2017). In DGVMs the parameters of biomass, turnover rate and residence time are used to capture ecosystem growth and mortality dynamics within mathematical approximations. This results in simplifying a very complex systems with multiple pools and fluxes into single pools. For example, by defining woody biomass based on stem biomass and tree mortality rate as woody turnover rate, while stem tissue and branch tissue fluxes differ in both stock and flux size as well as flux rate. This simplification and the use of a constant turnover rate for all woody tissues instead of adding variation in turnover time causes up to 30% of disagreement between model outcomes of predicting C budget (Xue et al., 2017). The use of a single biomass pool and flux rate for what is a more complex dynamic is largely due to the lack of observations available on this dynamic C output. Canopy damage is seen as a precursor of tree death. In tropical forest up to 42% of total AGB loss quantified is loss that happened due to tree damage (Zuleta et al., 2023). Assessment of canopy completeness in the field is challenging, and thus methods for observing the whole tree or partial tree mortality are focussing on the outcome of this process instead of categorizing canopy damage in trees, measuring branchfall and litterfall at the forest floor.

Research on capturing and quantifying the tissues that are lost from the canopy due to lethal and non-lethal canopy damage shows a variety of nomenclature and inclusion thresholds based on sample size and collection methods. Small material lost from the canopy is generally described as litter or litterfall in annual, monthly, or per-day timeframes. Well-established methods for collecting litterfall are litter traps (either square, circular/funnel or rectangle troughs of different sizes) and bark traps, either as squares on the forest floor or attached to the stem (Crockford & Richardson 1998; Pook et al., 1997). Material collected from these traps is often separated into leaves, wood or twigs, reproductive material, bark where relevant and “other”, representing frass, unidentifiable material. Captured woody material is sometimes further separated into different size classes (Crockford & Richardson, 1998).

Larger woody material is referred to as (downed) coarse woody debris or detritus (CWD) (Campbell et al., 2019) or downed dead wood (Russell et al., 2014). CWD inventories are undertaken to estimate total debris population density, which is relevant for biodiversity assessments, and to investigate fuel loads for fire safety, along with volume and subsequent carbon stocks. A review of the most common CWD inventory methods using fixed area transects with varying inclusion protocols determined all three unbiased for volume estimations (Gove & Van Deusen, 2011) although this report focussed on downed logs and not so much on dynamic branchfall. The line-intersect sampling method is more accurate with increasing transect length in mature northeast USA forests (Fraver et al., 2018). There is no universally agreed inclusion length or diameter inclusion threshold, and customisation for CWD inventory is expected if not unavoidable (Woldendorp et al., 2004) depending on the forest type and size, the main objective of inventory and scope of the project, increasing the difficulty of inter-publication comparison. Regardless, branches can make up 40% of total deadwood found on forest floors. It remains necessary to investigate branchfall dynamics, including under eCO₂, to predict the long-term C-sequestration withing forest ecosystems accurately.

Previous studies on eCO₂ impacting tree growth have also reviewed effects on litter production, which have yielded varying results. The results of young potted trees exposed to eCO₂ in open-top chambers show an increase in leaf biomass (Norby et al., 1999). In the WEB-FACE canopy exposure study, there were no significant differences in needle litterfall dynamics between treatments over 5 years (Klein et al., 2016). Diverging outcomes were observed in the DukeFACE experiment within a loblolly pine plantation; initial years showed a significant increase in pine needle and bark litter under eCO₂ treatment, yet the understory broadleaves showed no similar response. A higher branchfall of pine under eCO₂ was also observed, although these treatment effects were not sustained over longer years of exposure (Finzi et al., 2001). Despite a lack of long-term significant differences in litter production after the first six years of CO₂ fumigation, overall litterfall remained higher under eCO₂ (Lichter et al., 2008). An increase in coarse roots and a shift in allocation to wood was observed of the broadleaf species. At the same time, tree mortality decreased (Palmroth et al., 2024).

In mature forests, the ecosystem is presumed to be close to a quasi-equilibrium state (Norby et al., 2016). These forests are expected to be at a certain carrying capacity because environmental and resources impose restrictions on growth and if eCO₂ imposes more gain in biomass through increased assimilation, then increasing resource demands, adjustments through physiology, phenology, competition for nutrients or light and subsequent mortality will tend to move the

system towards the carrying capacity. In other words, over time, biomass turnover through pathways including mortality and litterfall, will balance biomass production, maintaining biomass stock at carrying capacity. Observation on the C input flux in mature forests under eCO₂ from the first-generation FACE experiments were varied, but mainly focussed on leaf level or stem growth, leaving a response in branch compartment un-investigated. In the second-generation FACE experiments of BIFoR FACE and EucFACE, photosynthesis was enhanced (19% and 33%, respectively) (Crous et al., 2015; Ellsworth et al., 2017; Gardner et al., 2022), and so was litterfall of the overstory leaves (Jiang et al., 2020a; Norby et al., 2024) but no measurements for productivity response of branches are available. This also goes for the mortality, or partial canopy mortality that the events of branchfall precedes. The assumption that mature forests are already at their carrying capacity, and thus any biomass gain through stimulated growth under eCO₂ will over time be followed by biomass loss provides opportunity to investigate this currently overlooked compartment in the fluxes that make up NEP. This comes with a set of assumptions and limitations such as if branch biomass (of both live and dead branches, in this case) is constant over time, that branch NPP equals branchfall and that there is no mass loss from dead branches. Branchfall and litter observations can then be used to approximate growth responses that occurred before deposition of the materials took place, and by quantifying different C output fluxes from the canopy (e.g. branchfall and litterfall) in existing forests exposed to eCO₂ in combination with different environmental stressors and competition for resources, is currently the only option we can utilise to reach to goal of C sequestering old-growth forest responses.

Notwithstanding, the largest opportunity that second-generation FACE experiments provide is the ability to gather observations on *in situ* productivity and mortality mechanisms on tree and stand level. The branch and litterfall processes impact both C fluxes, i.e. net increase or decrease in branch growth in support of metabolic tissues, and outward in creating a net higher or lower pool of woody substrate for decomposition. Locating the missing C flux after enhanced C assimilation is discussed in this thesis.

1.3 Thesis overview

1.3.1 Thesis objectives

This PhD thesis aims to detect an eCO₂ treatment effect on branch biomass distribution in a mature forest canopy and quantify the branchfall and litterfall from the canopy, to inform on woody turnover during the measurement period. Woody turnover in this thesis is defined as the fraction transitioning from wood biomass in the canopy (woody AGB pool) to deadwood

on the forest floor over time. Calculated as the sum of branchfall and twig litter fall divided by the size of the total woody AGB pool. Methods employed include Terrestrial Laser Scanning (TLS) for large-scale and detailed observations of canopy structure, Line Intersect Sampling (LIS) for branchfall monitoring and litter traps for quantifying litterfall. The observations were done in two mature forest stands in two second-generation FACE facilities: BIFoR FACE and EucFACE. Both forests are exposed to similar eCO₂ levels (150 ppm above ambient) and receive similar mean annual precipitation. However, the experiments' treatment exposure time, mean annual temperature, soil status, species composition, and canopy density differ (Norby et al., 2016). These differences provide an opportunity to assess whether and how tree growth and wood turnover vary under eCO₂ across different forest ecosystems and whether these responses vary over time. Specifically, this thesis aims to address the following research questions and hypotheses in the corresponding Chapters and by using observations from the following experimental research sites:

- 1) Has four years of eCO₂ treatment impacted the branch biomass distribution in the canopy dominant species? (Chapter 2, BIFoR FACE). The expected outcome is that at least a fraction of the additional C available from photosynthetic enhancement over the first years of fumigation has been invested in branch growth as a strategy by the trees and that this will be first detectable in small branch sizes, where tissue has mostly grown under eCO₂ and where support for increase light capture is expected to drive allocation.
- 2) Does eCO₂ treatment effect branchfall, litterfall, and or woody turnover of branch biomass in the canopy? If so, does this change across different branch sizes? (Chapter 3, BIFoR FACE). Tree mortality cannot be accurately assessed at the scale of FACE experiments, yet increased growth rate under eCO₂ is expected to negatively impact tree longevity. The mature forest is assumed to be in a quasi-steady state, where the ecosystem is at a carrying capacity. This thesis therefor assumes that loss of branch biomass from the canopy is a precursor to mortality and indicative of growth that happened in the past. If increased growth of small sized branch under eCO₂ was detected through TLS, then enhanced loss of this size compartment under will follow.
- 3) Does wood turnover of total biomass differ between two mature forests exposed to eCO₂ for different lengths of time? Are there differences in branchfall between dominant and understory species, differences throughout the year, and differences across size classes of branch or litter types? (Chapter 4, BIFoR FACE and EucFACE). It was hypothesized that prolonged exposure to eCO₂ would increase either the

magnitude or the branch sizes impacted by CFE on woody turnover, presuming resulting in larger percent of total biomass lost through branchfall at EucFACE 10-year exposure compared to BIFoR FACE's 4 years.

1.3.2 Thesis outline

Chapter 1 presented the general introduction to this PhD thesis.

Chapter 2 aimed to investigate the effect of eCO₂ exposure on fine woody material within the canopy of a mature forest stand of *Quercus robur* trees. Terrestrial laser scanning (TLS) captured the canopy structure at a second-generation Free Air Carbon Enrichment (FACE) facility. The distribution of tree height, canopy projected area, trunk and branch volume, and the density of branches of different size classes within the available canopy volume were assessed. Increased upper canopy volume, wood volume, and fine wood density were found in canopies exposed to 4 years of fumigation with eCO₂. This finding supports the hypothesis that trees with additional carbon available direct at least part of this towards increasing light capture. These results emphasise the need for incorporating observations of fine woody material into future research on the response of mature forest ecosystems to changing climate conditions.

Chapter 3 aimed to demonstrate the impact of eCO₂ on branchfall and woody turnover in a mature oak woodland. Line-transects and litter trap observations were used to determine the annual branchfall and litterfall at an oak-dominated, old-growth forest Free Air Carbon Enrichment experiment in the UK to investigate this. Woody turnover was determined by dividing the fraction of total branch biomass lost over 12 months through branch and litterfall, divided by total branch biomass. Leaf litterfall increased under eCO₂, but not twig litterfall, fine branch, or larger branchfall. The percentage lost in the fine material was ~ 0.5% less under eCO₂ compared to ambient. These chapter findings reveal no significant increase in woody turnover with earlier observed stem radial growth enhancement under eCO₂, underscoring the complexity of forest dynamics. Continuous, focused research on turnover and twig litter is essential for a deeper understanding of woody dynamics in forest ecosystems.

Chapter 4 aimed to investigate woody biomass loss in two mature forest stands treated with eCO₂ and determine if previously observed treatment effect on productivity are followed by similar branchfall and litterfall as expected in an ecosystem that has reaching carrying capacity, and if these are different between canopy positions or eCO₂ exposure times. Standing above ground biomass was captured through terrestrial laser scanning, allometric scaling, branchfall

by line intersect sampling, litterfall through litter baskets and bark shedding funnels monitoring. In the mature oak woodland exposed to eCO₂ for four years, an increase in branch or twig litterfall was not observed despite previously documented increases in woody net primary productivity (NPP). In a phosphorus-limited dry-eucalypt forest, the effects of eCO₂ on the turnover of multiple small branch size classes were noted, even in the absence of prior increases in woody NPP. These findings indicate that the impact of eCO₂ on mature forests may become more pronounced with longer exposure periods and is primarily observable in the smallest size categories of wood.

Chapter 5 synthesises the major findings of this PhD thesis and discusses the interrelations of the three separate experimental chapters. The results of these studies can improve a general understanding of branch biomass distribution and branchfall in current forests and future forests in changing climate conditions. The outcome of this thesis can aid in more accurate parametrisation of models which incorporate wood residence time to estimate global C budgets. The insights gained can provide a resource and baseline for further investigation of branch biomass that grows and branches that fall under eCO₂.

Chapter 2

Wood volume distribution in the canopy of mature *Quercus robur* trees under elevated CO₂

2.1 Introduction

Forests are an important component of the global carbon (C) sink by absorbing more CO₂ from the atmosphere during photosynthesis than is respired back into the atmosphere. The efficacy of this sink faces uncertainties as atmospheric CO₂ concentrations continues to rise (Ciais et al., 2013; Friedlingstein et al., 2022). C-rich compounds captured during photosynthesis (Gross primary production, GPP) can be transported into short-lived pools, or the compounds can be used to build long-lived wood, sequestering the C for the remaining lifespan of the tree. The difference between the C taken up through photosynthesis and that which is respired back into the atmosphere by the plants in an ecosystem is defined as Net Primary Production (NPP). NPP is partitioned among three main components: roots, which absorb minerals and water and transport these to the stem; leaves, which photosynthesise; and wood, which provide mechanical strength, storage, and conduct water and minerals via vessel tissues. The trade-off among these components is crucial for plant survival. It is influenced by past evolutionary pressures and current environmental conditions, including the abundance or limitation of resources like light, water, CO₂, nitrogen, and phosphorus (McNeil et al., 2023).

Human emissions exacerbate the sharp rise of CO₂ levels in the atmosphere and have been found to impact plant productivity via multiple processes. Elevated CO₂ (eCO₂) levels increase photosynthesis and reduce stomatal conductance, increasing the C availability and reducing water use. These leaf-level effects can increase whole plant growth by alleviating C and water limitations and cause secondary changes in plant morphology and biomass allocation (H. Poorter et al., 1997). There can also be positive feedback, whereby increasing leaf growth or optimising canopy morphology increases C uptake. These changes in plant functioning are known as the CO₂-fertilization effect and have been researched in several studies and on average cause a 24% increase in leaf area per plant (Pritchard et al., 1999). Although emerging evidence suggests that this also occurs in forests (Bonan, 2008; Friedlingstein et al., 2022; Quéré et al., 2018), the global fertilisation effect's occurrence, magnitude, and transience remain uncertain.

For instance, evidence suggests the long-term positive impact of the CO₂-fertilisation effect on C-sequestration might be limited in forest stands due to a reduction in tree lifespan associated with the faster growth rates under eCO₂ (Brienen et al., 2020; Green & Keenan, 2022; Körner, 2017). Observations of eCO₂ effects on a stand scale have been researched in Free Air Carbon Enrichment (FACE) experiments. The interaction of atmospheric CO₂ with plant physiology starts in the leaves, and increasing growth can also lead to increased leaf area index (LAI, m² leaf area per m² of ground surface), an important indicator of ecosystem productivity. The hypothesis of an increase in LAI under eCO₂ has been researched in first-generation Free Air Carbon Enrichment (FACE) facilities with closed canopy stands. The responses of LAI ranged from over 40% increase to an 8% decrease under treatment, with the differences in species composition, interannual variability and availability of other resources such as water all playing a role (Norby et al., 1999; Norby & Zak, 2011). More recently, crown and canopy structure were not changed after 12 years of eCO₂ exposure in the young plantation experiment of ORNL FACE.

Observations of wood growth in four forest FACE experiments have shown increased carbon allocation to wood and above-ground dry matter production under eCO₂ in the early phase of the experiments (Norby et al., 2005) but with large intra-site variability. The largest growth response to eCO₂ was seen in trees still in the phase of canopy expansion (Norby & Zak, 2011). At a young sweet-gum plantation at Oak Ridge, the eCO₂-fertilisation effect reduced over time due to increasing nitrogen limitations (Norby et al., 2010). Based on first-generation FACE observations, there is support for increased C-sequestration in wood under eCO₂. However, the magnitude remains uncertain (Walker et al., 2021), especially for trees beyond the first exponential growth phase or at an age where tree or branch biomass longevity changes can be considered.

Whilst the first-generation FACE experiments focussed largely on young plantation stands, the second-generation FACE facility designs provide the opportunity further to research the effects of eCO₂ on mature forest stands. Of these, an experiment in a mature Eucalypt woodland, EucFACE, found that an increase in GPP was not transferred into radial stem growth enhancement due to phosphorus limitation over four years of treatment (Ellsworth et al., 2017b; Jiang et al., 2020b). In an experiment in a mature oak forest, BIFoR FACE, the overstorey oaks had a sustained photosynthesis enhancement for the first three years for the experiment (Gardner et al., 2022). Most recent observations and use of allometric scaling show an increase

in radial stem growth and continued higher LAI, green leaf mass and litter mass under eCO₂ (Norby et al., 2024).

While extensive research on tree growth and LAI improves our understanding of forest growth, significant gaps in knowledge persist. Traditionally, research has predominantly concentrated on the leaves and stems of trees. However, trees comprise various compartments, such as branches and twigs within the canopy, which are frequently neglected due to their challenging study conditions. Additionally, the dynamics of wood in ecosystems extend beyond radial stem growth and single-tree mortality (Green & Keenan, 2022; Körner, 2017). Branches are long-lived components that can sequester carbon but have a shorter lifespan than the whole tree. While NPP and decomposition frame the boundaries of ecosystem C exchange, the woody C fluxes internal to the ecosystem, such as the structural support for metabolic tissues and the branch and litterfall, impact the C balance in both directions. Understanding the distribution and subsequent residence time of C-sequestered in different sized woody tissues under eCO₂ requires accurate measurements of within-canopy wood distribution.

Theories about canopy architecture are often based on mechanical considerations, for example the need for canopy form to counteract intrinsic forces from gravitational pull or external forces from wind throw (King & Loucks, 1978; Zeide, 1993). Other theories suggest that hydraulic transport through the sapwood is the major driver of canopy structure (Shinozaki et al., 1964; via McCulloh & Sperry, 2005). Based on hydraulic flow considerations, West, Brown, and Enquist (1997) generalised both the branching of animal cardiovascular systems and the branching of vascular systems in plants by power-law scaling to body mass and plant size, respectively. The importance of the trade-off with mechanical strength received little attention, causing critiques of the fractal-like model of West, Brown, and Enquist (Coomes, 2006; Petit & Anfodillo, 2009). Nonetheless, the theory of these models is comparable to the self-similar patterns observed in trees to a degree and thus useful in describing the branching patterns.

Allometric scaling, utilising tree diameter at breast height (DBH) or tree height, plays a vital role in measuring forest functionality and is essential for estimating above-ground biomass (AGB) and evaluating forest carbon stocks on a broad scale. However, while these equations are useful for basic scaling, they are less useful for accurately modelling stand growth dynamics or in formulating biomass and leaf area equations that allow for scaling up from individual tree measurements (Forrester et al., 2017). The role of branches within the complete tree biomass distribution has been mentioned in only a limited number of observation-based papers.

Branches are described as the morphological plasticity result of crown optimising for light foraging (Stoll & Schmid, 1998) or mentioned while looking at the first living branch height to determine canopy height (Poorter et al., 2012). Branch biomass research often conducts destructive measurements to determine tree biomass allocation (Calders, Burt, et al., 2015; Garcia Villacorta et al., 2015; Sillett et al., 2015; Uller et al., 2019). These methods have important limitations; destructive research involves time-intensive manual labour, and allometric scaling tends to be inaccurate. Scaling relationships themselves could even change under eCO₂ (Kim et al., 2020), due to the potential growth increase in the key height metrics and DBH (McCarthy et al., 2001) which further adds to the uncertainty of biomass allocation. It can be concluded that researching the within-tree and within-crown biomass distribution in mature trees has been restrained by their size and the inaccessibility of branches.

Terrestrial Laser Scanning (TLS) provides a non-destructive method for gathering large-scale tree data by sending out and registering the returning laser beams to create a point cloud copy of tree structures (Calders et al., 2015). Various software tools, such as TreeQSM and SimpleTree, use the point cloud generated by TLS to fit primitive building blocks, often cylinders, that make up quantitative structure models (QSMs), which subsequently provide ecologically relevant parameters like tree height, branching order and volume of the different canopy structures (Calders et al., 2020; Lau et al., 2019; Malhi et al., 2018; Raunonen et al., 2013). Multiple studies have utilised TLS and subsequently done (destructive) manual measurements post-scanning to determine accuracy (Dassot et al., 2019; Demol et al., 2022; Garcia Villacorta et al., 2015; Sillett et al., 2015; Uller et al., 2019). Moreover, research on tree height, canopy volume or width (Moorthy et al., 2011) or the impact of neighbouring trees on canopy projected area and canopy volume have been made more accessible using TLS (Georgi et al., 2021). However, to the authors knowledge, no research has been done on any within-canopy distribution of branch biomass under the impact of eCO₂ utilising TLS scans.

This chapter aims to leverage TLS data to test whether four years of eCO₂ exposure has initiated differences in branch growth of a mature oak stand. We hypothesise that a CO₂ limitation on growth has been alleviated, and the allocation ratio of biomass has shifted towards capturing more of another limited resource: light. For the canopy-filling oaks in this study, this can only be achieved by filling out the remaining available canopy volume. Given the short duration of the current experiment, we expect this shift to be most noticeable in the smaller wood sizes, which have had the opportunity for new growth in the fumigation timeframe and are supporting previously observed increased leaf tissues.

2.2 Methods

2.2.1. Site description

This research was conducted at the Birmingham Institute of Forest Research (BIFoR) Free Air Carbon Enrichment (FACE) Facility. Located in Staffordshire, United Kingdom (52.801° , - 2.301°) this site consists of mature northern temperate deciduous woodland. Fumigation of the treatment plots with eCO₂ started on the 3rd of April 2017. The daily operating target is an enhancement of 150µmol/mol above the ambient levels at the top of the canopy (Hart et al., 2020). The daily fumigation times are determined by solar elevation. Seasonal downtime starts after the completion of leaf senescence, usually at the end of November, and lasts until the spring flush of the dominant Oak (*Quercus robur*) trees commences. The forest site was planted 180 years ago, and the forest has been largely unmanaged for the last 30-40 years. This study's sample size is n = 3, representing the number of replicate experimental plots per treatment. Nested within each ring are multiple replicate trees. Figure 2-1 shows the location extent of A1 to A6 at the BIFOR FACE Facility. See Hart et al., (2020) for further details on the site.



Figure 2-1 Annotated top view image of the BIFoR FACE facility, showing the locations of the treatment rings (A1, A2, and A5), highlighted in orange, and the ambient control rings (A3, A4, and A6), highlighted in blue.

2.2.2 TLS protocol

Laser scans were done with a RIEGL VZ-400i (RIEGL Laser Measurement Systems GmbH, Horn, Austria) in all six experimental plots. Scans were made in leaf-off conditions between the 23rd of January 2022 and the 26th of February 2022. Scan dates were chosen to be as wind-still as possible, and during scanning days, minimal movement of the upper branches could be observed from the ground. The RIEGL VZ-400i works on a “time-of-flight” basis with an exit beam diameter of 7 mm and a beam divergence of 0.35 mrad, relating to the achieved resolution and extended range of the laser beam. Table 2-1 summarises the plot and scanning days, weather, and wind conditions.

There were eleven scan positions per plot, set up in a circular pattern with 3 around the middle tower, alternating with 4 positions in the centre, and alternating again with 4 locations between or just beyond the towers depending on available forest floor space. Figure A-1 shows the approximate scan positions in relation to plot infrastructure, trees and other research equipment. The pulse repetition rate used was 300 kHz with a 0.04 angular resolution. There were two rounds of scanning (~3 minutes per round) per position: one upright (360-degree panorama) and the one tilted at a 90-degree angle. Each plot took 3-4 hours to scan to completion.

Table 2-1 Date, time of day, and wind conditions measured at the central flux tower and plot infrastructure during scanning.

Plot	Date	Time	Wind speed flux tower	Wind speed plot
A1	11 February 2022	morning	2.10	7.56
A2	26 January 2022	morning	2.66	9.58
A3	26 January 2022	afternoon	2.66	9.58
A4	13 January 2022	afternoon	0.87	3.13
A5	11 February 2022	afternoon	2.10	7.56
A6	25 February 2022	afternoon	3.25	11.70
FC	25 February 2022	morning	3.25	11.70

Wind speed flux tower is the mean wind speed measured at the flux tower on site during the scan period ($m s^{-1}$), and Wind speed plot is the mean of wind speeds measured by four sensors on the top of the BIFoR FACE ($m s^{-1}$). Equipment used: R3-100 by Gill Instruments (Lymington; UK).

TLS scans were pre-processed using the scanner manufacturer's RiSCAN PRO software (version 2.0). Coarse and fine registration, including multi-station adjustment (MSA) 1 and 2, were used, where iterative scans are aligned based on minimising the distance between overlapping detected planar surfaces. In addition, MSA 2 uses information from an inertial measurement unit for more refinement (Demol et al., 2022). Each merged point cloud was filtered by removing points closer than 0.25 m from the scanner, with a reflectance below 17dB or over 24dB and a pulse shape deviation larger than 12. This avoids including points originating from merged echo pulses and faulty points coming from backscattered pulses instead of the emitted laser beam. After these steps, the point clouds were subsampled to 0.005 m density and exported in both .txt and .las files for further processing. Target trees were manually extracted, the understory was removed, and infrastructure was isolated using the open-source GNU General Public License software of Cloud Compare (Figure 2-2). The orientation of the point cloud of the fallen canopy section (see 2.3.3 below, Figure A-4) was changed to accommodate for the height variable in further analysis steps.

A1



A2



A3





Figure 2-2 Post processing spatial arrangement of Oak trees in relation to other trees and surrounding infrastructure at BIFoR FACE [front view]. Isolated trees are ordered by decreasing height. Trees omitted from analysis are also omitted here.

2.2.3 Manual measurements of fallen canopy

A large portion of the canopy structure of one tree, outside of the treatment and control plots at BIFoR FACE, came down in late 2021. Opportunistic sampling was done on the entirety of this fallen canopy (FC) to allow for validation of the TLS protocol, by comparing volume results of both QSM and manual measurements. Scans of the fallen canopy were done with a TLS set-up mimicking distance and angles occurring in plot scan protocols. We manually measured all branches' total height, length and diameter following an adjusted protocol from Demol et al., (2022). The stem compartment of the fallen canopy was determined by following the branch with the largest diameter after bifurcation until the 2.50cm diameter was reached, and a tape measure was attached to the stem for future length reference. Branching of the first order was noted and coded with A, B, C, etc. Sprouting height on the main stem/branch was measured, followed by the branch length at 10 cm diameter, 7 cm diameter, 5 cm diameter and 2.50 cm diameter if available. Diameters were determined with an electronic calliper, and the average of 2 perpendicular measurements was used. A tape measure was also used for the circumference of larger branches (Figure A-2).

Between 24 and 26 April 2023, all material smaller than 2.50 cm in diameter was removed from the FC and stored. The smaller material was measured as follows: first, branch diameter was measured at the base, middle and end in mm with a vernier scale calliper to 0.02 mm precision. Then, the total length was measured with fabric tape to the closest full cm. For the smallest twig material, the number of samples was noted. Then, the average of the smallest and largest samples was determined for the diameters at the base, middle, and end.

2.2.4 Quantitative Structure Models

The TLS point cloud was converted to single tree QSMs that comprise tree and stand scale properties. To achieve the most accurate QSM, the patch sizes used to fit the cylinders to the point cloud are important, as well as the construction of multiple models with the same parameter inputs to accommodate the stochastic elements in the reconstruction process. The algorithm *Optqsm* (github.com/apburt/optqsm) was run in MATLAB 2023b, and the best parameter sets for each tree were determined by calculating the vertically resolved nearest neighbour distance for each point cloud. We used these parameter sets (Table A-1) to construct 30 QMS per tree. Tree ID 8546 was omitted here due to processing errors. While *optQSM* optimises the parallel use of algorithm *treeQSM* v2.3.2, it is restricted in the number of

properties included in the output. By using the calculated parameter sets in the v2.4.1 version of *treeQSM* (Raumonen et al., 2013), another 5 QSMs per parameter set were generated. The lowest point cloud to the model distance determined the final cylinder model per tree. Figure 2.1 shows a flowchart with the steps to create the final QSM per tree. Table A-2 contains the mean and standard deviation of total volume across the *optQSM*-generated models and the final *treeQSM*-generated models per tree. Table A-3 shows the difference in total volume between the final QSM from *optQSM* and the final QSM from *treeQSM*.

From the final *treeQSMs*-generated model, tree height, average canopy projected area, and trunk and branch (both living and dead) volumes were determined for each tree. The trunk and branch volumes are distinct by branch order 0 for the trunk and above for the branches, with canopy metrics defined by the first major branch encountered along the trunk (MATLAB-software *TreeQSM* manual, version 2.4.1). The radii from the canopy centre to the canopy boundary per layer (1/20 of tree height) in 18 directions are also exported. From this, we determine 18 x- and y- coordinates on the outer canopy boundary to more accurately calculate the canopy's projected area. The sum of the area of each trapezoid that fits within these coordinates determined the layer's total canopy area (hereafter, “projected canopy area”). Tree IDs 6581 and 8544 were removed due to unreliable projected area output. Finally, the diameter at the base, the length, and the height along the tree of each cylinder (hereafter, “branch”) are exported and further analysed with RStudio (R core team 2024). Trunk data and branches with diameters smaller than 0.5 cm were omitted.

Cumulative distribution functions (CDFs) were made of length and volume across the ordered diameter of the branch data. To determine canopy filling, the projected canopy area and branches datasets were scaled based on average tree height across each plot (eq.1).

$$\text{Scaling Factor} = \frac{\text{Tree height}}{\text{Average tree height plot}} \quad (1)$$

By scaling the branch data based on average tree height per plot, the layers for each projected canopy area at that given height also become more similar in depth (perpendicular to the diameter of the projected area). This allows for determining canopy volume, branch volume and branch density on a plot level while not reducing the impact of neighbouring trees during pre-treatment growth. Canopy volume is the volume enclosed by each layer's canopy projected area and depth boundaries (eq. 2) and represents both airspace and wood.

$$\textit{Canopy volume} = \textit{canopy projected area} * \textit{depth} \quad (2)$$

Where canopy volume is m³, projected area is m² and layer depth in m. Branch volume is defined as the total sum of volume (m³) of the branches present in each layer. Finally, the canopy filling of the branches is analysed by calculating branch density (branch volume m³/canopy m³) per height layer per plot.

Statistical analyses were performed in R software (version 4.4.2). Variables were tested for normality using the Shapiro-Wilk normality test and homogeneity of variances using Levene's test. For parameters that met assumptions of normality and homogeneity 2-sided t-tests were performed. For non-normally distributed data, differences between treatments were assessed using a permutation t-test. In both cases $\alpha = 0.05$.

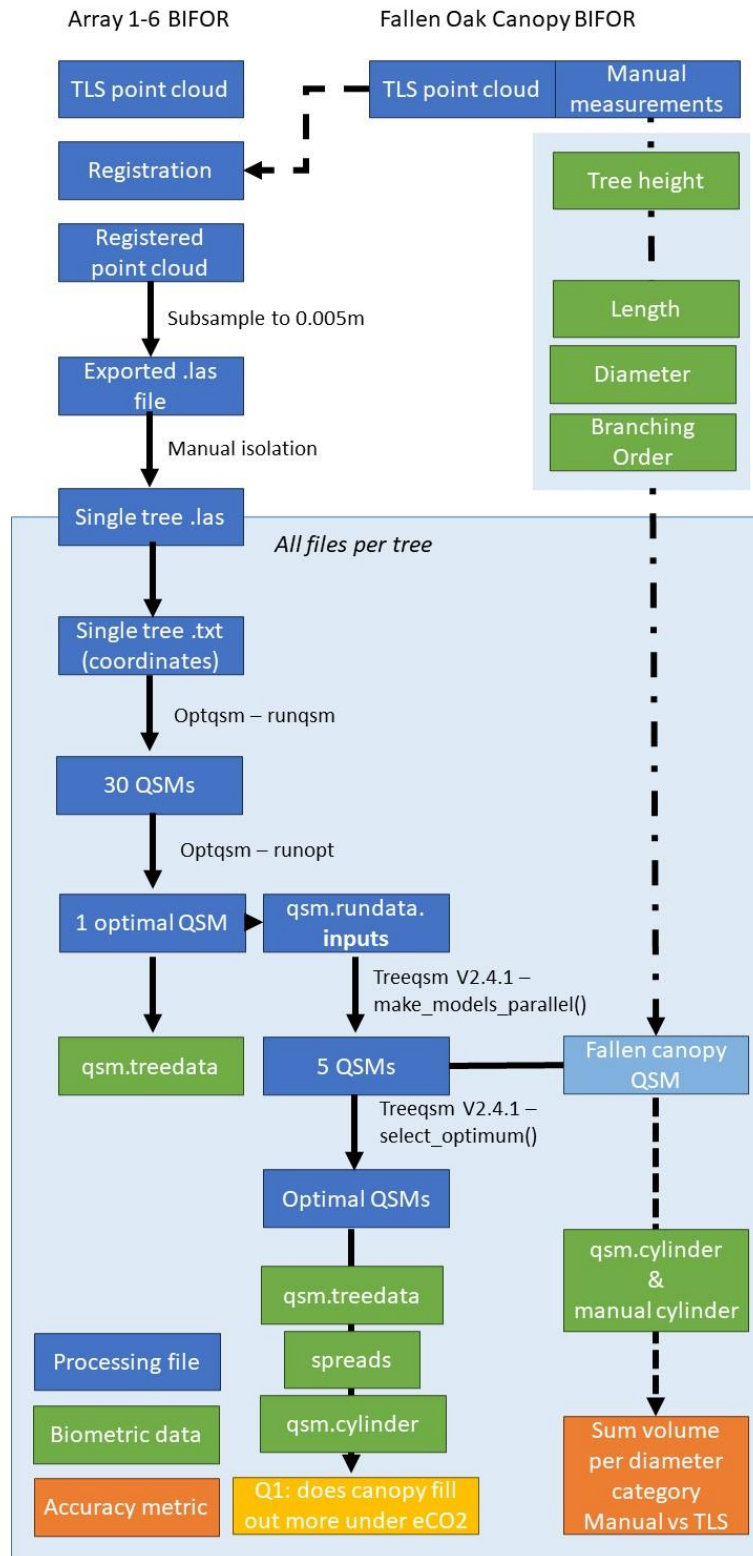


Figure 2-3 Flowchart of processing steps from TLS point clouds to optimal QSM per tree and the fallen canopy section for validation. Blue boxes show processing file type and repetition when relevant, green boxes show utilized biometric data generated by the algorithm or manual measurements. Orange squares represent the metric for determining accuracy of biometric output of the algorithm.

2.3 Results

2.3.1 Quantitative structure models versus manual measurements

The branch volume of the fallen canopy (FC) was manually measured to be 1.37 m³ while calculated as 1.13 m³ by treeQSM with an underestimation of 0.24 m³ or 20% overall. Figure 2-3 compares the branch volume in each diameter class between measurement types and shows a similar pattern of overestimation in size classes to other validation comparisons (Demol et al., 2022). However, here, TLS underestimated the > 10 cm diameter volume, which was most likely caused by the proximity of the trunk to the ground at the time of scanning (Figure A-4).

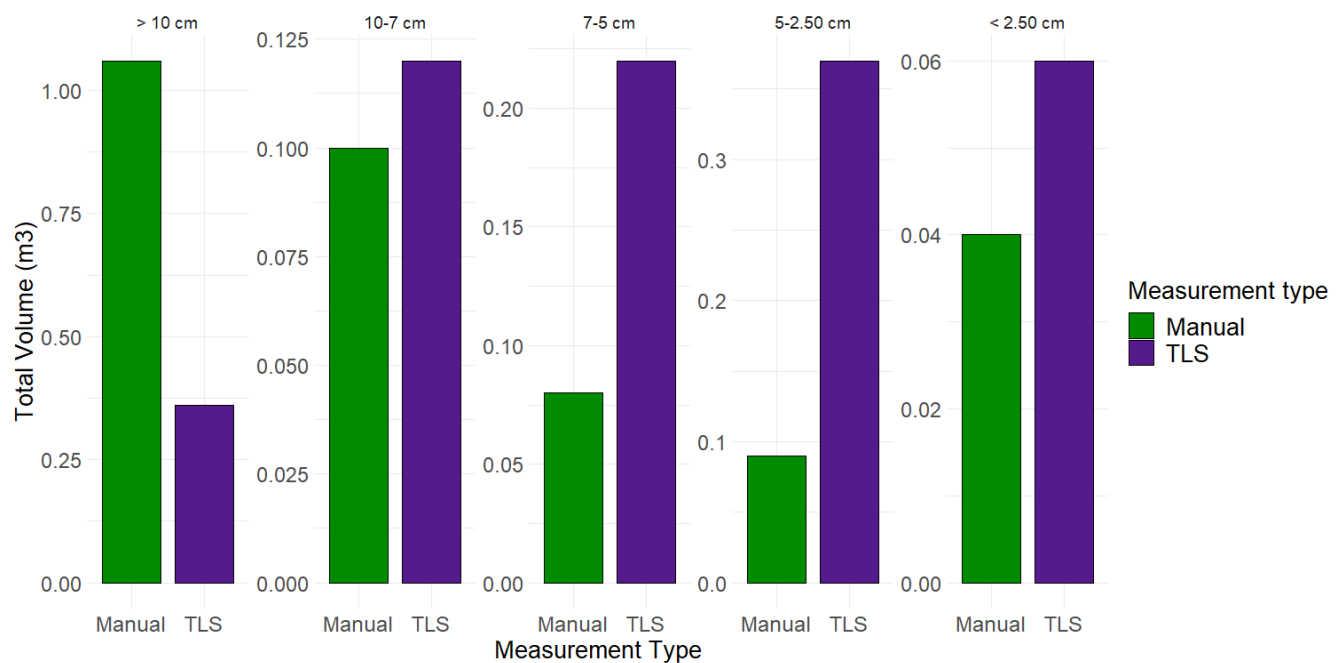


Figure 2-4 Branch volume per diameter class of branches from manual measurements (n = 728) and TLS-derived QSM branches (n = 6651) from the same fallen canopy section. All diameters smaller than 0.5 cm were omitted from TLS data

2.3.2 Tree data across plots

Figure 2.4 shows the variation in the commonly used forestry metrics of tree height, canopy projected area, and trunk and branch volume, across plots and treatments, with each dot representing one of 46 individual trees. Tree height ranged from 16 to 29 m (Fig 2-5 A), and canopy projected area from 33 to 210 m² (Fig 2-5 B). The total trunk and total branch volume per tree ranged from 2 to 7 m³ and 1 to 13 m³, respectively (Fig 2-5 C, D). The mean tree height was 25 ± 2 m (mean $\pm$ SD) for aCO₂ and 24 ± 3 m for eCO₂, with no significant difference between treatments (permutation t-test, $p = 0.4427$). Similarly, the mean canopy projected area of 90 ± 39 m² under aCO₂ and 92 ± 43 m² eCO₂ were not significantly different (2-sample t-test, $p = 0.7617$). The mean trunk volume under aCO₂ (4 ± 1 m³) was not significantly different from eCO₂ (4 ± 2 m³) shown by 2-sample t-test ($p = 0.6124$). Likewise, the mean total branch biomass under aCO₂ (6 ± 3 m³) was not significantly different from eCO₂ (4 ± 3 m³) (Welch t-test, $p = 0.0796$).

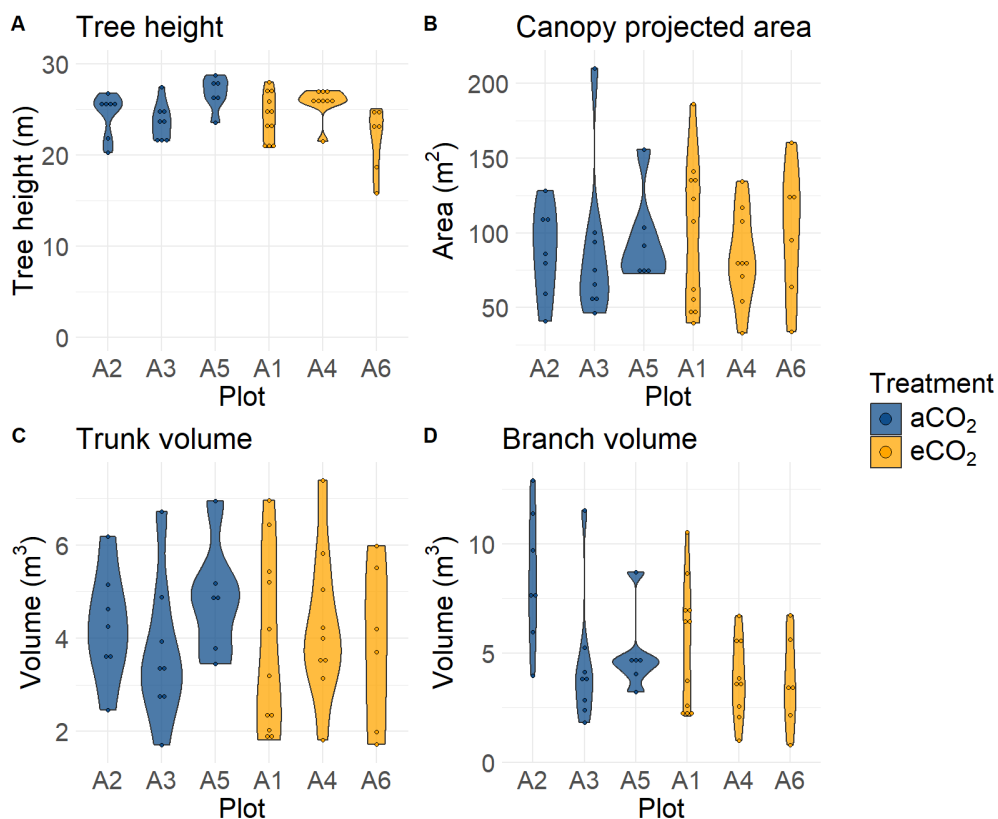


Figure 2-5 Violin and dot plots per plot across treatments. A) Tree height in m. B) Mean canopy projected area in m². C), Trunk volume in m³. D), Branch volume in m³. The dots within the violin plots reflect the number of QSM trees from each plot, with nA1 = 11, nA2 =, nA2 = 7, nA3 = 8, nA4 = 9, nA5 = 6, nA6 = 5.

2.3.3 Branch volume and length distribution per plot and treatment

To compare branch size distributions between treatments, Figure 2-5 shows the cumulative distribution functions of branch volume and length per plot, coloured per treatment. The 50th percentile (probability = 0.50) represents the median diameter size where 50% of the total accumulated volume or length is reached. For branch volume under aCO₂, the 50th percentiles occur at 8.23 cm, 4.58 cm, and 4.95 cm diameter in plots A2, A3 and A5, respectively. For eCO₂ the 50th percentile of branch volume occurs at 5.37 cm, 5.99 cm, and 3.99 cm diameter in plots A1, A4 and A6, respectively (Fig 2-6 A). The means ($\pm$ SD) of these 50th percentile diameter thresholds (5.12 ± 1.02 cm and 5.92 ± 2.01 cm for eCO₂ and aCO₂ respectively) are not significantly different (Welch t-test, df = 2.9731, p = 0.5812). For length distribution per diameter (Figure 2-6 B), the 50th percentiles across the treatments are 4.34 cm, 3.14 cm, and 2.97 cm for aCO₂ plots (A2, A3 and A5) and 2.92 cm, 2.90 cm, and 2.77 cm for eCO₂ plots (A1, A4 and A6). Mean 50th percentile for aCO₂ (3.48 ± 0.75 cm) did not differ from eCO₂ (2.86 ± 0.08 cm) (df = 2.0476, p = 0.2864).

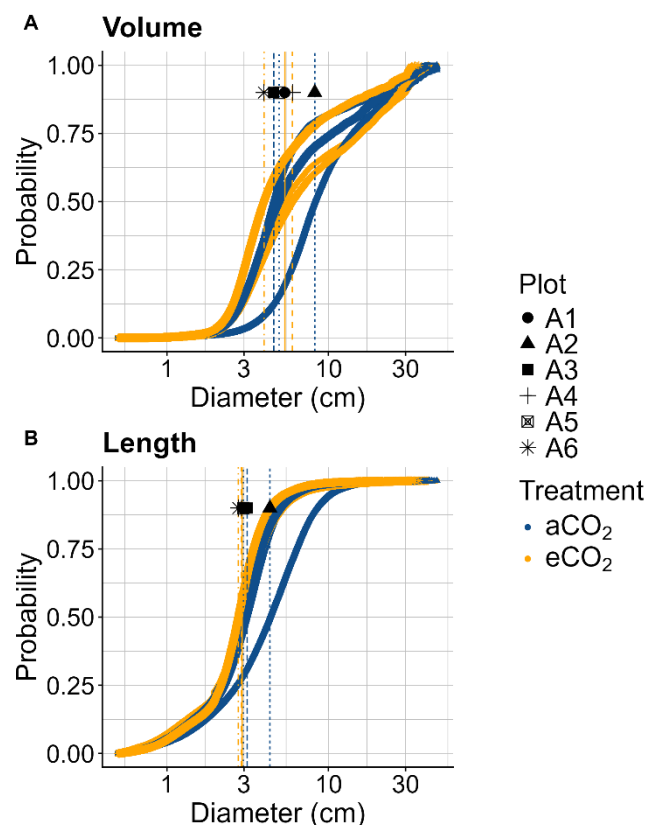


Figure 2-6 Cumulative distribution functions of branch volume (A) and length (B) as a function of diameter, shown per plot and coloured per treatment. Dotted lines indicate the diameter at which 50% of cumulative branch volume or length (probability = 0.50) is reached for each plot.

2.3.4 Branch volume per diameter class

Figure 2-7 shows the total branch volume per diameter class, averaged across the plots and subsequent per treatment ($\pm$ SE). In the < 2.50 cm class, branch volume per plot appears higher under eCO₂, although the difference is not statistically significant (Welch t-test, $p = 0.3926$). In contrast, in the > 10 cm, 10–7 cm, 7–5 cm, and 5–2.5 cm classes, mean branch volume is seemingly higher under aCO₂, but these differences are also not statistically significant ($p = 0.5641$, $p = 0.4203$, $p = 0.2444$ and $p = 0.8578$ respectively).

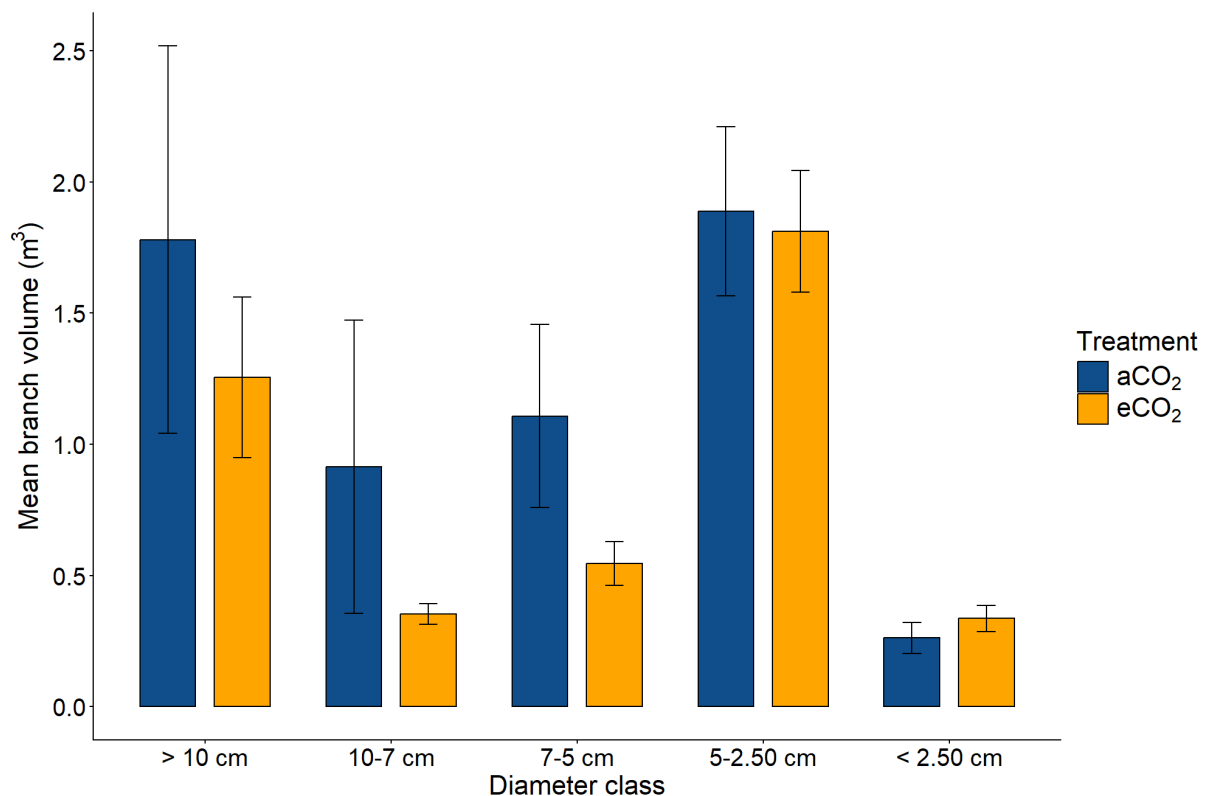


Figure 2-7 Barplot showing the mean ($\pm$ SE) branch volume (m³) for different diameter size classes, colored per treatment. Branch volume was first summed per tree within each diameter class, then averaged per plot, and finally averaged across the plots ($n = 3$) for each treatment.

2.3.5 Canopy volume, branch volume, and branch density

The average available canopy volume per height layer are displayed in Figure 2-8. For the layers 11 to 20 the canopy volume under eCO₂ appears higher compared to aCO₂. However, none of the differences between total canopy volume between treatments on any of the height layers are significant (Welch's t-test, $p = 0.192$ to $p = 0.913$).

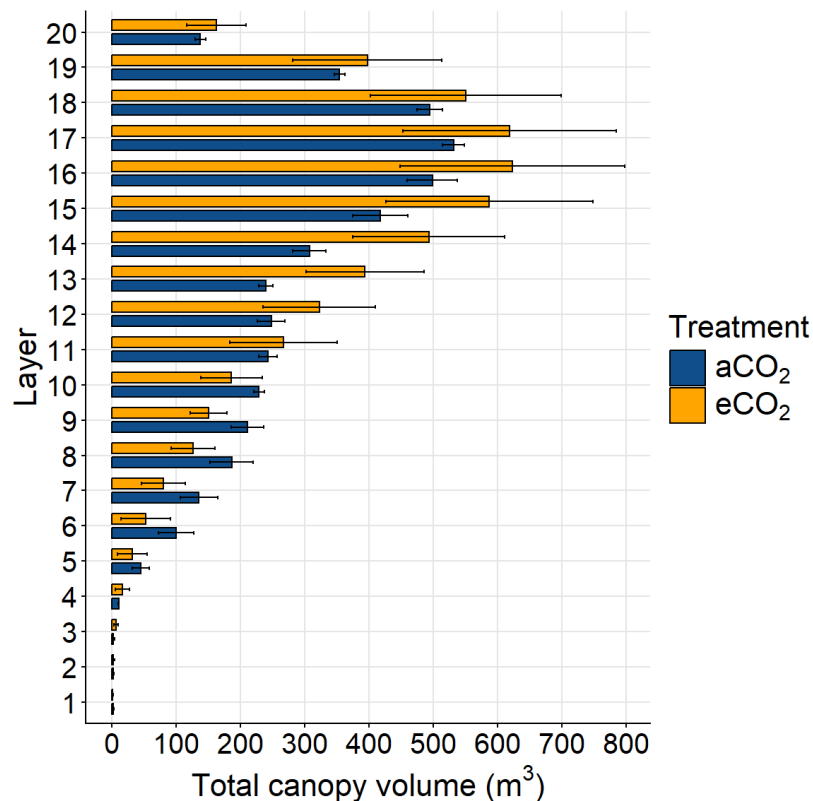


Figure 2-8 Total canopy volume per layer. The total canopy volume (m³) is calculated based on layer depth (m) and layer canopy projected area (m²). Layers are numbered from 1 (stem base height) to 20 (canopy top). Horizontal bars represent the total canopy volume means across the treatment plots ($n = 3$), with error bars showing the standard error.

The branch volume distribution pattern per diameter class (Figure 2-7) looks to be consistent across the different height layers (Figure 2-9) for diameter class > 10 cm and more clearly in 10-7 cm and 7-5 cm where there is a trend of a larger branch volume present in all layers under aCO₂ compared to eCO₂. The apparent higher total branch volume for eCO₂ is not clear in the 5-2.50 cm diameter class in any of the layers, but a contrast stands out in the layers 11 up to 20 for the < 2.50 cm class. Two sample t-test shows significantly higher volume in wood < 2.50 cm in diameter in layers 13 and 14 (p = 0.01479 and p = 0.01483 respectively). The branch density (m³/m³) of size class < 2.50 cm displayed in Figure 2-10 also appears to be higher in layers 11 and upwards under eCO₂ compared to aCO₂, although none of the differences are significantly different (p = 0.0801 to p = 0.9878).

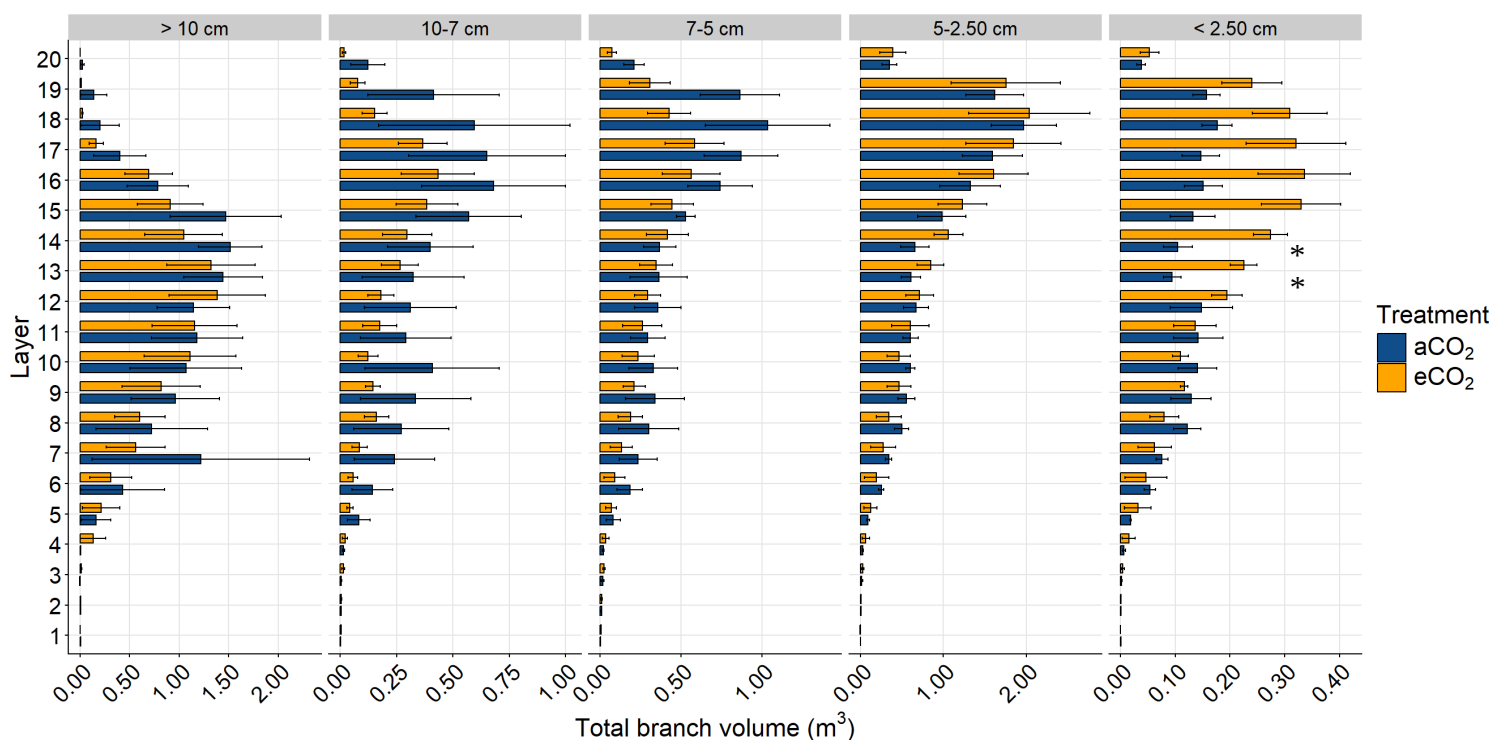


Figure 2-9 Total branch volume within different diameter size classes per height layer. Bars represent the mean total branch volume (m³) across treatment plots (n = 3), with error bars showing standard error. Layers are numbered from 1 (stem base height) to 20 (canopy top). Significant differences between treatments with p < 0.05 are highlighted with *.

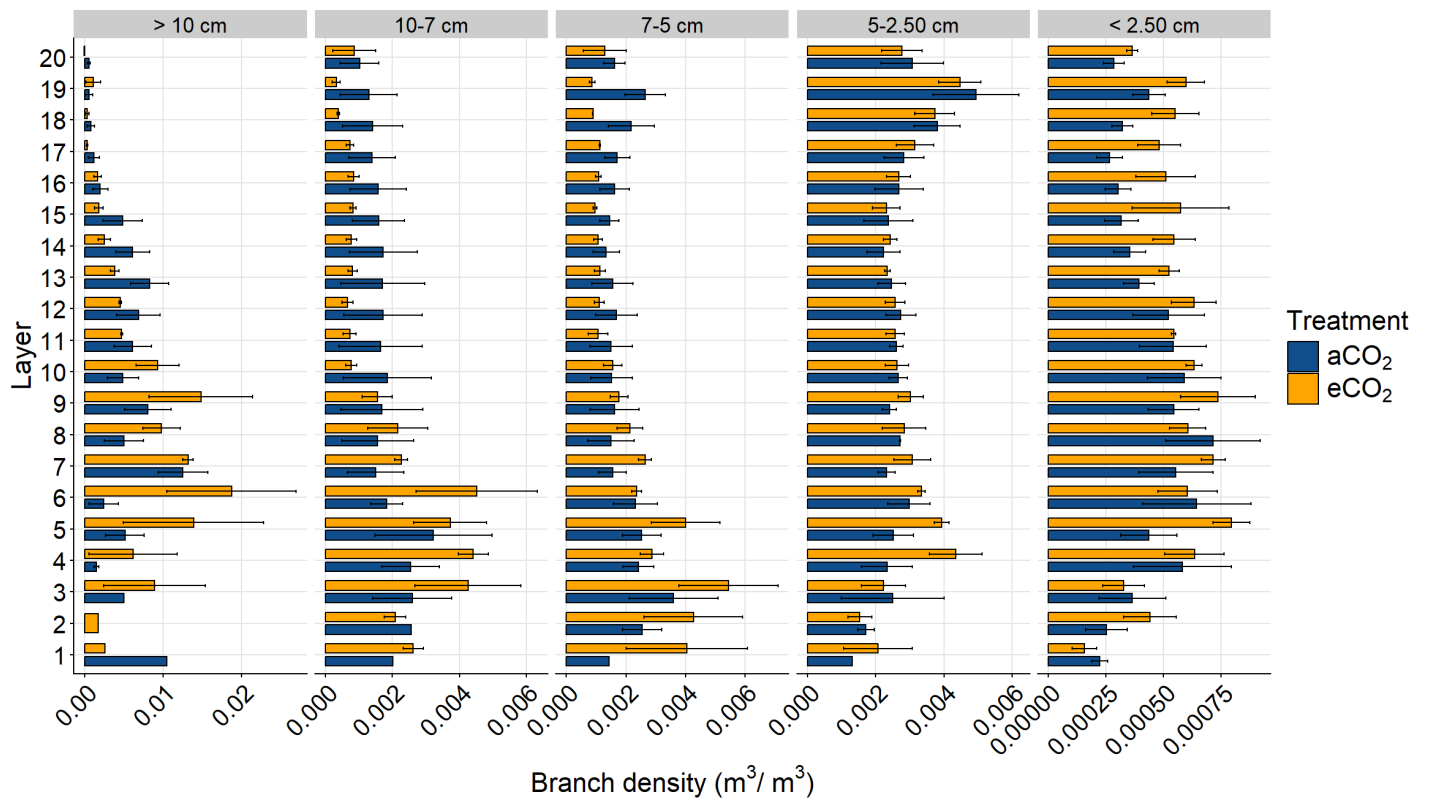


Figure 2-10 Branch density (m^3/m^3) of different diameter size classes per height layer. Bars represent the mean branch density across treatment plots ($n=3$), with error bars showing standard error. Layers are numbered from 1 (stem base height) to 20 (canopy top).

2.4 Discussion

This chapter examined the biomass distribution of a mature oak stand exposed to eCO₂ using TLS to inform on detailed branch volume and density across different height layers. The hypothesised eCO₂ alleviation of C-limited growth and the subsequent increase in mostly finer branch material to facilitate previously observed could not be disproven. We found a higher fine branch density in the upper canopy of *Quercus robur* trees exposed to elevated CO₂ levels (eCO₂) for four years compared to ambient conditions. The QSMs of the trees under eCO₂ treatment contained a tendency towards more branches of 2.50 cm or smaller diameters in the highest six layers compared to the same canopy volume in ambient conditions.

These results point towards an increase in small sized woody tissues under eCO₂, which aligns with the hypothesized positive feedback of the CFE by investing surplus of C into metabolic tissues and the structures supporting these tissues. If this impact of eCO₂ on the internal ecosystem C fluxes was one-directional, the positive CFE could be sustained and a new carrying capacity in this mature forest can be reached. The uncertainties of DGVMs NEP projections for future temperate forest with rising CO₂ concentrations (Ciais et al., 2013) might be partially resolved by including these results. The previously observed enhanced photosynthesis (Gardner et al., 2020), with the preliminary NPP_{stem+branch} increase (Norby et al., 2024) and the indication for positive feedback of eCO₂ by increasing branch support for leaf structures accounts for a part of the missing C flux. It is still to be determined if the eCO₂ impacts the internal C flux through branchfall and litterfall with a negative treatment effect and if so, with similar magnitude and if this positive CFE is sustained over time.

2.4.1 eCO₂ treatment results in increased branch volume and branch density

The eCO₂ tree canopies contain slightly more volume in the smaller diameter classes of < 2.50 than aCO₂, while the reverse is seen in the four larger classes (Figure 2-7). This is in line with the hypothesis of shifting growth towards smaller wood diameter sizes driven by light capture using newly available carbon. The increased light capture efforts are noted at increased LAI, as observed in multiple other studies looking for eCO₂ impact on plant structure (Pritchard et al., 1999). The results of increased branch density under eCO₂ in the top of the canopy are not completely in line with results from younger potted birch tree experiment on a crown structure, where eCO₂ caused an increase in the number of metamers (sub-sections of a shoot) when in light competition with neighbouring trees, yet only in the lower branches of the canopy (Kull et al., 2003). Longer internodal lengths were observed after two years of eCO₂ exposure in PopFACE (Gielen et al., 2002) in line with the slight increase in cumulative length distribution

under eCO₂ in our results in Figure 2-6. From TLS scans and subsequent QSMs, the details of the internodal level cannot be determined. However, longer internal lengths could explain the higher fraction of total length captured in smaller diameter sizes in eCO₂ canopies.

What stands out in Figures 2-8 and 2-9 is that the larger average proportion of canopy volume under eCO₂ in the upper canopy is only mirrored in a larger proportion of wood volume under eCO₂ in the material with < 2.50 cm diameter. Larger canopy volume can be caused by more area (i.e., caused by more trees in the plots) or more depth (i.e., taller trees). It is necessary to look at branch density to determine if this difference was caused by horizontal canopy expansion or optimising the use of available canopy volume. Figures 2-10 show that we cannot reject the optimal canopy volume usage hypothesis because the wood volume per canopy volume remains, on average, higher in the upper canopy under eCO₂ than in aCO₂. It corroborates the most recent results on continued higher green leaf mass and litter mass under eCO₂ at the BIFoR FACE site during scanning (Norby et al., 2024).

2.4.2 Branch volumes can be overestimated without impacting effect size

The canopies' cumulative distributions of branch volume in Figure 2-6 align with the variability shown in Figure 2-5 D. It is striking, yet not unsurprising, that in most plots, half of the branch volume is captured in branches smaller than 4 - 6 cm in diameter. Examination of multiple *Quercus petraea* trees showed an overestimated volume of up to 32% for the smallest wood sizes in other research utilising TLS (Hackenberg et al., 2015). This overestimation happens due to the faulty cylinders fitting to the points; their scans were made in non-advantageous weather circumstances, high wind speeds, and precipitation. In the context of this studies results, it could mean the absolute canopy volume (Figure 2-8), and the absolute density of these branches in the upper canopy might be overestimated (Figure 2-10). However, the effect size of eCO₂ in these figures is not expected to be impacted, as Figures 2-5 B and D show a wide range of canopy projected area and branch volumes. We assume that the volume overestimation caused by this method refers to all the trees, plots, or treatment means equally.

2.4.3 Impact of understory presence on branch volume distribution in dominant species remains inconclusive

There is some variance among the plots. Figure 2-6 shows how ambient plot A2's distribution curve diverges the most from the other ambient plots, with a 50% volume probability reached at 8 cm diameter. Similarly, the probability of 50% length is reached at a larger branch diameter. A possible explanation for this difference may be the higher density of understory

vegetation in plot A2 (Hart et al., 2020). This could have caused a shift in prioritising height increase over canopy expansion, likely years before fumigation started. The difference in plot A2 is also reflected in the relatively small projected canopy area despite not having the least number of trees (Figure 2-2, 2-5). This contrasts with the finding from Georgi et al., (2021), that higher neighbourhood species richness increased branch length and fine wood (< 7 cm diameter) volume in the canopy. This experiment focussed on canopy overlap and not understory-overstory structure dynamics, so additional examination of the canopy placement at BIFoR FACE would be worthwhile to investigate this dynamic further.

2.4.4 Limitations

The findings of this chapter are subject to at least a few limitations. A study in a mature, 175-year-old BIFoR FACE woodland faces challenges in observing immediate eCO₂ treatment effects, primarily because detectable changes might not be present after only four years of fumigation. The outer boundaries of the canopies were established long before the infrastructure was placed, and the scans were made. Hence, we hypothesised that first treatment effects would be discernible in the smallest sizes classes and that it would happen driven by optimising the available space within canopy borders in contrast to outward growth foraging light. The trees have not been grown or fumigated in a controlled environment but have been exposed to light competition or nutrient limitations, insect plagues like in 2019 (Norby et al., 2024) and extreme weather events such as droughts and storms. These are all factors that shape tree growth and canopy plasticity. Hence, sum per plot level was chosen to test the hypothesis instead of per tree, as canopy shape and branch density are also inherently impacted by neighbouring trees. By doing this, the individual distribution of branches that make up the trees remained the same but made height layers comparable between the plots per treatment. This allowed for a more relevant analysis of the differences between the treatments.

The manual measurement of a fallen canopy section that was used to validate the TLS-derived QSM metrics was an opportunistic use of a large section accessible to both researcher and laser scanner. The use of this validation method in literature generally starts with scanning a standing living tree or trees, followed by the destructive harvest and thereafter manual measurements (Garcia Villacorta et al., 2015; Sillett et al., 2015; Calders et al., 2015; Uller et al., 2019). This chronology was not an option at BIFoR FACE as the surrounding woodland, like the FACE experiment, is a highly regulated research site. Although BIFoR FACE has a canopy access points, these did not provide enough or consistent access to branches of critical sizes. Thus the alternative was to scan a canopy section already fallen to the forest floor to provide some

measurement of accuracy for the critical size classes instead of solely the DBH. However, scanning after harvest comes with other caveats. The proximity to the forest floor restricted scanning angles and made a 360-degree scan pattern impossible, especially in the largest diameter size, closest to the forest floor showed incomplete point cloud coverage (Figure A-4). Since these points guide the fitting of cylinders by the treeQSM algorithm, this lack of coverage caused the underestimation of stem volume, in comparison to other research using manual validation results of same size class (Demol et al., 2022). It is therefore necessary to approach this validation method with some caution, yet the overall overestimation of volume in our comparison between manual and scanned method aligns with that of Demol et al., (2022). It is important to note that smaller branch sizes are often omitted from QSM derived volume calculations and manual comparison studies to avoid overestimation; below 5, 7 or even 10 cm in diameter (Burt 2017; Dassot et al., 2012; Gonzalez de Tanago et al., 2018). While a risk of overestimation in these size classes is acknowledged, this study aimed to quantify relative treatment effects rather than achieving absolute volumetric accuracy. In this context, any systemic bias that is consistent across aCO₂ and eCO₂ plots is expected to cancel out in ratio-based comparisons, as it affects both the numerator and denominator proportionally. Therefore these results still provide valuable insights into future research.

Weather conditions during scanning can impede the accuracy of the output of TLS-derived QSM data, where wind and precipitation can cause tree movement, especially in specimens over 15 m tall. Multiple scan positions were employed in leaf-off conditions to mitigate inaccuracies, angled scans were added to include upper canopy capture otherwise missed, and scans were conducted under the most optimal weather conditions offered within the timeframe of access to the scanner. Exclusion of specific trees due to unreliable output the TreeQSM algorithm and omitting all branches of 0.5 cm diameter from the analysis further ensured data quality but compromised data completeness.

The use of a single set of scans offers a highly detailed representation of tree a detailed tree model but captures only a single timepoint after 4 years of fumigation. A before-after comparison was beyond the scope of this study. Additionally, the TLS derived estimates of stem and branch structure do not differentiate between living and dead components. At least some fraction of the captured branch volume and branch density described in this chapter is represented by non-living material. This study assumes that branch biomass in the canopy remains constant over time, reflecting the equilibrium between growth and mortality of a mature forest that has reached closed-canopy state. Alternative methods like allometric scaling

would not have resolved the challenges in differentiating between living and death material and would not have provided the detail in size compartments hypothesized to show the preliminary treatment effects. Although the TLS outcomes come with uncertainties, it's the continuation of repetitive scans over multiple years that will allow for comparison of outcomes, and the preliminary results in this Chapter offer a piece of this timeline that will help determine if the distribution changes in these smaller size branches and canopy layers are sustained over longer periods of time.

2.5 Conclusions and future work

The aim of this study was to understand whether eCO₂ affects branch volume distribution within the canopy, and if so, what mechanisms might drive this change. The expected outcome was that with previously observed increases in C assimilation in this stand, a CO₂ limitation on growth has been alleviated and would lead to increased branch growth in support of light capture. With this mature stand canopy already closed, this growth would need to take place within the canopy's existing boundaries. This hypothesis could not be disproven. The results of this study revealed a noticeable increase in the smallest size woody volume per available canopy volume, particularly in the upper canopy layers. In general, therefore, it seems that these results are aligning with both the theorized proximity to the light resource and the smallest size consistent with the argument for leaf support. In future investigations it would be recommended to repeat the single time scans used in this study over multiple years to determine if the observed difference between treatments is sustained after longer exposure than 4 years. This study also shows that while TLS has greatly improved the accessibility and detail of observations of forest canopy structure, which previously were restricted by time and labour costs, the validation of these observations still requires a lot of manual processing and ideally destructive harvesting. There is abundant room for further progress in testing and improving the accuracy of TLS derived volume calculations and potentially making the requirement of destructive harvesting obsolete in the future. Considering the potential overestimation of branch biomass of the smallest branches with the current processing protocol, continued investigation on improving accuracy is important for future work. This could be through improvement of the algorithms used to better fit cylinders to the point cloud or by adjusting the scan placement protocol by including different heights as well as angles to optimize accessibility to the upper canopy. Overall, collecting more observations on branch growth in a mature forest exposed to eCO₂ was achieved, and a future study investigating how including this preliminary increased

branch growth would improve model projections of different C fluxes that make up the NEP of global forest ecosystems, especially in response to future atmospheric CO₂ concentrations.

Chapter 3

Woody turnover in mature oak woodland under elevated CO₂

3.1 Introduction

Forests play a vital role in the global carbon (C) cycle, constituting a significant sink for atmospheric CO₂. The net primary production (NPP), e.g., the difference between the C that is taken up through photosynthesis (Gross Primary Production, GPP) and the C that respired back into the atmosphere in each time, is a vital metric for models in projecting the global C capture from the atmosphere. Plants use the assimilated C to grow biomass in the form of roots, leaves, stems, and branches. Mature and old-growth forests are particularly important for long-term carbon (C) storage, as they contain larger trees that have accumulated more C over time, e.g. large standing crop, along with increasing amounts of deadwood on the forest floor (Burrascano et al., 2013). The time that C is sequestered in an ecosystem is largely driven by the longevity of the woody above-ground biomass (AGB); e.g., the stems, branches, and twigs. The longevity of wood determines the long-term C sequestration of the whole ecosystem since C can remain in stem and branches for several decades. In contrast, the C that is used to construct tissues with shorter lifespans, such as leaves or fine roots, is quickly released into the atmosphere via litterfall and subsequent decomposition by other organisms. The rate by which this occurs for woody tissue, e.g. the fraction transitioning from wood in the tree canopy (woody AGB pool) to deadwood on the forest floor over time, divided by the size of this woody AGB pool can be defined as woody turnover rate. The inverse of this, e.g. the time a tree stem, branch or twig remains in canopy of a tree, or a forest stand is defined as woody residence time (Xue et al., 2017). Understanding how long C remains sequestered in all wood sizes and the factors that influence the turnover rate from one C pool into another is crucial for predicting future global carbon dynamics.

Dynamic global vegetation models (DGVMs) use the parameters of biomass, turnover rate and residence time to predict the C budget on global or regional scale and partition the AGB pool into wood (which includes both stem and branch), leaf, and root tissues (Yu et al., 2023) and often assume the residence time is constant for the entire wood biomass pool. This assumption overlooks critical differences in forest dynamics, as branches are more dynamic than the stem compartments of trees. The reduction of wood dynamics to this single biomass pool instead of

differentiating between stem and branch causes up to 30% more uncertainty in the overall C budget predictions (Xue et al., 2017). This is especially pressing considering accurate turnover rates can predict long-term C sequestration in above-ground biomass (AGB) better than NPP itself (Malhi et al., 2015; Yu et al., 2023) and potentially determine the difference between a forest acting as a C sink or source (Gough et al., 2007). These the branch and litterfall fluxes can impact the productivity capacity, by removing from branch biomass in place to support metabolic tissues. The branchfall also impact substrate availability for decomposition, eventually leading to C release back into the atmosphere, Observing woody residence time at the stand scale is challenging due to the long lifespan of trees, which exceeds the typical duration of most research projects. However, quantifying woody turnover rates through measurements of accumulated deadwood on the forest floor, branchfall, and litterfall over time can provide insights into past and present forest dynamics.

To accurately determine the woody turnover rate through branch and litterfall, quantification of the biomass pool present the canopy is required. This can be done through manual measurement (Silett et al., 2019) but is more often done by using allometric equations (Forrester et al., 2017). The use of terrestrial laser scanning (TLS) is becoming more coming in forestry research as it provides a non-destructive but high detail method to estimate above-ground biomass (Calders et al., 2015). TLS provides detailed canopy architecture data, including the angle, height, length and diameter of branches throughout the canopy (Dassot et al., 2019; Demol et al., 2022; Lau et al., 2018) and can be used to supplement or replace another commonly used method of airborne remote sensing (Liu et al., 2017). Aerial remote sensing can be utilised to supplement field data by capturing canopy gaps formation on a large scale. Yet up to 17% of tree-mortality and branchfall occurrences impact only understory or lower canopy, making ground-based field observations of continued importance (Simonetti et al., 2023). Methods are characterised by tissue type, size and data can be utilised to determine a variety of forest functions, structures or dynamics. Typically, the rate of the smallest tissue (litter) falling from the canopy onto the forest floor is measured using periodic collection from litter traps. Total litter mass can be used to indicate the general production and turnover dynamics of a stand (Lichter et al., 2008; Norby et al., 2024), and it is often separated into leaves, twigs, reproductive material, and bark (Crockford & Richardson, 1998; Pook et al., 1997; Finzi et al., 2000). Leaf litterfall, for example, can be used to estimate total canopy leaf area and thus understand stand-scale photosynthetic tissue per area of forest stand (Norby et al., 2024; Ellsworth et al., 2017). Reproductive material, such as flowers, fruits, and seeds,

provides insight into tree phenology, reproductive investment, and regeneration potential, making it a useful indicator of ecosystem productivity and species recruitment. Litterfall, but also branches and bark (Grootemaat et al., 2017) contribute to forest floor fuel loads, a metric used to interpret and predict forest fire dynamics. For example, observations of the diameter distribution of downed tree trunks and larger branches on the forest floor can be used to estimate the duration of fire events (Graham & McCarthy, 2006)

The larger the tree components, the more difficult it is to capture within traps, so subsampling methods are utilised to quantify the frequency and biomass of larger branches falling from the forest canopy. This is categorised as (downed) coarse woody debris or detritus (CWD) (Campbell et al., 2019; Miehs et al., 2010) or downed dead wood (Russell et al., 2015). Common methods to subsample CWD in large forest areas are quadrants or line intersect sampling (LIS), which involves one or multiple lines placed on a forest floor. When CWD in the form of logs, snags, stumps, or branches are encountered crossing this transect line, they are measured for diameter and length (Woldendorp et al., 2004). Noting the decay class of encountered CWD can also inform on previous stand dynamics (McCarthy et al., 2001) or determine the transition between mature forest and stand old-growth forest stands in undisturbed scenarios. The orientation of the line, as well as the type of CWD and size threshold for inclusion, vary greatly between studies. There is no commonly agreed-upon threshold for the size of what is included in the term CWD, but inventories often start measuring samples above 5 cm diameter (Woldendorp et al., 2004; Miehs et al., 2009), 10 cm (Busing & Fujimori, 2005; Killey et al., 2010) or 20 cm diameter (Cobb et al., 2012). Some studies include “fine” CWD consistent with branches < 7 cm in diameter (Korboulewsky et al., 2021; Lang & Forman, 1978).

Across different forest ecosystem, reported C input to the deadwood C pools due to tree mortality and branchfall range from 0.54 Mg C ha⁻¹ yr⁻¹ to 4.9 Mg C ha⁻¹ yr⁻¹ (Wijas et al., 2024). In tropical forests for example, AGB loss through a combination of tree mortality and branchfall is estimated at 8.72 Mg ha⁻¹ yr⁻¹ (95% confidence interval [CI]: 5.57–12.86). Of this, 42% (3.62 Mg ha⁻¹ yr⁻¹, 95% CI: 2.36–5.25) is attributed to branchfall from living trees (Zuleta et al., 2023). Branches up to 7 cm in diameter can make up approximately 40% of the total deadwood volume on a temperate forest floor, highlighting how non-fatal crown damage of relatively small branches, contributes substantially to forest C dynamics (Korboulewsky et al., 2021; Teissier et al., 2009). Tree mortality and branchfall in forest ecosystems is influenced by multiple factors, including disturbances such as droughts, windstorms, and lightning strikes

(Wijas et al., 2023). Climate change, particularly through increasing extreme weather events, is expected to accelerate both tree mortality and branchfall (Allen et al., 2010; Wijas et al., 2024). However, beyond these external disturbances, tree physiological responses to the continuing elevation of atmospheric CO₂ (eCO₂) may also play an important role determining future woody C output flux and associated impact on long-term C sequestration.

The CO₂ fertilization effect on the plant level, in which higher atmospheric CO₂ enhances photosynthesis and reduces stomatal conductance, increases C assimilation while decreasing water loss, leading to improved water-use efficiency and greater C availability for growth (Ainsworth & Long, 2005; Pritchard et al., 1999). Additionally, this effect can generate a positive feedback loop when increasingly available C is allocated to metabolically active tissues, further optimizing photosynthetic capacity and enhancing growth potential (Walker et al., 2019). Potentially provide positive feedback for the canopy, resulting in increased leaf growth or changing canopy morphology for optimal light capture (Poorter et al., 1997). The rate at which this occurs can differ by forest type (Bölöni et al., 2021) and structural characteristics of forest stands such as tree height (Piponiot et al., 2022). On a global scale this positive eCO₂ feedback on growth is uncertain, especially in temperate zones (Ciais et al., 2013).

In summary, there is a need to observe woody biomass growth and woody turnover of different diameter size branches, as these are more dynamic than stems, in a forest stand scale under elevated eCO₂ treatment. This will increase understanding of the forest carbon cycle and will add accuracy to current DGVM parameterizations (Körner 2017).

First generation Free Air Carbon Enrichment (FACE) experiments have provided the opportunity to research eCO₂ effect on young forest stands dynamics by conducting periodic litterfall collections. In open-top chamber CO₂ enrichment experiments with younger trees, leaf biomass in the traps increased under eCO₂ (Norby et al., 1999). In a WEB-FACE system, needle litterfall showed large variation due to forest structure heterogeneity and wind, with no significant difference in annual needle litterfall between treatment and control (Klein et al., 2016). In a larger loblolly pine plantation experiment (DukeFACE) the litterfall in the first two years differed significantly in pine needle mass and bark between treatments, while the litter of deciduous leaves produced under eCO₂ did not increase relative to control plots. A higher mass of pine branches was also observed, albeit not significant, due to large variations among the rings (Finzi et al., 2001). Follow-up research after nine years of fumigation showed no

significant treatment effect on litterfall past the first six years of the experiment, although the C annual and cumulative inputs to the forest floor remained higher under eCO₂ (Lichter et al., 2008). For the broadleaf species an increase in coarse roots and shift in allocation to wood was observed, while tree mortality was decreased (Palmroth et al., 2024). At ORNL FACE, a young even aged sweet gum plantation, canopy structure did not show an enhancement of canopy structure change, or tree stand development, and no increase in litterfall (Norby et al., 2022). Overall, first generation FACE experiments show species-specific and site-specific variability in litterfall responses to eCO₂, with some studies indicating increases in turnover that diminish over time. All studies have in common that no branchfall has been measured.

The second-generation FACE experiments provide opportunity to measure the changes to growth and mortality in mature and undisturbed forest ecosystems, with the assumption that these have reached a quasi-steady state (Norby et al., 2016). In these forests a certain carrying capacity of biomass is reached by the limitations imposed by resource competitions and resource demands. Since at least some fraction of enhanced C input flux will result in increased woody NPP (Walker et al., 2019), the expectation is that bringing the biomass above carrying capacity will eventually result in increased mortality, increasing the C output flux, bringing the ecosystem back to the carrying capacity baseline. Observations on the flux of litterfall are available, yet data on CWD in mature forest stand exposed to eCO₂ (second-generation FACE experiments) are rare and inconclusive. In a mature Eucalypt Forest, while photosynthetic enhancement of 19% occurred under eCO₂ (Ellsworth et al., 2017), no treatment effect on stem growth followed and the twig fraction of litter remained lower than the control across the first four years of fumigation (Jiang et al., 2020ab). In contrast, during the first three years of fumigation at a mature Oak woodland prolonged photosynthetic enhancement of 33% was observed in the dominant species (Gardner et al., 2022) in combination with a higher total litter mass, and radial stem growth under treatment (Norby et al., 2024). No data on CWD in either second generation FACE experiment has previously been collected, which means possible within ecosystem C fluxes are currently overlooked.

The aim of this paper is 1) to contribute to the understanding of branchfall and litter dynamics of different size classes in a mature oak woodland and to examine whether 2) eCO₂ treatment impacts branchfall, litterfall and woody turnover after 4 years of fumigation. We hypothesise an increase in smaller branches and twig litterfall under eCO₂ given the already observed sustained enhancement of photosynthesis (Gardner et al., 2022) and increased litterfall (Norby et al., 2024). We expect no treatment effect for medium to larger branchfall, as these sizes will

have experienced most of their growth prior to the start of eCO₂ treatment. At the same time, the small woody material has potentially grown in tandem with the increased leaf production and thus may also have increased with eCO₂.

3.2 Methods

3.2.1 Description of Field Site

This study was conducted in the temperate broadleaf deciduous woodland research facility of BIFoR FACE, Staffordshire, UK. The forest consists of 150-year-old pedunculate oaks (*Quercus robur*) as canopy dominant species and a dense understory with coppice common hazel (*Corylus avellana*) and hawthorn (*Crateagus monogyna*) and sycamore (*Acer pseudoplatanus*). The woodland has been largely unmanaged for the past 30-40 years. Three plots receive 150 ppm above ambient CO₂ concentrations, and three plots receive ambient air (Figure 2-1). Each plot contains free-standing towers of canopy height outfitted with pipes that omit the (enriched) air to be dispersed by wind throughout the canopy. The towers are positioned in an approximate circular pattern and placed to avoid the existing vegetation. As a result of this, each plot differs in area, ranging from 626 m² to 728 m². See Hart et al. 2022 for extended site characteristics.

3.2.2 Branchfall and litterfall inventories

Branchfall over time was observed using a Line Intercept Sampling (LIS) method for larger branches. In each plot, an octagonal line transect of approximately 80 m total length was placed in April 2021 (Figure 3-1). Before the start of the LIS inventories (hereafter referred to as “inventory”), the already present stock of branch deadwood crossing the newly placed transect was observed (hereafter referred to as “pre-transect”), so that the results of past branchfall events, of which most occurred before start of treatment, can put the observations in this measurement period into perspective and determine overall deadwood biomass stock. Afterward, new branches falling on each transect were monitored, measured and tagged at monthly or bimonthly intervals from the start of May 2021 to the end of May 2022. Both pre-transect counts and (bi)monthly inventory counts are upscaled to the total branchfall for the whole plot (see section 3.2.3). For each (fallen) branch sample that crossed the transect, the diameter was measured at base, middle and end with a digital calliper, and length to nearest cm with a tape measure. The minimum thresholds to be included was set at 20 cm in length and at least 1 cm in diameter at the base. The maximum threshold for branchfall only was 7.50 cm diameter at base.

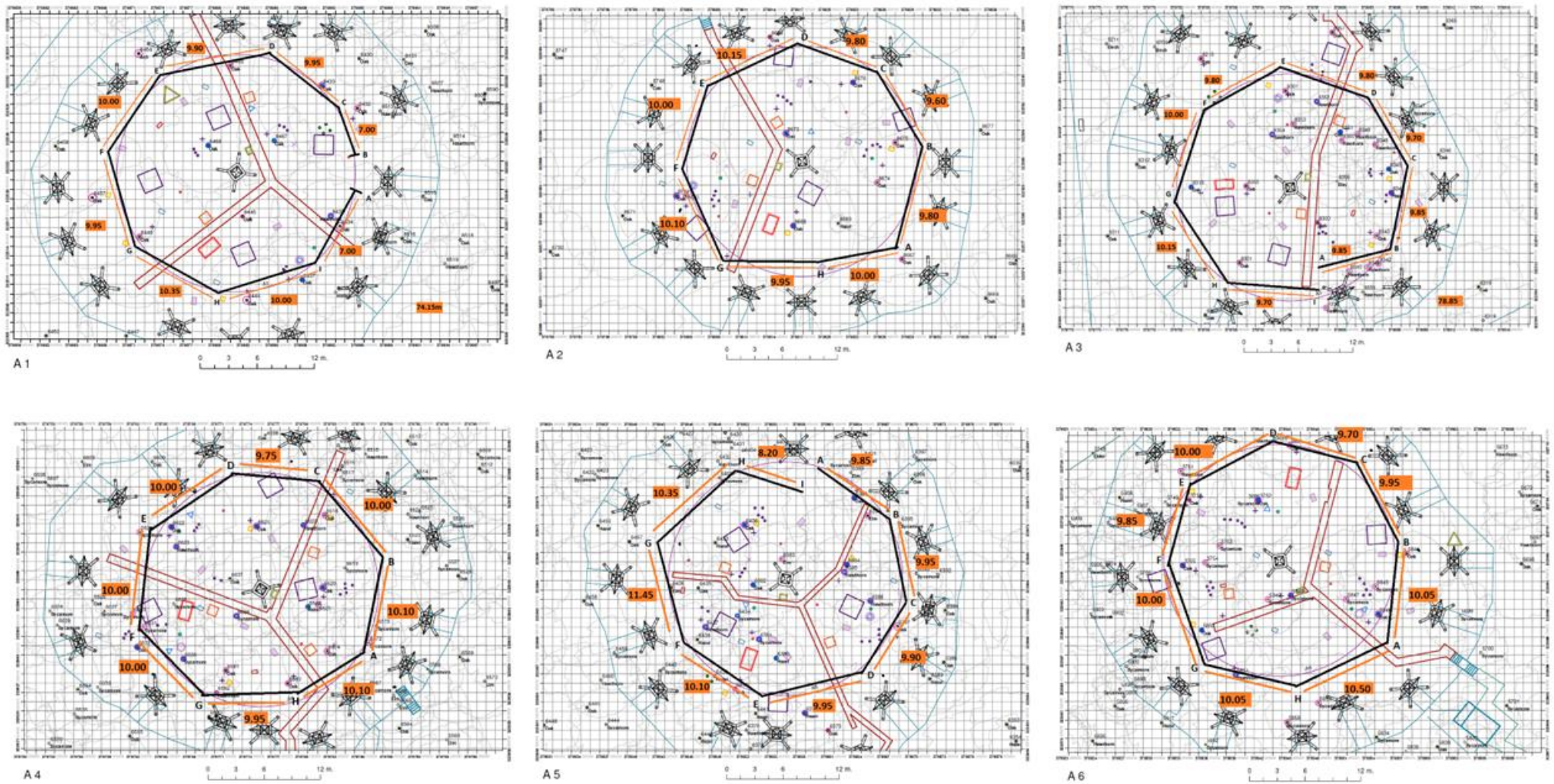


Figure 3-1. Top-down view of BIFoR FACE plots A1 to A6, including transect orientation and length. Black lines indicate transect and orange boxes show the length of transect compartments A to H in meter. Red lines are walkway infrastructure. The total transects lengths; A1: 74,15 m, A2 79,40 m, A3: 78,85 m, A4: 79,90 m, A5: 79,75 m, A6: 80,10 m.

Species and branching occurrences meeting the same thresholds and decay classes were noted. Five decay classes were used, following (Hunter, 1990; via Di Lella et al., 2019): (1) Recently downed, with bark intact; (2) Bark becoming loose or sloughing off, no sapwood degradation; (3) No bark present with some sapwood degradation; (4) No bark and considerable sapwood degradation; (5) Sapwood and heartwood degradation.

The total volume for each sample was determined by assuming the branch consisted of two separate truncated cones sharing one of the two surface areas.

$$V_{total} = V_{base-middle} + V_{middle-end} \quad (3)$$

$$V_{base-middle} = \left(\frac{1}{3}\right) * \pi \frac{1}{2} l * (R_{base}^2 + R_{base} * R_{middle} + R_{middle}^2) \quad (4)$$

$$V_{middle-end} = \left(\frac{1}{3}\right) * \pi \frac{1}{2} l * (R_{middle}^2 + R_{middle} * R_{end} + R_{end}^2) \quad (5)$$

Where V_{total} is determined by l of length from base to end, and R_{base} , R_{middle} and R_{end} are the radii of the truncated cone surfaces. From the samples containing one or more side branches meeting the same inclusion threshold of 20 cm in length and 1 diameter at base, the branch volumes are added to the final sample volume. Wood density of 580 kg m⁻³ for oak and 500 kg m⁻³ for understory species was used to calculate dry mass. A single wood density was used for all decay classes, as the main use of pre-transect inventory is to gauge previous branchfall dynamics and fluxes as they occurred when no or little decomposition and loss of wood density had taken place.

Litterfall is measured using six 0.25 m² traps placed in each plot. Litter was collected at monthly intervals. The samples were oven-dried for 48 hours, sorted by type (total leaves, oak leaves, sycamore leaves and petioles, hazel leaves, hawthorn leaves, unsorted leaves, reproductive output, twig and other) and weighed. We used data on twig litterfall collected between the start of May 2021 and the end of May 2022.

3.2.3 Upscaling branchfall data

The line-transect observations were upscaled to a plot-wide estimate by assessing the probability that a branch of a certain length would cross the transect line within a plot. The probability was first derived analytically and then verified using a numerical simulation (see below). Figure 3-2 A depicts how the probability of a branch of length l falling on the transect is determined by the transects radius T and the area S of the plot. A branch will intersect with

the transect if it falls in the shaded area, an ellipse. If the branchfall at a different angle than depicted, we assume symmetry, and the probability remains the same. See equations A-1 to A-6 in Appendix A for the complete derivation. The equations 6 to 8 show the main steps:

$$Probability = \frac{\text{shaded area}}{\text{plot area}} \quad (6)$$

$$\text{Shaded area} = 2 * \left(\frac{\pi}{2}\right) * T * l = \pi * T * l \quad (7)$$

$$Probability = \frac{\pi * T * l}{S} \quad (8)$$

3.2.4 Validation upscaling method

To test the accuracy of Equation 6 in section 3.3.3, a numerical comparison was implemented to calculate the probability of transect intersection of random generated branches of length l using the R *LearnGeom* package (version 1.5, 2022). An octagon with radius T is plotted within a square with area S . A single branchfall is simulated by randomly generating x and y values for the branch base and a random angle between 0° and 360° , and then drawing a line of length l , to the branch tip. Whether or not the branch crosses the transect is determined by cross comparing the coordinates of the transect lines with the base and tip of each branch. This process is repeated 1000 times to generate 1000 branches “dropped” in area S per round, and then each round is repeated 500 times. Figure 3-2 B shows a still of a subset of 10 branches. Probability is calculated for each round by dividing the mean count of crossing with the transect by 1000; this is the average over the 500 repetitions. The process is repeated for six lengths l ranging from 25 to 155. Figure 3-2 C compares the scaling factors (1000/ probability) calculated from Equation 6 with the branch drop simulations for the case when $S = 9000000 \text{ cm}^2$ and $T = 1273.24 \text{ cm}$. The agreement between the simulation and Equation 6 with identical T and S values supports using the scaling factors derived from the equation for upscaling the observed samples to plot wide numbers.

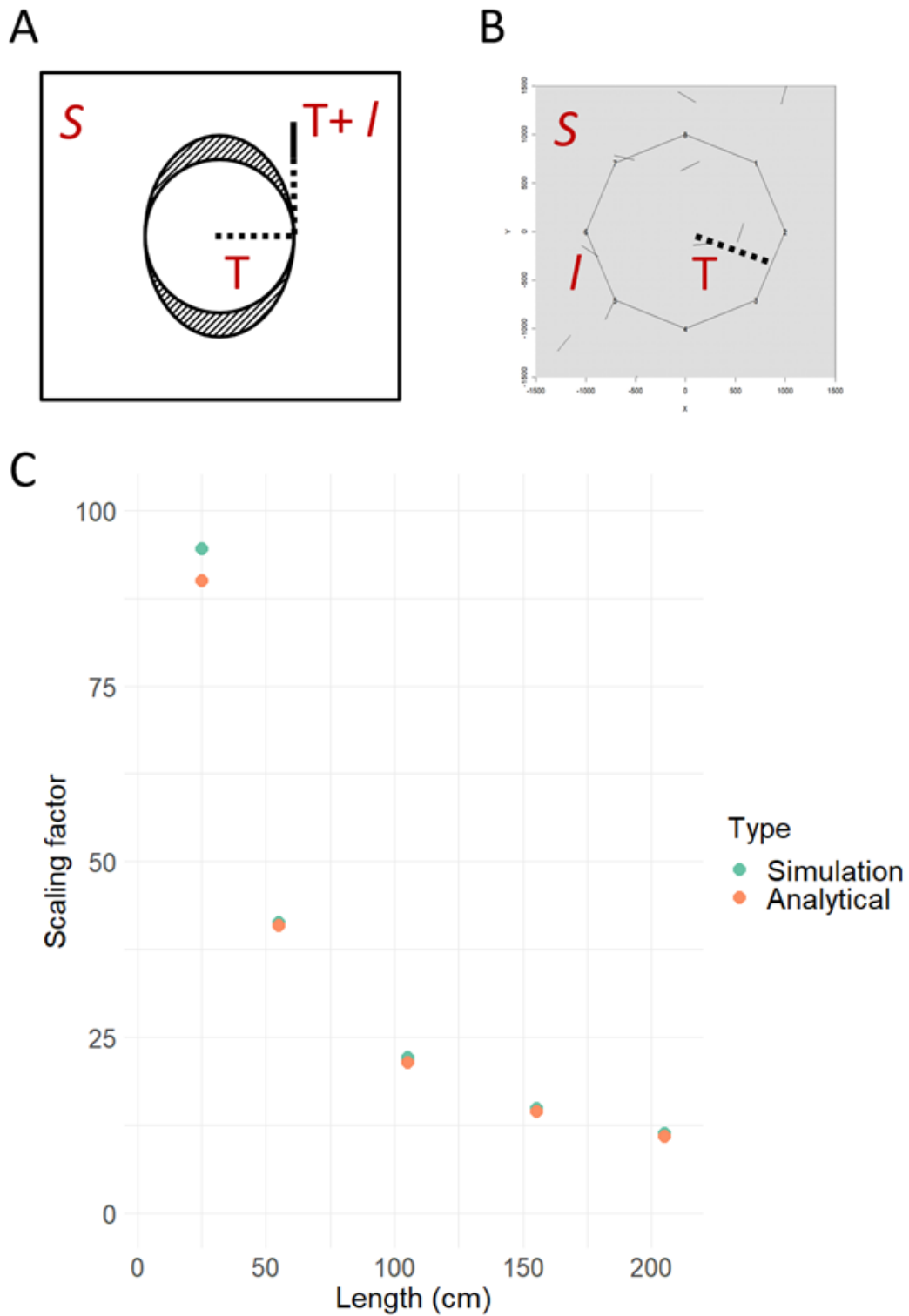


Figure 3-2 Analytical and simulation for upscaling octagonal Line Intersect Sampling. A) Illustration of analytical approach determining the probability of branch of length l intersecting a transect with radius T , within a plot of size S . B) Still of the subset in random branch drop simulation ($n = 10$) with branches of length l , a transect with radius T 1273.24 cm within a plot of size S . C) Scaling factors for the numerical and analytical derived probabilities per length.

Each observation is put into a length class (20-40; 40-60; 60-80; 80-100 and > 100) as well as diameter class (> 3.00, 3.00-2.50, 2.50-2.00, 2.00-1.50 and 1.50-1.00). The mean of each length class is used as input for l , and all samples above 100 cm are given l of 155, which is the mean length of all branchfall observations longer than 100 cm. The area of the plot is used for S , and the radius of T is a constant of 1273.24 cm across each length class and plot. The upscaled dataset is made by repeating each branch observation times their respective scaling factor rounded up to the nearest full number.

3.2.5 Determining above ground woody biomass of oaks and understory

To quantify the flux of living and dead branch biomass from canopy to forest floor, first the above ground woody biomass ($AGB_{stem+branch}$) present in each plot is assessed. The oak woody biomass is determined by using TLS data supplemented by allometric scaling for missing trees to account for the trees that did not meet quality checks in Chapter 2 but nonetheless are still present in the plot and contributing to branchfall. The TLS data was collected using a RIEGL VZ-400i scanner (RIEGL Laser Measurement Systems GmbH, Horn, Austria) during leaf-off conditions between January 23 and February 26, 2022. Chapter 2 provides a detailed description of the construction of the qualitative structure models (QSMs) in MATLAB (2022b) using *optqsm* and *treeqsm* algorithms from the generated point clouds. The fitting of cylinder primitives to the processed point clouds of each isolated tree gives detailed information on branch diameter and length and subsequently volume and biomass in each tree's canopy. To use the TLS derived volume, a wood-specific density of 580 kg m^{-3} was used to calculate biomass for each branch. The allometric equation for the missing trees (eq. 10) is based on the metrics derived from the TLS data of the oaks at the BIFOR FACE research site (Norby et al, 2024).

$$\ln(\text{Oak } AGB_{stem+branch}) = 2.312 * \ln(DBH) - 1.0862 \quad (9)$$

where Oak $AGB_{stem+branch}$ is in kg, and DBH is the diameter at breast height in centimetres.

To obtain an estimate of $AGB_{stem+branch}$ for other species that are present in the plot contributing to branch and litterfall, species-specific equations for sycamore and other understory species, such as hazel or hawthorn are used (Forrester et al., 2017; Norby et al., 2024).

$$\ln(\text{Sycamore } AGB_{\text{stem+branch}}) = 2.4186 * \ln(\text{DBH}) - 2.3116 \quad (10)$$

$$\ln(\text{Other understory } AGB_{\text{stem+branch}}) = 2.4143 * \ln(\text{DBH}) - 2.1653 \quad (11)$$

Where DBH is the diameter at breast height. The five thickest sprouts on each hazel stool are measured for multi-stemmed coppiced hazel samples. Oak branch biomass (Oak AGB_{branch}) in the trees that were successfully processed to QSMs was determined by omitting all branches with BranchingOrder = 0 (stem) from each dataset ($n = 46$) and then divided into two size classes: 6.00 cm – 3.00 cm and 3.00 cm – 1.00 cm diameter. The relation between Oak $AGB_{\text{stem+branch}}$ and Oak AGB_{branch} in these size classes was calculated for each plot. The resulting linear equations (Figure A-6), together with $AGB_{\text{stem+branch}}$ calculated using Eq 10, were used to include the contribution of the missing oak trees ($n = 7$) to Oak $AGB_{\text{stem+branch}}$ and Oak AGB_{branch} in each plot. Woody turnover per size class is determined by dividing 12 months' worth of Oak branchfall in $\text{g m}^{-2} \text{ yr}^{-1}$ by the Oak AGB_{branch} in g m^{-2} multiplied by 100. Two-tailed t-tests were used to determine P-values to test for the significance of the treatment effect at the $\alpha = 0.05$ level.

3.3 Results

3.3.1 Pre-transect observations and upscaled deadwood biomass

The total number of pre-transect branches observed before the branch turnover monitoring started was 429 across the six plots. Diameter size at the base ranged from 1.06 cm to 29.30 cm and length from 20 cm to 1260 cm. Table 3-2 shows the probability for crossing the transect calculated for each plot and length category using Equation 6, the observed crossing count and subsequent upscaled counts. After upscaling, the total number grew to 12394 samples of pre-transect deadwood and made for deadwood biomass stock ranging from 3334 g m^{-2} to 8449 g m^{-2} across the six plots, with a site-average ($\pm$ SD) of $4800 \pm 2818 \text{ g m}^{-2}$. The pre-transect deadwood represents the cumulation of woody biomass resulting branchfall and tree death events from years prior to fumigation, with Figure 3-3 B) showing a large portion of deadwood mass in the advanced decay classes of IV and V. The largest fraction of pre-transect deadwood is found within the oak species, $6096 \pm 3024 \text{ g m}^{-2}$ and $2376 \pm 870 \text{ g m}^{-2}$ for aCO₂ and eCO₂ respectively, followed by understory with $433 \pm 213 \text{ g m}^{-2}$ and $563 \pm 816 \text{ g m}^{-2}$ for aCO₂ and eCO₂ respectively. Differences between means are not significant (Welch's t-test, $p = 0.159$ and $p = 0.812$).

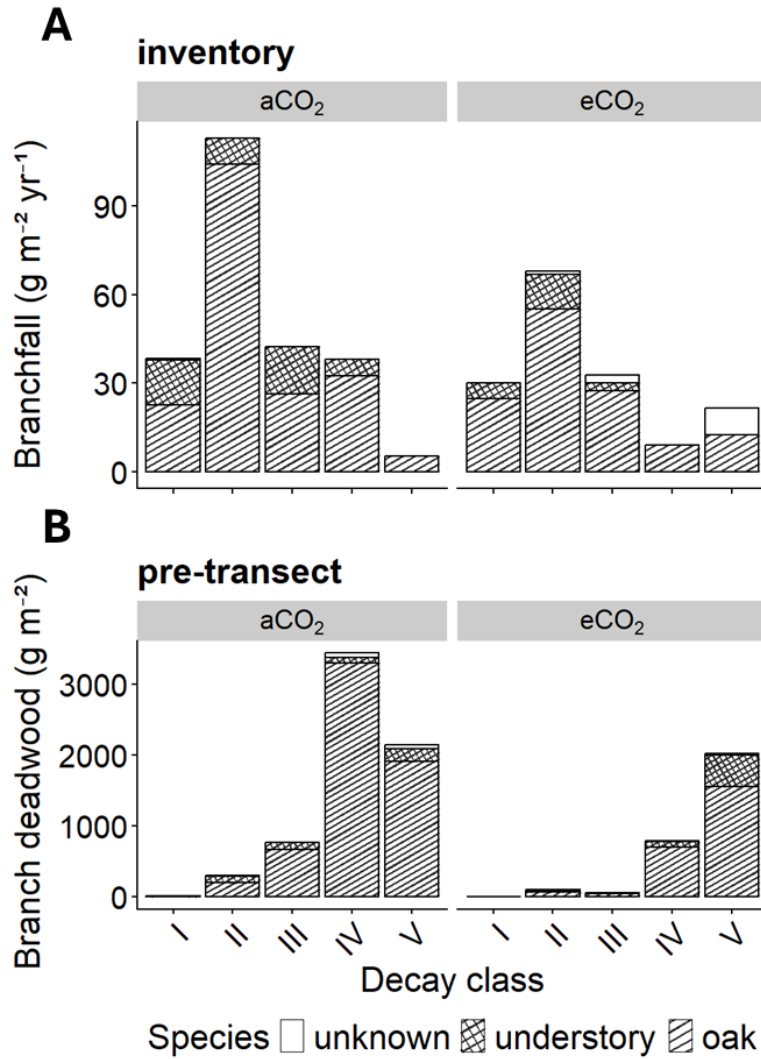


Figure 3-3 Deadwood biomass before and after transect placement collected at BIFoR FACE under eCO₂ and aCO₂. A) Branchfall across decay classes per treatment over 12 months in g m⁻² yr⁻¹. B) Pre-transect placement deadwood stock across decay classes per treatment in g m⁻². Species means across treatments (n = 3) are stacked.

Table 3-1 Probability, observation count of 12 months inventory, upscaled count per length category, and plot using equation (6). T = 1273.24 cm in each plot. Areas eCO₂ plots: S_{A1} = 24 m², S_{A4} = 702 m², S_{A6} = 678 m². Areas aCO₂ plots: S_{A2} = 628 m², S_{A3} = 661 m², S_{A5} = 668 m².

Plot	Length category	Probability	Observation count	Upscaled count ^a
A1	> 100 cm	0.0829	9	117
	100 - 80 cm	0.0497	7	147
	80 - 60 cm	0.0387	9	234
	60 - 40 cm	0.0276	15	555
	40 - 20 cm	0.0166	8	488
A2	> 100 cm	0.0955	10	110
	100 - 80 cm	0.0573	2	36
	80 - 60 cm	0.0446	5	115
	60 - 40 cm	0.0318	9	288
	40 - 20 cm	0.0191	12	636
A3	> 100 cm	0.0908	26	312
	100 - 80 cm	0.0545	5	95
	80 - 60 cm	0.0424	13	312
	60 - 40 cm	0.0303	13	442
	40 - 20 cm	0.0182	17	952
A4	> 100 cm	0.0855	16	192
	100 - 80 cm	0.0513	4	80
	80 - 60 cm	0.0399	10	260
	60 - 40 cm	0.0285	16	576
	40 - 20 cm	0.0171	12	708
A5	> 100 cm	0.0872	6	72
	100 - 80 cm	0.0523	4	80
	80 - 60 cm	0.0407	3	75
	60 - 40 cm	0.0291	13	455
	40 - 20 cm	0.0174	11	638
A6	> 100 cm	0.0885	8	96
	100 - 80 cm	0.0531	5	95
	80 - 60 cm	0.0413	3	75
	60 - 40 cm	0.0295	12	408
	40 - 20 cm	0.0177	13	741
1. Upscaled to nearest whole number				

3.3.2 Branchfall observations and upscaled cumulative branchfall

During the 12 months of monitoring, 296 branches fell on the transects across the six plots, collectively containing 37 side branches within the length and diameter threshold. Of the observations, 222 came from oak, 66 from understory trees and 8 samples could not be identified. During the measuring period complete canopy sections with base diameters larger than 7.50 cm were found on the transect during high wind speed events. Although an important contribution to total turnover in the multi-year context of the BIFoR FACE experiment, these were omitted. The diameter size at base ranged from 1.01 cm to 7.46 cm, and length from 20 cm to 650 cm. The upscaled dataset consists of 9334 samples, with the number of samples for oak, understory, and unknown upscaled to 7565, 1465 and 304, respectively. The total branchfall biomass ranged from 124 g m⁻² to 284 g m⁻² across the 6 plots. Figure 3-3 A) shows that more branchfall occurs in the plots with the largest mean deadwood stock, and oak branches make up the majority of branchfall mass, analogous to the species distribution in the pre-transect deadwood stock. Close to 66% and 62% of the mean total oak branchfall biomass are in decay categories I and II for aCO₂ and eCO₂ respectively.

Figure 3-4 shows the cumulative branchfall of the oaks and understory throughout the monitoring period of 12 months. At the end of this period, the total branchfall for oak and understory was significantly higher in under aCO₂ (Table 3-2, $p = 0.021$ and $p = 0.016$ respectively). Branches fall roughly evenly throughout the year, with a peak between November and February for both species' groups. The mean branchfall is seemingly consistently higher for oaks throughout the year, and shortly after August 2021 under aCO₂ for understory species driven by large input from one plot.

The branchfall of different diameter classes and twigs from the litter traps is shown in Figure 3-5, where in most classes, the turnover is lower under eCO₂, except for classes 3.00-2.50 cm and 1.50-1.00 cm, where the values are almost identical between treatments. The twig litter in aCO₂ was roughly the same weight as aCO₂ coarse branchfall in > 3.00 cm class, but twig litter in eCO₂ was almost triple the weight of > 3.00 branchfall in the same treatment.

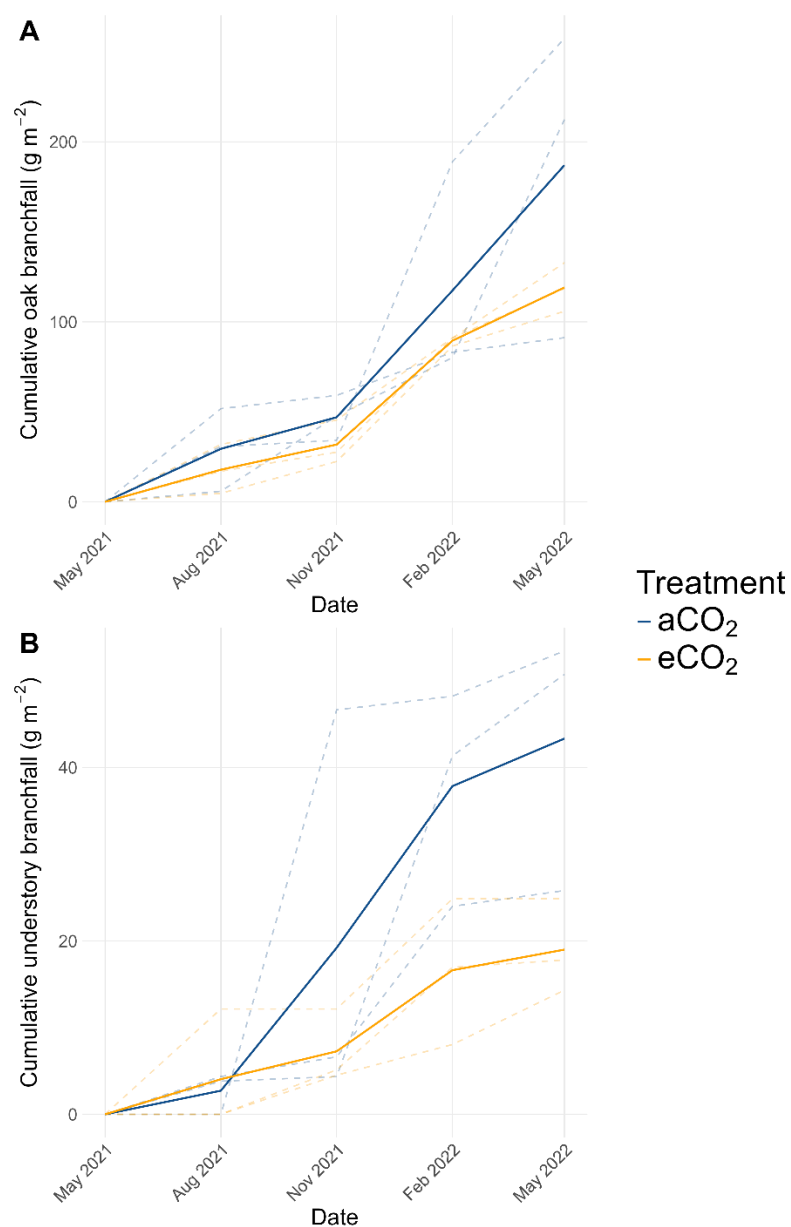


Figure 3-4 Cumulative oak and understory branchfall over 12 months in g m^{-2} per plot and average per treatment. The dashed lines represent cumulative branchfall in each separate plot; the solid lines are the mean across plots per treatment ($n = 3$).

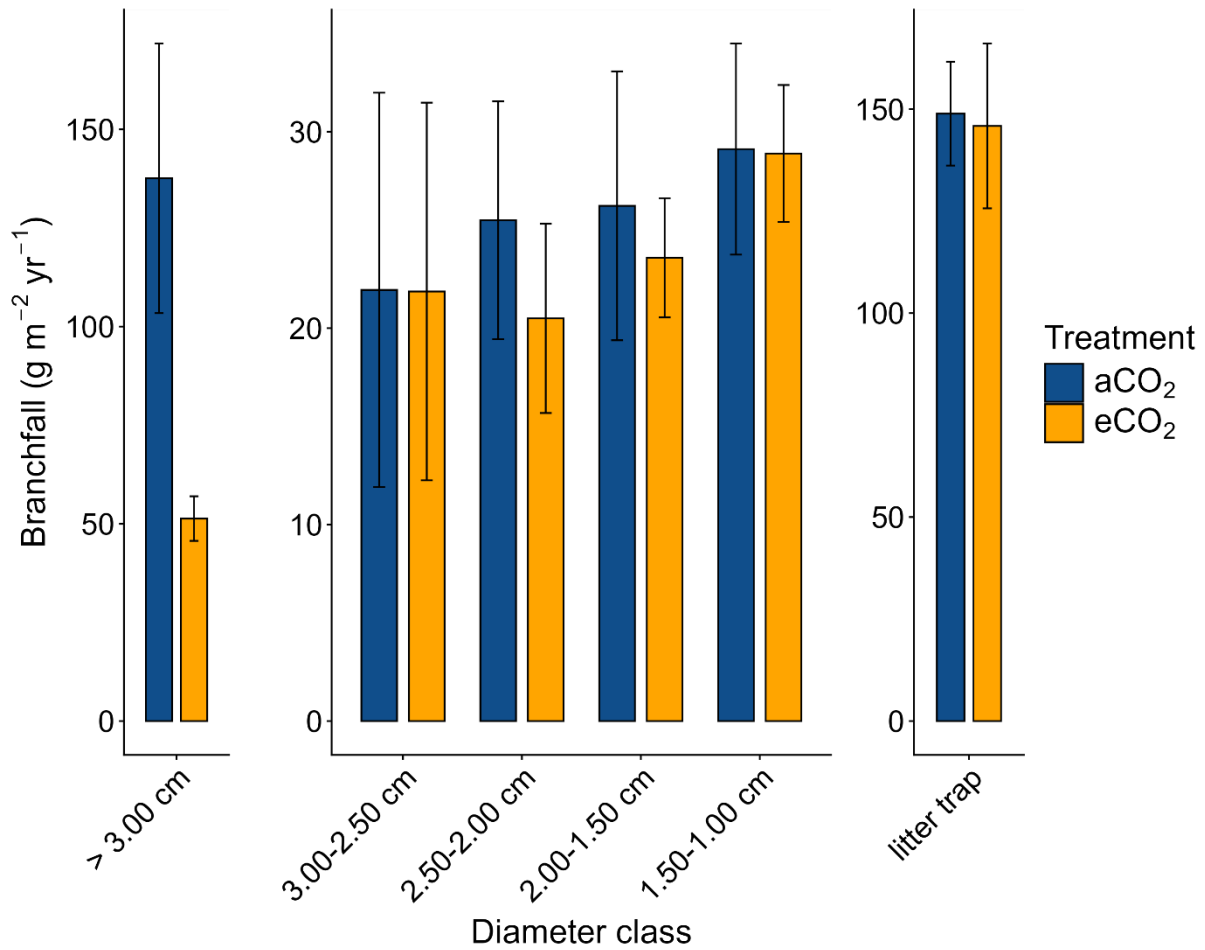


Figure 3-5 Branchfall across different diameter sizes and twig litterfall coloured per treatment. Bars represent the means and error bars show the standard error across the plots per treatment (n = 3).

The branchfall is separated into oak and understorey and their respective diameter class components in Table 3-2. The $AGB_{\text{stem+branch}}$ in 2022 for oaks and understorey is included to provide a reference for magnitude of branchfall in relation to the total stem and branch biomass. The oak branchfall within diameter size class > 3.00 cm is seemingly higher under aCO₂ compared to eCO₂ (p = 0.176). The oak leaf litterfall fraction is significantly higher under eCO₂ (p = 0.017), and while the understorey leaf litterfall fraction and the sum of both species' leaf litterfall together also appear to be higher under eCO₂, these are not significantly different from aCO₂ (p = 0.309 and p = 0.0519 respectively). The e/a ratio in oak $AGB_{\text{stem+branch}}$ (0.9) is similar throughout the branchfall of branches smaller than 3.00 cm (between 0.8 and 0.9).

Table 3-2 Mean ($\pm$ SE) above ground stem and branch biomass ($AGB_{\text{stem+branch}}$), branchfall across diameter ($\varnothing$) classes in cm and litter fractions of BIFoR FACE species per treatment. The ratio of the value in eCO_2 to the value in aCO_2 is e/a. Two-sample t-test determined the significance between treatment means, p values < 0.05 are highlighted in bold.

	AGB _{stem+branch} 2022	Total	Ø > 3.00	Ø 3.00-2.50	Ø 2.50-2.00	Ø 2.00-1.50	Ø 1.50-1.00	Twig litter traps	Leaf litter traps
	<i>g m⁻²</i>		<i>Branchfall g m⁻² yr⁻¹</i>						
Oaks									
eCO ₂	67561 ± 6992	122 ± 10	48 ± 3	17 ± 7	19 ± 5	16 ± 4	21 ± 3		330 ± 5
aCO ₂	74156 ± 7286	189 ± 50	114 ± 32	18 ± 6	23 ± 7	18 ± 7	22 ± 3		290 ± 19
e/a	0.911	0.642	0.425	0.948	0.828	0.866	0.949		1.138
P value t-test	0.445	0.021	0.176	0.924	0.682	0.785	0.803		0.017
Understory									
eCO ₂	234 ± 46	19 ± 3	NA	7 ± 3	5 ± NA	7 ± 2	6 ± 1		122 ± 21
aCO ₂	166 ± 40	43 ± 9	36 ± 7	8 ± NA	4 ± 1	8 ± 3	6 ± 2		93 ± 14
e/a	1.418	0.443	NA	0.921	1.183	0.913	0.915		1.302
P value t-test	0.613	0.016	NA	0.869	NA	0.711	0.513		0.309
								<i>g m⁻² yr⁻¹</i>	
							Species combined		
							eCO ₂	146 ± 20	464 ± 16
							aCO ₂	149 ± 13	396 ± 17
							e/a	0.980	1.171
							P value t-test	0.895	0.0519

NAs in means are caused by 0 observations in a category within all plots, and NA in SE and p values are caused by observations from only one plot included per treatment.

3.3.3 Woody turnover from mature oak canopy

Oak branchfall over 12 months was used to quantify the flux from AGB_{branch} to the forest floor over time. The AGB_{branch} in diameter size class 6.00 – 3.00 cm shows a non-significant ($p = 0.310$) lower average under eCO_2 ($13056 \pm 2048 \text{ g m}^{-2}$) compared to aCO_2 ($15826 \pm 865 \text{ g m}^{-2}$). For the 3.00 – 1.00 cm size class a non-significant ($p = 0.236$), but positive treatment effect was observed; on average $6288 \pm 1088 \text{ g m}^{-2}$ of branch biomass was present under eCO_2 treatment, while only $4199 \pm 1031 \text{ g m}^{-2}$ under aCO_2 . When stacked mean AGB_{branch} in these size classes make up $\sim 28\%$ and $\sim 27\%$ of $AGB_{stem+branch}$ (Table 3-2) under eCO_2 and aCO_2 respectively. Figure 3-6 shows the woody turnover rate as the percentage of AGB_{branch} lost through branchfall over 12 months in these size classes. In the smallest size class, almost 1.5% of AGB_{branch} is lost under aCO_2 , compared to 1% under eCO_2 , making woody turnover of branches between 3.00 and 1.00 cm in diameter seemingly 0.5% lower under eCO_2 compared to aCO_2 . In the larger size class the woody turnover is close to a tie between aCO_2 and eCO_2 conditions, which is most likely a pre-treatment effect. None of the differences in woody turnover between treatments were significant (6.00 – 3.00 cm: $p = 0.901$ and 3.00 – 1.00 cm: $p = 0.393$).

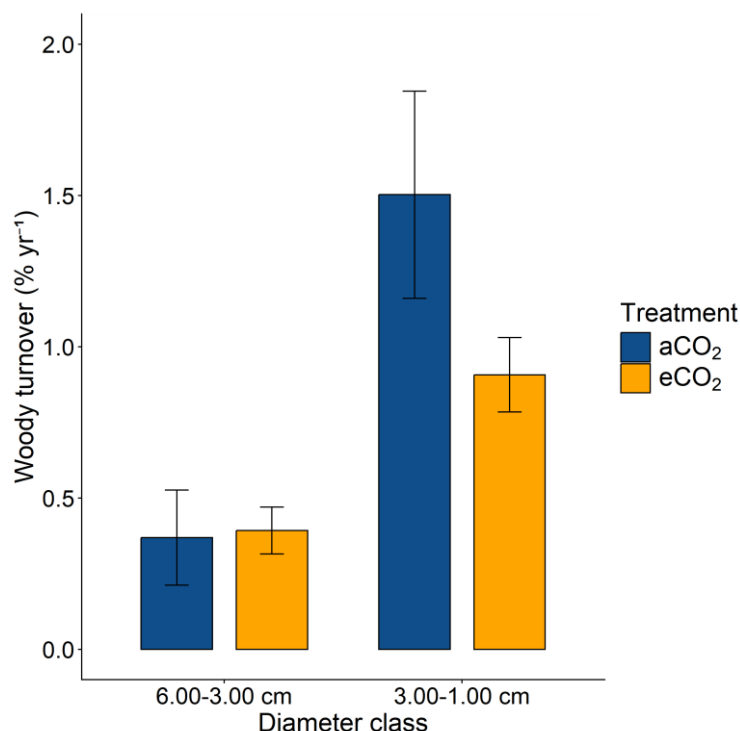


Figure 3-6 Woody turnover of oak branch biomass in canopy to forest floor as percentage lost over 12 months. The bars represent the means and standard error bars across plots ($n = 3$) per treatment.

3.4 Discussion

For both pre-transect deadwood and subsequent collective branchfall over 12 months (Figure 3-3), in all diameter sizes (Figure 3-5) and species types (Figure 3-4, Table 3-2) and regardless of the AGB_{branch} present in the size class (Figure 3-6), branchfall or woody turnover was higher under aCO_2 compared to eCO_2 . The hypothesis that increased twig litterfall and branchfall in smallest branches would follow previously observed enhanced photosynthesis and C assimilation (Gardner et al., 2022) and stem NPP (Norby et al., 2024) under eCO_2 was not supported. There was an increase in leaf litter for both the dominant oaks and understory species, consistent with previous observation at the same site (Norby et al., 2024). Chapter 2 described increased branch volume of smaller diameter sizes (> 2.50 cm) in the highest layers of the oak canopy under eCO_2 . These branches are hypothesised to be there to facilitate increased leaf tissues grown and subsequently lost under eCO_2 (Table 3-2), and potentially for that reason not (yet) lost from the canopy (Figure 3-5).

When assuming this enhancement in smaller woody turnover under eCO_2 is the direct outcome of enhancement in small branch growth for supporting optimal light capture, these results are in line with a proposed positive feedback loop due to CFE (Poorter et al., 1997). The results indicate that enhancement of a C input flux is not directly associated with a C output flux after 4 years of fumigation. If this effect does not change over time due to i.e. progressive nutrient limitation, it would mean that this mature forest has reached a new carrying capacity previously unattained due to a C resource limitation in the ecosystem. The implications for future forest response to increasing atmospheric CO_2 concentrations are an even higher C sequestration capacity and increased priority to protect mature and old-growth forest against harvest.

3.4.1 Interpretation of pre-transect deadwood dynamics and mass

The mean pre-transect CWD mass of 4800 g m^{-2} sits at the upper range compared to other old-growth deciduous forests: *Fagus-Betula* forest ($3000\text{--}4900\text{ g m}^{-2}$), *Pinus* forest ($2900\text{--}4200\text{ g m}^{-2}$), and *Acer* forest ($790 - 1620\text{ g m}^{-2}$) (Harmen & Hua, 1991). When taking the absolute number of this deadwood pool in consideration this might suggest that BIFoR FACE woodland is transitioning from mature to old growth since unmanaged mature forests are expected to hold more deadwood over time due to accumulation combined with an increased tree mortality rate, of which canopy breakage is often a precursor (Zuleta et al., 2013). There was, however, no site-specific data available on interaction of eCO_2 and decomposition rates, and no measurements of wood density per decay category were made for both pre-transect and inventory samples. Using one woody density number for all decay categories will have likely

overestimated the deadwood mass to a certain extent, since wood density will decrease as decay advances, e.g. for *Quercus robur* from 580 kg m⁻³ to 380 kg m⁻³ (Bitunjac et al., 2023). The main argument for conducting a pre-transect survey was to investigate previous branchfall dynamics and fluxes as they occurred when no or little decomposition had taken place. So, these numbers still reflect important information on the varied dynamics in these plots; deadwood mass in largest plot is almost 3 times that of the smallest. Additionally, both treatment means have over 90% of their deadwood mass represented in the > 3.00 cm diameter classes and within the III to V decay classes (together 73%). The latter is also likely caused by large debris decomposing at a slower rate, the species difference in decomposition rates (Russell et al., 2015), and potentially the large CWD being recognisable as deadwood on top of the forest floor for longer. The higher deadwood mass in > 3 cm diameter sized deadwood under aCO₂ shows that the stands in these ambient plots have been impacted by larger canopy breakage in the past, relative to eCO₂ plots, while still having a higher AGB_{stem+branch} at present than forest in eCO₂ plots (Table 3-2), implying that plots have since these large branchfall events have recovered from these events back into to a state of equilibrium.

3.4.2 Increased leaf litterfall is not followed by increased twig or branchfall

The significant increase in oak leaf litter and apparent rise in total and understory leaf litterfall under eCO₂ were consistent with observations of increased total litterfall from earlier years at the same site (Norby et al., 2024). However, despite the enhanced photosynthesis and C assimilation (Gardner et al., 2022) and increased litterfall of short-lived tissues like leaves, the loss of other presumed shorter-lived woody tissues like twigs, fine branch material or larger branches did not increase in the fourth year of fumigation (Table 3-2). This lack of increased loss of short-lived tissue could either indicate that a response is delayed, and the mature oaks retain twigs and smaller branches to support the increased leaf production until a new steady state is reached, after which litter and branchfall will catch up. Alternatively, it could indicate a persistent increase in C allocation towards woody tissue (Walker et al., 2019) as was observed after 6 years of fumigation at the younger Duke FACE pine and broadleaf forest. Litterfall and branchfall did not increase in proportion with (above + belowground) NPP either under eCO₂, and cumulative tree mortality was lower under eCO₂ (Palmroth et al., 2023). Further supporting a shift towards small branch production, the percentage of Oak AGB_{branch} within 3.00 – 1.00 cm diameter class lost from the canopy in 12 months (Figure 3-6) is appearing to be lower under eCO₂, while the branch volume present per available canopy volume appeared higher in the same range under eCO₂ (Chapter 2). This suggests that after 4 years of fumigation the

mature oak canopy shows increased the growth of small branches without increased turnover, which is not expected in an ecosystem that is presumed to be at an equilibrium between new growth and mortality (Brienen et al., 2020). To confirm if this is a temporary delay or sustained treatment effect, yearly or bi-yearly scans to continuously determine branch density in all canopy levels as well as continued monthly monitoring of branch and litterfall are needed. This underscores that a previously observed treatment effect in photosynthesis, C assimilation, leaf litterfall or increased branch density (Chapter 2) cannot be used to directly extrapolate proportionate twig litterfall or branchfall after 4 years of fumigation of a mature oak dominant forest.

3.4.3 Intra-annual variability, branch size variability and under/overstory variability

The cumulative branchfall over 12 months (Figure 3-4) shows that branchfall was consistently higher under aCO₂ throughout the collection year, with substantial variability between plots and steep increases at autumn and winter. Continued monitoring of branchfall would inform if this variability in a single year aligns with long-term interannual variability as seen for litterfall in other FACE experiments. For example, in the first year before and the year after fumigation started at DukeFACE, twig litter was lower than eCO₂, while this dynamic flipped in year 2. Observations of eCO₂ deciduous leaf litterfall were consistently higher under aCO₂ compared to aCO₂ across the three years (Finzi et al., 2001), like the higher leaf litterfall over three years at BIFoR FACE (Norby et al., 2024). In contrast, the EucFACE overstory leaves and twig litter fractions under eCO₂ remained equal or lower compared to aCO₂ litter fractions across four years (Jiang et al 2020b).

The steep increases in the dotted and averaged solid lines in Figure 3-4 highlight the substantial impact of major branchfall events on the wood dynamics for each separate plot and the averaged treatment effect. The relatively large contribution of branches beyond twigs in the litter traps to these dynamics is further illustrated in Table 3-2 and Figure 3-4, where collective branchfall in the 3.00 cm to 1.00 cm diameter classes already reaches ~ 66% of the annual twig litterfall. The difference between > 3.00 cm diameter class under eCO₂ and aCO₂ also shows that the branches in the > 3.00 cm diameter class are driving the negative treatment effect seen in the total branchfall. In line with this, extreme weather events can mask or overwhelm expected treatment effects due to disproportionate increased inputs, as seen in a case where branchfall following an ice storm likely obscured an CO₂ fertilization effect on litterfall for 2 whole years before returning to significant difference (Lichter et al., 2008). This underscores

the importance of multi-year inventories that include the monitoring of partial canopy mortality and larger sized branchfall, in addition to the continuation of litter collection and complete tree mortality surveys.

3.4.4 Limitations of this study

This chapter's research had to rely on a pioneering transect placement for the LIS method with and use an expansion method not used before in forestry research to the authors knowledge. And while the probability of branchfall falling on the octagon transect shape was validated by a random branch drop simulation, the upscaled branchfall mass could be inflated. For example, each observed branch in the largest length class was repeated ten times in both the upscaled deadwood and the upscaled branchfall dataset (Table 3-1). Long branch samples were often the samples with relatively large base diameters, this means high volumes and thus relatively large contributions to total g m^{-2} . It is untested how the use of octagon transects to monitor branchfall compares to the use of the conventional straight-line linear sampling or alternative set-ups. The measuring of base-middle-end diameters was chosen to improve volume estimations that could be compared to canopy biomass, instead of solely the measuring of base and/or diameter at intersections. The largest base diameter in the branchfall dataset is 7.46 cm, a size that is often not even included in the threshold for CWD inventories that start measuring only from 5 or 10 cm in diameter (Woldendorp et al., 2004; Busing & Fujimori, 2005), which makes comparing this C output flux through branches to other repeated measurements of branchfall challenging. A full analysis of all branchfall at the site is beyond the scope of this thesis. As seen with the ice storm at DukeFACE (Lichter et al., 2008), high-wind events at BIFoR FACE (December 2021 and April 2022) caused major canopy damage, with large branches landing on transects but also obstructing critical infrastructure. For safety, these branches were moved and disassembled before measurements could take place. Due to time constraints, the fact that growth of these large branches predates the start of fumigation and the risk of overwhelming predicted treatment effects, an upper threshold of 7.50 cm in diameter was set for the turnover dataset analysis. The large branches were measured later with an adjusted protocol, and this data (not shown) could still be valuable for future studies that assess interannual branchfall variation, post storm recovery and canopy closure dynamics.

Although the majority of branchfall in the 12 months of measurement period was categorized in decay category I or II (Fig 3-3), which can be interpreted as recently broken from living canopy section and only just started decomposition, there are also cases where branches with

advanced decay markers fell on the transect. This shows that observations with this survey method will include branches that died in canopy before measurement period, or even before treatment start, and fell to forest floor on a later date. Additionally, it may miss branches that have died during measurement period but have not yet detached from the tree or have but are captured and held by understory branches. The author assumes that the fraction of branchfall that is missed and the fraction that is surplus are close to the same, yet future research might be able to confirm or deny this. In addition, using TLS to determine $AGB_{\text{stem+branch}}$ and AGB_{branch} , makes it impossible to differentiate between living and dead branches. It is therefore assumed that branch biomass in the canopy of this mature forest which achieved a closed canopy threshold, remains constant over time and that branch NPP is equal branchfall for branches < 7.50 cm in diameter in this study. In essence, disregarding the impact of large branch death events, which drastically alter canopy structure which could take multiple years to recover from and are thus outside the scope of this study.

Another limitation is a misalignment of time of scans and the start and duration of the transect observations included in the analysis. Branchfall has been monitored for a 12-month period and the possible variation in a season's cycle of weather conditions and subsequent effects on branchfall is included, the scans were, however, made close to the 6-month mark. It was considered that the completeness of branchfall data over 12 months in all plots, the seasonal variation and consistency in observer took president over the timepoint of scans made at t_0 .

Finally, a limitation that all FACE experiments face is lack of replicates when a mechanism behind the occurrences of branchfall or litterfall is investigated, as the outcomes can generally only be observed on a plot scale with subsampling methods like LIS and litter traps. Additionally, looking at a treatment effect on stand scale comes with compounding variability due to factors such as local microenvironmental differences and weather conditions or soil status between rings. The scope of this thesis could not include multiple timepoints, but continuing the observations will also increase statistical power besides capturing a wider size range of branchfall occurrences. It cannot be overstated, however, that these experiments provide the only current day *in situ* observations for forest responses to future conditions.

3.5 Conclusion and future works

This chapter set out to determine if eCO_2 impacts branch and litterfall and woody turnover of branch biomass in the canopy of a mature forest stand over 12 months measuring period. The

first objective was to fill a research-data gap on branchfall under eCO₂ in mature forest as by reviewing the literature, little data was found on these dynamics in these forest stands exposed to eCO₂ treatment. Specifically, it tested the hypothesis that previously observed increased leaf litterfall and preliminary enhanced stem and branch growth under eCO₂ would be followed by increased twig litter and smaller sized branchfall with similar magnitude. However, the results did not support this hypothesis. In contrast, a non-significant but higher total branchfall in both dominant and understory under aCO₂ instead of eCO₂ was observed. Additionally, a lower turnover rate of smallest branch size was measured. The precise mechanisms for growth of “long-lived” woody tissues with additional C available under eCO₂ and if extra growth is sustained over time remain uncertain, for instance, considerably more work will need to be done to determine if the lower woody turnover observed in this study is sustained over time. In future research the interaction between eCO₂ and larger canopy death events, woody biomass lost through dead branches of all sizes, and subsequent re-closure of the canopy cover should be investigated. Although multiple years of observation may be required to discern effects. Additionally, a methodological gap on observing branch biomass dynamics beyond twig litterfall in circular plots was filled by creating and validating an octagonal LIS method to upscaled plot wide counts. This approach was effective in observing branchfall up to 7.50 cm in diameter, which makes comparison to other forest floor inventories of branchfall or deadwood stock using higher minimum diameter thresholds challenging. However, these findings highlight the currently overlooked contribution of the smaller than stem, but larger than twig biomass to overall forest biomass dynamics, and that treatment effect cannot be directly extrapolated from previous increasing leaf litterfall. Further work to optimize the observation of branchfall for this and other branch sizes is required, and a natural progression of this work would be to extend the measurement period over multiple years instead of months. More broadly, it would be interesting to review a multitude of different forest stands with CWD inventories especially focussed smaller sized branchfall, repeated over time, and AGB_{branch} at these time points, as well as surveys on stand age, species, management history and environmental variables. Such a synthesis would help determine if any changes in branchfall of smaller branches in the FACE experimental plots are site-specific or reflect broader trends in mature forests.

Chapter 4

Woody turnover under elevated CO₂ in two mature forest ecosystems

4.1 Introduction

Forests are of fundamental importance in the global carbon (C) cycle. These ecosystems act as a large C sink by assimilating more CO₂ from the atmosphere by a surplus of photosynthesis than is released back into the atmosphere, through autotrophic and heterotrophic respiration. The difference between the C that is captured (Gross Primary Production, GPP) and the C that is released back into the atmosphere via this respiration is net primary production (NPP). The NPP is allocated to grow different plant organs such as roots, photosynthetic tissues, and woody stem and branch material. Trade-offs in partitioning NPP among these compartments are a key part of adaptive strategies acquired through evolution to optimise plant production, competition, reproduction, and survivorship, impacted by prevailing growing conditions and past evolutionary pressures (Brienen et al., 2022). Quantifying C input and C output fluxes are vital metric for Dynamic Global Vegetation Models (DGVMs) to simulate vegetation dynamics over time and project the continuation of forest C sinks in the future (Sitch et al., 2015; Li et al., 2022). In DGVM models it is common to represent biomass as stem, leaf, and root tissues, putting the long-lived branch and stem compartments under the same constant residence time, the inverse of turnover rate (Xu et al., 2007). While these turnover rates can so inform dynamics of large-scale tree mortality events, the more frequent but smaller scale occurrences of branchfall or litterfall goes unnoticed in these predictions. The lack of observational data to inform on these models, along with the variety in growth–mortality trade-offs among species, and their outcome dependence on factors such as stand composition, environmental stress, soil nutrient status as well as the timing and pathways of carbon output fluxes, and the impacts of changing growing conditions on these processes all contribute to uncertainty in model outcomes. (Ciais et al., 2013; Friedlingstein et al., 2022; Quéré et al., 2018).

Elevated CO₂ (eCO₂) has been found to impact plant productivity on multiple levels. On the leaf level, increased photosynthesis and reduced stomatal conductivity have caused increased C assimilation from the atmosphere and lessened water loss through evaporation. This, in turn, increases the C availability for growing biomass and reduces water usage needs. This increased C availability can also generate a positive feedback; the additional C is allocated to growing more metabolic tissues such as leaves, leading to more photosynthesis and C assimilation, known as a CO₂-fertilization effect (CFE) (Walker et al., 2019). When positive feedback of CFE occurs, it remains unknown if or to what extent plants would invest the additional C into leaves and woody tissue or if one compartment is prioritized over another. Or if C allocation ratio would shift the longer plants are exposed to eCO₂ and C limitation is alleviated, since most plant level experiments do not last longer than 2 years at the most (Poorter & Navas, 2003). Other research suggests that the positive feedback loop on C uptake will decrease over time and lead to the flux returning to baseline levels due to CFE outpacing the nutrient supply (Finzi et al., 2008). There is evidence that the availability of resources other than C, particularly soil-based macronutrients, like as nitrogen (Crous et al., 2015, 2021; Norby et al., 2010) or phosphorus (Ellsworth et al., 2017), may limit the ability of plants to capitalise on increased C availability or result in a reduction in a positive CFE over time (Norby et al., 2022).

Besides investing surplus of C in additional photosynthetic capacity, an increased allocation to wood growth has also been predicted (Walker et al., 2019), and extensive research shows that saplings and young forest trees in the exponential growth phases are indeed growing faster when exposed to eCO₂ (Ainsworth & Long, 2005; Norby & Zak, 2011), although geographic location and environment, as well as temperature (Hyvönen et al., 2007; Norby & Luo, 2004)), impact the magnitude of the eCO₂ response. It is both the fluxes of C input and several C output fluxes that define the Net Ecosystem Productivity (NEP). Assimilated C that is used to grow woody biomass of trees, shrub stems, and coarse roots keep C locked in these “long-lived” tissues, potentially with C residence times of centuries. By comparison, “short-lived” tissues such as leaves, fine roots and most reproductive organs have short C residence times. These compartments enter the litter and soil decomposition stage of the C cycle faster, which in turn causes the return of C back into the atmosphere over time through heterotrophic respiration by (mainly) fungi and bacteria. For the long-lived wood, this transfer can take a long time, so dead wood, particularly larger branches and standing dead stems, are an important carbon pool of ~3.3 Pg C, and 5% of the global total deadwood is stored in temperate and subtropical forests (Wijas et al., 2023). In addition, 40% of deadwood on the forest floor of mature forests are

branches, and evidence shows that canopy breakage is a precursor to tree death (Zuleta et al., 2013). The impact of eCO₂ on mechanisms that drive the internal net ecosystem fluxes after the enhanced C input through photosynthesis, but before the final C output flux during decomposition of the deadwood causing C to return to the atmosphere remain ill-understood. Especially since the mechanisms of branch growth and branchfall are bi-directional and can impact net productivity through branch growth supporting metabolic tissues and impact substrate availability through loss of these compartments over time. Understanding and investigating the impact of eCO₂ on both the growth and mortality, including precursory branchfall, responses of different tree species with different growth-mortality trade-off traits required to accurately predict NEP and long-term C-sequestration of forests.

It has been hypothesised that fast growing species could be more responsive to eCO₂ compared to slow growing species. A very slight increase in eCO₂ biomass increase response of fast growers compared to slow growing herbs in short term competition experiments was observed, but no relationship between competitiveness of species and response to eCO₂ was found (Poorter & Navas, 2003). Conversely, on larger timescales even minor magnitudes of competitive edge in fast growers could still lead to NEP to decrease in C gain, as less wood dense species hold less C captured. Especially Liana's are likely to take advantage of high eCO₂ concentrations and would potentially shift tropical forest back to earlier successional stages by increasing tree turnover (Körner 2004). But most-time depending changes have not been investigated and although in isolated plant-level experiments most of the CO₂ induced growth stimulation is found at the beginning of the treatment (Poorter & Navas, 2003), it remains unclear how long-term exposure to eCO₂ on stand level with corresponding competition will impact growth and turnover or evolve over time.

Observations on whole tree mortality or the precursory branchfall cannot accurately be investigated in the small-scale and highlight controlled environments that have provided valuable evidence on eCO₂ effect on productivity on the individual plant level. The first generation (Free Air Carbon Enrichment) FACE experiments provided data on larger trees of different species mixtures, that exist in competition for resources and are exposed to environmental stressors. The investigations conducted in these young, mesic temperate plantation forests, provided some preliminary insights on woody tissue loss from the canopy through litterfall (Norby & Zak, 2011). Within the DukeFACE research site, early observations over the first two years showed significant more pine needle and bark litterfall under eCO₂, in contrast to unchanged deciduous leaf litterfall in eCO₂ plots. However, follow-up analyses after

nine years of CO₂ enrichment revealed that these early differences in litter deposition between pine needle and bark dissipated after the experiment's initial six years, but that the annual and total C inputs to the forest floor remained slightly elevated in eCO₂ environments (Lichter et al., 2008).

Although pine bark dynamics were observed in DukeFACE, the causes and mechanics behind the regular bark-shedding species are relatively unknown. Suggested is a connection to facilitate the growth in tree height or change lateral growth by shedding bark at regular intervals (Crockford & Richardson 1998) or speculated if the shedding causes an increased competitive position during fires (Gould et al., 2011). Observations are that shedding happens primarily in Australian summer and is also impacted by (seasonal) weather conditions (Pook et al., 1997; Crockford & Richardson 1998). The amount of bark shed observed can vary considerably between locations on stem, captured with funnel traps, and branches higher in the canopy, captured with litter traps (Pook et al., 1997). It is clear bark makes up a large portion of the total litter layer on eucalyptus Forest floors (~20-45%), and a change in biomass loss through shedding under CO₂ fertilization could be similarly relevant for long term C-sequestration as branchfall as well as e.g. nutrient availability or fire behaviour in the future (Grootemaat et al., 2017).

Accurate turnover rate estimated provide a stronger predictor for long-term biomass accumulation, and thus C sequestration, than the NPP in an ecosystem alone (Malhi et al., 2015; Yu et al., 2023). The term of *turnover time* is commonly used to refer to the ratio between total C stock and C input or output flux, making *turnover rate* in this case indicative of the fraction of total stock is gained or lost with the flux per unit of time. In complex models that use a process-based approach, using one turnover rate for a complete biomass pool, i.e. wood or leaves will overlook the dynamics of branchfall which is likely to be in between these outskirts on the dynamics spectrum (Sitch et al., 2015; Xue et al., 2017; Li et al., 2022). In field experiments with mature forests that are presumable at a carrying capacity, quantifying a change in branch and litterfall can inform on previous productivity changes in standing stock, under the assumption that these changes are directly or indirectly caused by treatment. And by comparing different sites, with different soil status and environmental stressors, the potential impact of these characteristics on canopy dynamics can start to be disentangled (Medlyn et al, 2015).

The first evidence on eCO₂ fertilisation on productivity in mature forests from observations at two second-generation FACE experiments are still inconclusive. Old-growth dry-eucalyptus forests showed enhanced photosynthesis, but no response to eCO₂ in stem biomass growth linked to phosphorus limitation (Elsworth et al., 2017; Jiang et al, 2020), while a mesic mature oak woodland also showed enhanced C assimilation in oaks (Gardner et al., 2022) and woody biomass increase during the first 3 years of eCO₂ exposure (Norby et al., 2024). The woody biomass loss data from these mature forests refers only to bark and twig litter captured in traps (Jiang et al. 2020b, Norby et al., 2024), leaving branch dynamics of mature forests unquantified. This lack of data on larger non-stem woody material in both experiments means a possible eCO₂ treatment effect of NPP allocation to branches or branch turnover is currently overlooked, which is contributing to uncertainty of NEP projections of future forests (Sierra et al., 2017).

This chapter aims to examine branchfall, litterfall and woody turnover, defined as fraction of standing stock biomass lost through branchfall and litterfall over time, in two mature forests stand exposed to eCO₂. 1) The first question is how branchfall and twig litterfall differ between two different forests subjected to similar eCO₂ treatment but with different productivity responses. Additionally, 2) if the impact of eCO₂ treatment on branchfall and twig litter varies between different canopy positions of dominant and understory is investigated. Finally, 3) if woody turnover through branchfall differs between branch sizes and between different eCO₂ exposure times is researched.

It is hypothesised that 1) when eCO₂ increased woody NPP in a mature steady state forest, this would also increase woody mortality rates, in this study quantified as increased branch and twig litterfall. Conversely, in forests where no NPP increase in wood was observed, it's expected that little to no increase in wood turnover rate would take place. 2) The eCO₂ treatment effect on branch and litterfall is expected to vary among species or canopy position due to their varied growth-mortality trade-offs, age, and size. The smaller, understory species that tend to show fast growth as part of the growth-mortality trade-off compared to larger, long-lived dominant species, are expected to show a positive and larger eCO₂ treatment effect on branchfall as well. 3) If eCO₂ treatment effect can result in additional C allocation to single compartments, e.g. only leaves, or branches to support leaves, and that such an allocation ratio doesn't change over time, a longer exposure time would result in larger treatment effect as trees will have had more time to grow branches and allocate the surplus C available to branches.

This would be discernible by an increase in relative contribution of larger branches to the total branchfall or woody turnover.

4.2 Methods

4.2.1 Site description

Two second-generation FACE experiments were used to monitor annual branch and litterfall: BIFoR FACE and EucFACE. EucFACE was established in 2010, and eCO₂ treatment started in 2012. The facility is situated in a native Cumberland Plain Forest with ~ 100-year-old *Eucalyptus tereticornis* as the canopy dominant species, a sparse understory of coffee bush (*Breynia oblongifolia*) as well as lianas (*Parsonsia straminea*) present in most of the plots. The removal or cutback of liana growth has happened twice since the start of the experiment as a maintenance measure, most recently in November 2022. The mean annual temperature (MAT) and precipitation (MAP) are 17.2 C° and 800 mm respectively. EucFACE is characterised by P-limited soil. BIFoR FACE is situated in a temperate broadleaf deciduous woodland in Staffordshire, UK. *Quercus robur* is the canopy-dominant species, 175 years old and unmanaged for the last 30-40 years. It has a dense understory consisting of coppice common hazel (*Corylus avellana*), hawthorn (*Crateagus monogyna*), and sycamore (*Acer pseudoplatanus*). The MAT and MAP are 9 C° and 690 mm, respectively. The eCO₂ treatments started in April 2016.

Both forests receive eCO₂ treatment via wind dispersal from integrated infrastructure enhanced to 150 ppm above ambient levels. The treatment plot sizes are varied at BIFoR FACE to avoid interference with dense vegetation, with an average plot diameter of 28 m. EucFACE plot diameter consistently 25 m in all treatment plots.

4.2.2 Transect, litter trap and stem bark observations

On the forest floor of each plot, octagon-configured line transects of 80 m circumference at BIFoR FACE (Figure 3-1) and 60 m circumference at EucFACE were used. The fall of the new branch and bark was monitored and tagged every month or two months at BIFoR from the start of May 2021 to the end of May 2022 and at EucFACE from the start of July 2022 to the end of July 2023. At BIFoR, a pre-transect inventory was also done to establish a baseline of deadwood on the forest floor. The observed branches and bark were then upscaled to the total branchfall for the plot (see section 4.2.3). In both forests, observations were made on species, side branches occurrence and decay, categorised into 5 stages: I) newly fallen, bark firmly attached; II) bark sloughing started, wood still intact; III) bark absent and start deteriorating of

sapwood; IV) bark gone, deterioration sapwood and hardwood present; V) extensive deterioration present, affecting both sapwood, hardwood and soft to the touch (Hunter, 1990; via Di Lella et al., 2019). Base, middle and end diameters were measured with a digital calliper of each sample. With a tape measure, the length to the closest cm. No minimum or maximum diameter size threshold was set to be included in the inventory at EucFACE, at BIFoR FACE the minimum base diameter was 1.00 cm. Both inventories had minimum branch length of 20 cm.

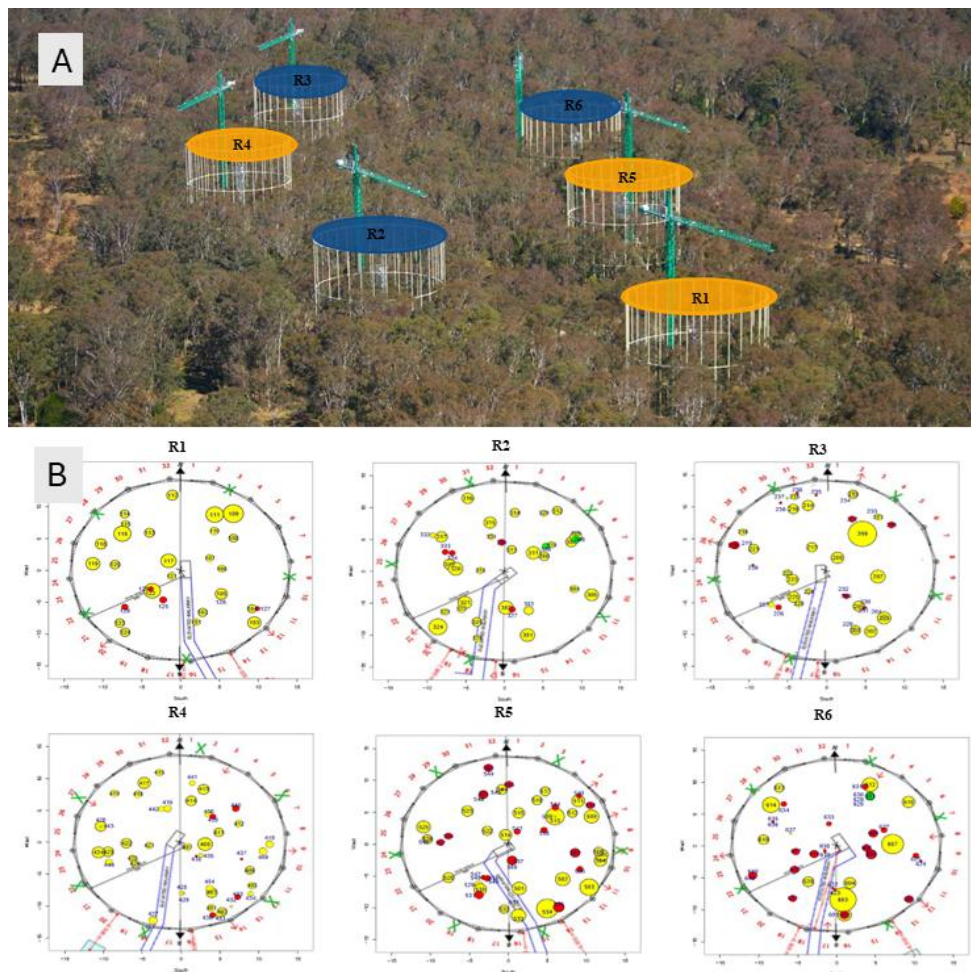


Figure 4-1 Annotated top view image of EucFACE forest with infrastructure and within infrastructure tree map. A) rings are coloured per treatment; orange for eCO₂ and blue for aCO₂. B) yellow circles indicate living trees, red show dead trees. Sizes of circles reflect relative size to other trees.

Wood volume per sample was determined by assuming the sample to be shaped as two truncated cones stacked, thus sharing one of the two surface areas.

$$V_{total} = V_{base-middle} + V_{middle-end} \quad (12)$$

$$V_{base-middle} = \left(\frac{1}{3}\right) * \pi \frac{1}{2} l * (R_{base}^2 + R_{base} * R_{middle} + R_{middle}^2) \quad (13)$$

$$V_{middle-end} = \left(\frac{1}{3}\right) * \pi \frac{1}{2} l * (R_{middle}^2 + R_{middle} * R_{end} + R_{end}^2) \quad (14)$$

In the equations above V_{total} in cm is determined by l as the length of the samples in cm and R_{base} , R_{middle} and R_{end} are the radii of the different diameters measured. When side branching occurred at EucFACE, an additional base-middle or middle-end equivalent volume was added per side branch longer than 20 cm. Species for branches was noted to be eucalyptus, understory, or liana. The side branches at BIFoR FACE that met the 20 cm and 1.00 diameter at base threshold were added to V_{total} .

Wood density was used to calculate the biomass of the observed volumes. The density for *Eucalyptus tereticornis* branches was 827 kg m⁻³ and eucalyptus bark 530 kg m⁻³ (Zanne et al., 2009), the understory species *Breynia oblongifolia* 500 kg m⁻³ (Zanne et al., 2009), and liana wood density measured at the site itself to an average of 528.5 kg m⁻³ (Coleman, personal communication). A specific wood density of 580 kg m⁻³ and 500 kg m⁻³ was used to calculate the dry mass of oak and understory, respectively.

At EucFACE, bark deposition on the transect that was larger than 20 cm in length was also noted. During the first month bark thickness in mm (with digital calliper) and bark width to nearest 0.5 cm at the middle of the sample was measured. This data was used for volume calculations of each sample in this month, and the relation between length and volume was determined after log-log transforming the length and volume to estimate volume of samples in the subsequent months. See Figure A-7 for length volume relation of bark per plot.

At EucFACE fine litterfall is collected using eight 0.20 m² circular traps placed randomly in each plot. Trap contents were collected monthly and then airdried in paper bags for at least two months. The litter was sorted by type (eucalyptus leaf, liana leaf, twig, reproductive flower/buds, reproductive fruits/seeds, and other, bark was only sorted at EucFACE) and

weighed to second decimal. At BIFoR FACE, litterfall was captured in six traps per plot, each with an area of 0.25 m². The collection of litter was performed monthly. Following collection, the litter samples underwent a drying process in an oven for 48 hours, after which they were sorted by type (total leaf mass, leaves of oak, leaves of sycamore (including petioles), leaves of hazel, leaves of hawthorn, reproductive materials, pieces of wood, and miscellaneous categories before being measured for their weight to the second decimal. No bark fraction is sorted from litterfall or captured on transects at BIFoR FACE as there are no bark-shedding species in the woodland.

Bark trap funnels were used to collect bark shedding directly from the eucalyptus stems of three trees in two of the three-ring pairs at EucFACE. The trees were chosen to have DBH closest to plot means. The funnels were made of fine mesh attached to PVC pipes with 3.65 m total length, which were bent to a circle around each stem, creating a collection area of one square meter around the stem (Figure 4-2). Funnels were mounted with an elastic wire so as not to obstruct stem expansion and bark shedding itself. Monthly collections were made between November 2022 and November 2023, and samples were airdried for several months before being sorted and weighed per type (eucalyptus leaf, twig, woody stem bark, finer bark and others). Weight was measured to 0.01 g.

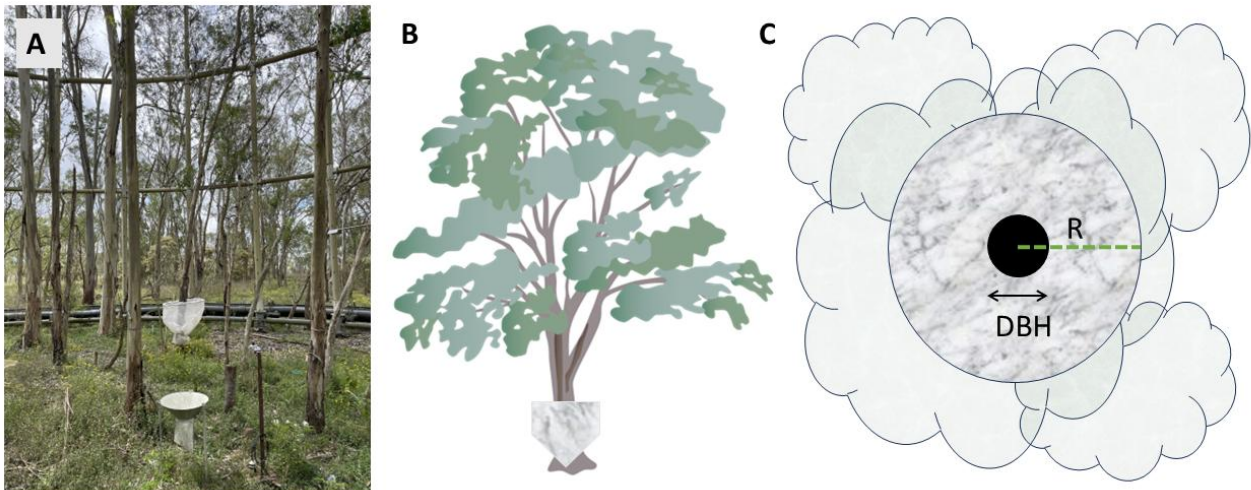


Figure 4-2. Images of bark trap for shedded stembark collection. A) Picture of bark trap attached to tree in the field. B) Diagram of bark trap. C) Top view diagram of bark trap and the capture area around the stem.

4.2.3 Upscaling branchfall data, litter data and bark trap data

The inventory on the line transects were upscaled to reflect plot-wide estimates using probability assessments described and validated in Chapter 3. The complete derivation of the analytical probability is described in equations A-1 to A-6. Equation 16 shows the probability of a branch of length l falling on a transect with radius T in a plot of size S :

$$Probability = \frac{\pi * T * l}{S} \quad (15)$$

Where length l is in cm, transect radius T is in cm, and plot area S is 4907000 cm² for each ring at EucFACE. At BIFoR FACE, the plot sizes S varied per plot: 7240000 cm² (A1), 7020000 cm² (A4), 6780000 cm² (A6), 6280000 cm² (A2), 6610000 cm² (A3), and 6680000 cm² (A5).

The probability for each length category was then divided by 1000 to determine the scaling factor by which each observation with measured attributes would be scaled up to plot quantity. The litterfall fraction weights were averaged across traps and then multiplied by the corresponding plot size. Bark stem weights were averaged across traps and then multiplied per number of trees within each ring to plot scale stem bark shedding.

4.2.4 Above-ground biomass

Allometric scaling was used to determine the $AGB_{eucalyptus}$ (whole tree, stem, branch and leaves), and diameter at breast height (DBH) was measured in September 2022 with vernier dendrometer bands.

$$\ln(AGB_{eucalyptus}) = -2.15 + 2.34 * \ln(DBH) \quad (17)$$

Where $AGB_{eucalyptus}$ is in kg and DBH in cm (Paul et al., 2016).

A combination of TLS-derived volume and subsequent biomass of stem and branch per tree ($n = 46$) and allometric scaling-derived kg ($n = 7$) was used to determine the AGB of 53 oaks across the 6 treatment plots. For TLS-derived volume, a wood-specific density of 580 kg m⁻³ was used to determine mass.

$$\ln(AGB_{oak}) = 2.312 * \ln(DBH) - 1.0862 \quad (18)$$

Where AGB_{oak} (whole tree, stem and branch) is in kg and DBH in cm (Norby et al., 2024).

The woody turnover was then determined as percentage loss of $AGB_{\text{eucalyptus}}$ and AGB_{oak} respectively, to determine how much of the total woody standing stock was lost through branch and litterfall. By dividing the mass of branchfall within 6-3 cm diameter and 3-1 cm or < 3.00 cm diameter classes over 12 months of both oaks and eucalyptus.

Treatment effects and p values to differences were determined by Welch's t-test if $n > 2$.

4.3 Results

The total number of branches observed on the transect at BIFoR FACE before monitoring started was 429 and thereafter upscaled to 12394 samples. This mostly represents the cumulation of branchfall and tree mortality events over time and before the start of eCO_2 exposure treatment. The total branches observed and tagged on the transect during the inventory year was 296; 222 came from oak, 66 were from understory trees, and 8 could not be identified as either oak or understory. The branchfall dataset was upscaled to 9390 individual branches across the 6 plots. At EucFACE the total number of samples observed on the transects was 2999 samples, of which 980 bark pieces and 2019 branches, subdivided into 778 from eucalyptus, 123 from understory and 118 liana samples. The upscaled dataset counted 85451 across the 6 plots.

Figure 4.3 presents the distribution of inventory and pre-transect at BIFoR FACE and inventory at EucFACE across decay classes I to IV. At EucFACE the majority of branchfall was allocated to the I decay category for both eCO_2 and aCO_2 , while at BIFoR FACE's inventory a greater proportion is in category II for both eCO_2 and aCO_2 . At both research sites, the species distribution in the branchfall is similar; dominant trees make up most of the branchfall, with the BIFoR FACE understory making up more of the branchfall biomass than the EucFACE understory. There were no significant differences in treatments between groups of the same species and decay class ($p = 0.494$ to $p = 0.992$).

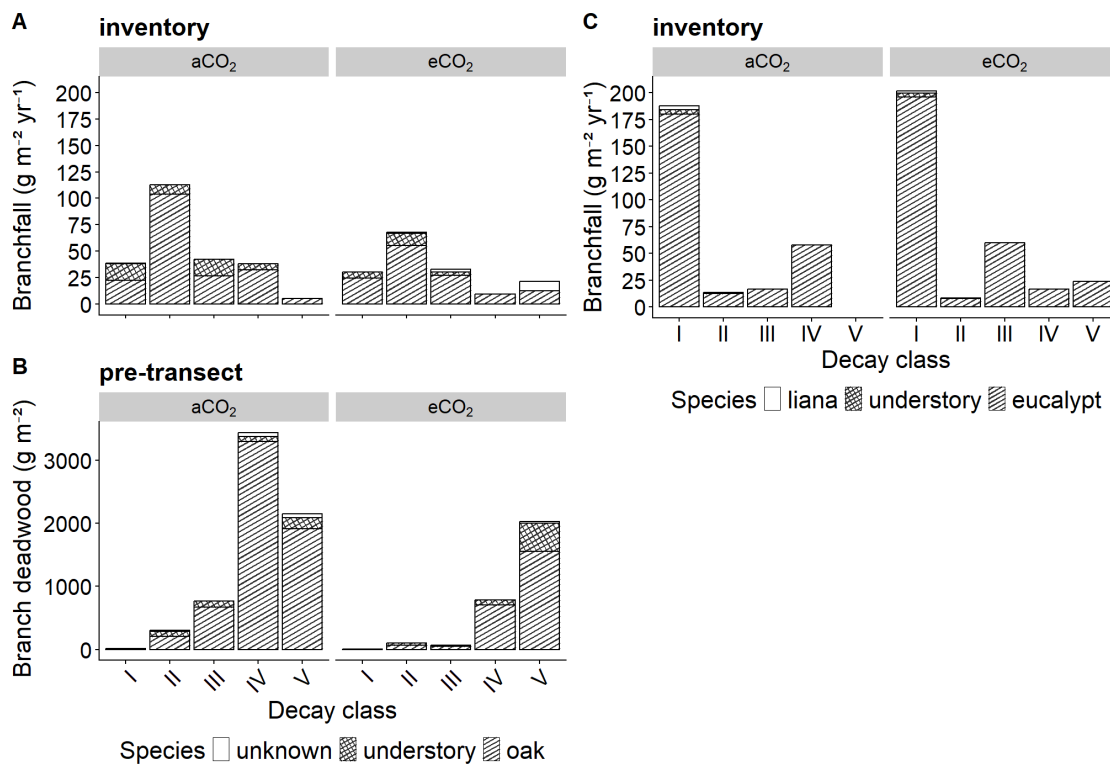


Figure 4-3 Branchfall biomass and pre-transect deadwood biomass. A) Branchfall of > 1.00 cm in diameter over 12 months across decay classes per treatment at BIFoR FACE. B) Pre-transect deadwood across decay classes per treatment at BIFoR FACE. C) Branch branchfall over 12 months across decay classes per treatment at EucFACE. Means of all species per treatment (n = 3) are stacked.

In Figure 4.4 the overview of the mean branchfall in different size classes including twig litterfall over 12 months at EucFACE and BIFoR FACE is provided. The left panels show branchfall in size class > 3.00 cm in diameter, which is seemingly lower in eCO₂ compared to aCO₂ for EucFACE (p = 0.579) and BIFoR FACE (p = 0.124). The middle panel for EucFACE, the branchfall is higher under eCO₂ than aCO₂ for all classes of 2 cm and smaller, including the twig litter. However, none of these differences were statistically significant (p values ranging from 0.093 up to 0.721). The branches larger than 2 cm in diameter show non-significant negative treatment effect (p = 0.547). For BIFoR FACE, all the size classes < 3.00 cm under eCO₂ are consistently similar or lower than aCO₂, but with no statistically significant differences in any size class (p values ranging from 0.555 to 0.974).

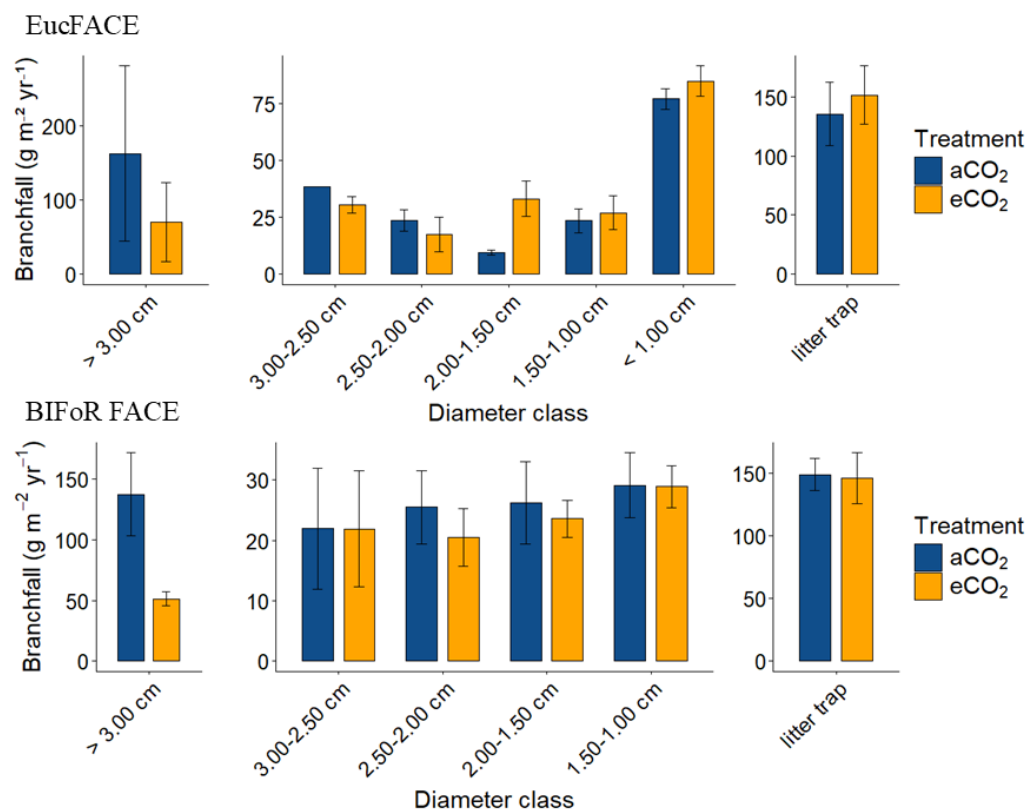


Figure 4-4 Branch and twig litterfall over 12 months at EucFACE and BIFoR FACE per diameter size. Each bar represents mean plot sum of mass per diameter size category. Error bars represent the standard error across plots (n = 3).

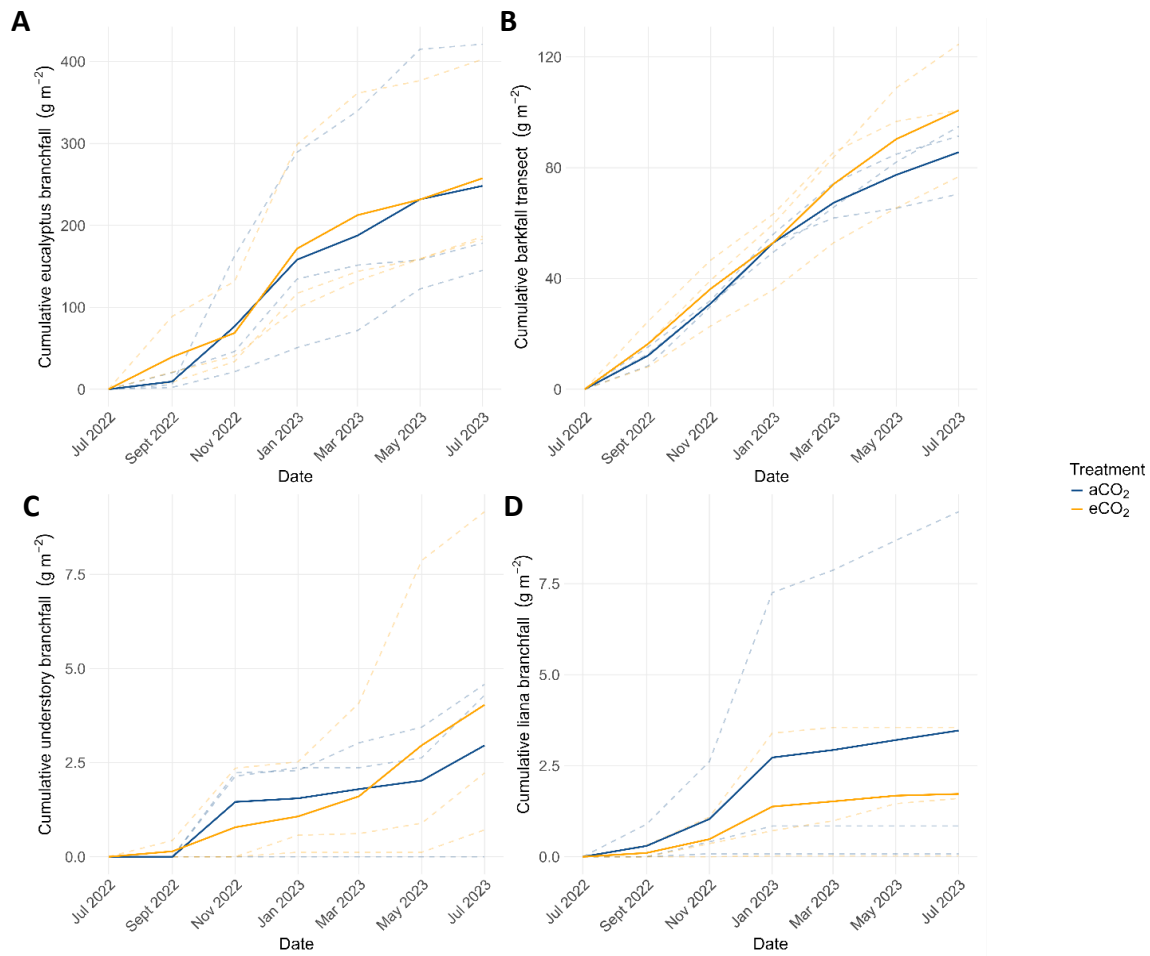


Figure 4-5 Cumulative branchfall and bark fall from upscaled transect observations, separated by species over 12 months at EucFACE. A) Cumulative branchfall eucalypt branches in g m⁻². B) Cumulative eucalyptus bark fall in g m⁻². C) Cumulative understory branchfall in g m⁻². D) Cumulative liana branchfall in g m⁻². Dashed lines represent cumulative branchfall in individual plots, and solid lines show the mean cumulative across the plots (n = 3) coloured for treatment.

Figure 4-5 shows the mean cumulative branchfall and barkfall on the transects over 12 months of collection. The variation between plots, e.g. the distance between dotted lines, is the lowest for eucalyptus bark litterfall, and a consistent increasing line shows relative consistent shedding throughout the year. The cumulative eucalyptus branch and bark litterfall are seemingly slightly higher under eCO₂ than aCO₂, although not significantly different at any point throughout the 12 months of collection ($p = 0.350$ or higher). The cumulative understory branchfall after a year is higher biomass under eCO₂. Liana branchfall appears to remain lower under eCO₂

compared to aCO₂ throughout the year, but also not significantly different at any date ($p = 0.571$ or higher).

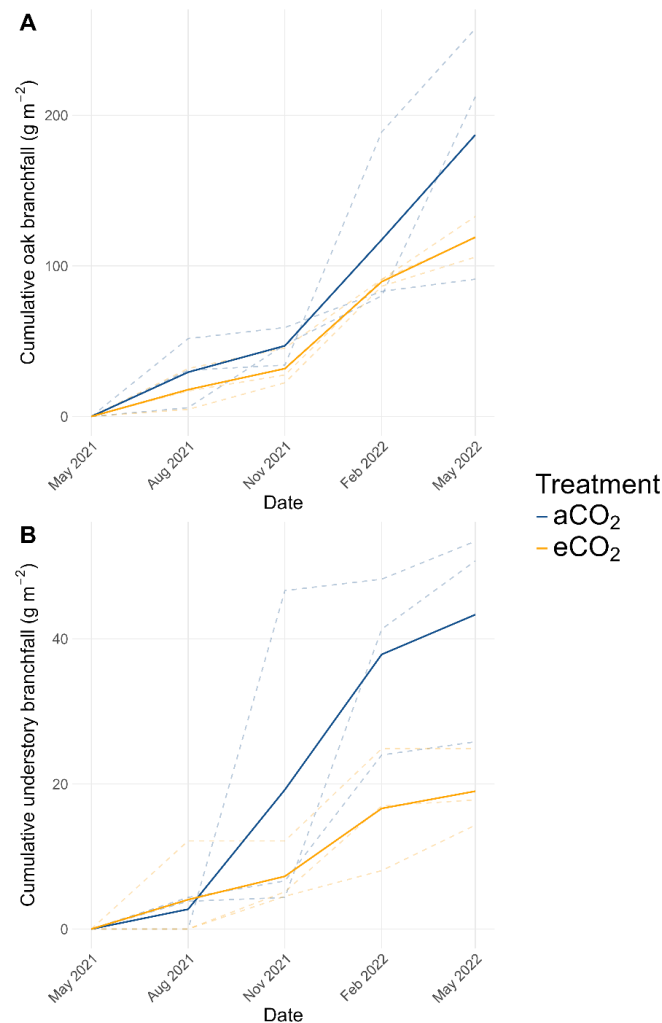


Figure 4-6 Branchfall at BIFoR FACE A) Cumulative branchfall of oak in g m⁻², B) Cumulative branchfall of understory g m⁻². Dashed lines represent cumulative branchfall in individual plots and solid lines the mean cumulative across the plots (n=3).

At EucFACE, the cumulative understory branchfall and the canopy dominant eucalyptus branchfall in Figure 4-5 show similar variations per plot, with the mean branchfall of both eucalyptus and understory seemingly, but not significantly ($p = 0.910$ and $p = 0.892$ respectively) higher under eCO₂ at the end of the collection year. In both the canopy dominant oak and understory branchfall at BIFoR FACE (Figure 4-6), the mean cumulative branchfall appears to show a negative treatment effect and remain lower under eCO₂ instead of higher, but also not significantly different at any of the timepoints ($p = 0.097$ or higher).

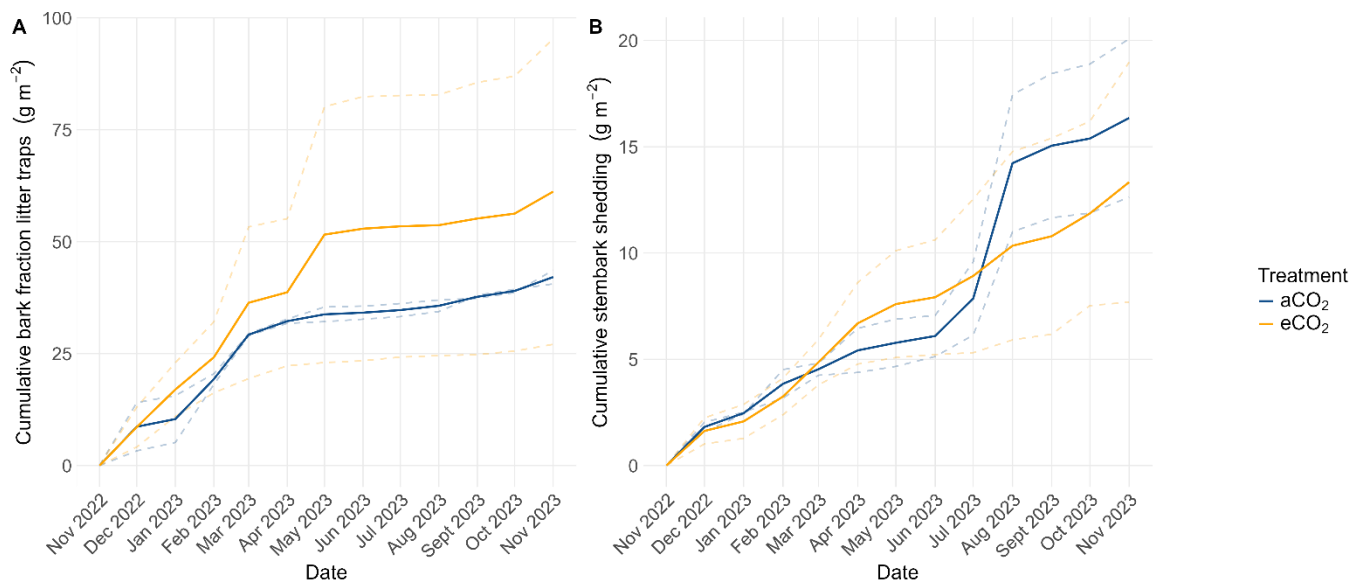


Figure 4-7 Bark litterfall and bark stem shedding at EucFACE. A) Cumulative bark fraction of litterfall caught in the litter traps over 12 months and B) cumulative shedding of stem bark in the bark traps over 12 months. Dashed lines are cumulative falls in plots. The solid line is the mean across these plots (n = 2).

The difference in bark fraction of litterfall between the eCO₂ plots is quite high for both collection methods, ~ 50 g m⁻² after 4 months in the litter traps, while aCO₂ plots show similar trends and biomass weights throughout the year. Due to the low number of repetitions (n = 2) no significance test was applied.

Table 4-1 Mean ($\pm$ SE) above ground biomass (AGB), branchfall across diameter ($\emptyset$) classes and litter fractions of EucFACE species per treatment. The ratio of the value in eCO₂ to the value in aCO₂ is e/a. Two-sample t-test determined the significance between treatment means, p values < 0.05 are highlighted in bold

	AGB 2022	Total	Ø > 3.00	Ø 3.00-2.50	Ø 2.50-2.00	Ø 2.00-1.50	Ø 1.50-1.00	Ø < 1.00	Twig litter traps	Bark litter traps	Leaf litter traps
	<i>g m⁻²</i>			<i>Branchfall g m⁻² yr⁻¹</i>							
Eucalypt											
eCO ₂	12372 ± 1916	258 ± 73	71 ± 53	30 ± 4	18 ± 8	33 ± 8	26 ± 7	79 ± 4		93 ± 19	310 ± 41
aCO ₂	12275 ± 399	248 ± 87	163 ± 118	38 ± NA	24 ± 5	10 ± 1	23 ± 5	71 ± 1		72 ± 10	273 ± 41
e/a	1.01	1.04	0.44	0.79	0.75	3.3	1.13	1.12		1.3	1.14
P value t-test	0.965	0.910	0.227	0.156	0.513	0.095	0.629	0.204		0.386	0.561
Understory											
eCO ₂		4 ± 3					2 ± NA	3 ± 2			
aCO ₂		4 ± 0					1 ± 1	3 ± 1			
e/a		1.1					1.23	1.14			
P value t-test		0.892					NA	0.851			
Liana											
eCO ₂								2 ± 1			36 ± 22
aCO ₂								3 ± 3			68 ± 49
e/a								0.499			0.531
P value t-test								0.230			0.598
									<i>g m⁻² yr⁻¹</i>		
								Species combined			
								eCO ₂	151 ± 25		346 ± 63
								aCO ₂	135 ± 27		341 ± 90
								e/a	1.19		1.014
								P value t-test	0.683		0.966

NAs in means are caused by 0 observations in a category within all plots, and NA in SE are caused by observations from only one plot included per treatment.

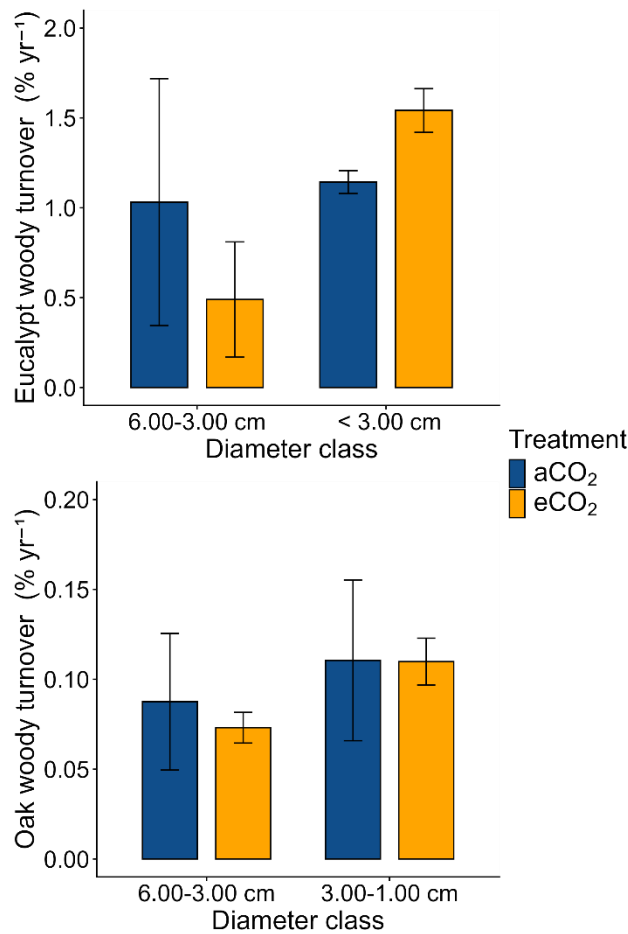


Figure 4-8 Eucalyptus and oak woody turnover as percentage lost from AGB through branchfall in different diameter size classes. Bars represent means across treatment plots ($n = 3$), error bars are the standard error.

Branchfall over 12 months in diameter class < 3.00 cm under eCO₂ made up ~ 1.55 % of AGB_{Eucalyptus} under eCO₂ in 2022, which is slightly higher than the ~ 1.15 % under aCO₂. This difference was not significant ($p = 0.062$). For the 6.00-3.00 cm diameter class a negative treatment effect is shown, with woody turnover over 12 months reaching ~ 1.00 % of AGB_{Eucalyptus} under aCO₂ and appearing higher than the $\sim 0.5\%$ under eCO₂, yet also not significant ($p = 0.572$). The woody turnover of AGB_{oak} through branchfall in the two size classes remains around 0.1%, with no significant differences between treatments ($p = 0.742$ for 6.00-3.00 cm and $p = 0.989$ for 3.00 – 1.00 cm)

4.4 Discussion

This chapter explored the litterfall, branchfall and woody turnover across different branch sizes in two mature forest stands exposed to eCO₂ for 4 years (BIFoR FACE) and 10 years (EucFACE). Contrary to expectations, the absence of enhanced NPP_{wood} under eCO₂ in EucFACE was not accompanied by a similar absence of increased woody turnover. Instead, although not significantly different, branchfall < 2.00 cm in diameter (Figure 4-4, Table 4-1), bark litterfall (Figure 4-5, Figure 4-7) and woody turnover through branches smaller than 3.00 cm in diameter (Figure 4-8) were noticeably higher under eCO₂ at EucFACE. In contrast, no evidence of any eCO₂ enhancing treatment effect on branchfall or twig litterfall at BIFoR FACE was observed, despite NPP_{wood} increases under eCO₂ (Norby et al., 2024). The hypothesised difference between dominant and understory species response to eCO₂ was not observed. In both BIFoR FACE and EucFACE, there was no consistent difference in treatment response or magnitude in branchfall between understory compared to canopy dominant species (Figure 4-5 and Figure 4-6). The final hypothesis that eCO₂ effect size would scale with exposure time, i.e., a treatment effect would be more discernible the longer exposure takes place, was only partially supported by the results. Preliminary treatment effects showing increased, but non-significant, branchfall and woody turnover through multiple smaller branch size classes in the EucFACE with exposure of 10 years (Table 4-1, Figure 4-8). In contrast to an noticeable negative, also non-significant, treatment effect in branchfall or woody turnover in any of the smaller branch sizes at BIFoR FACE, which has relative short eCO₂ exposure time (Table 3-1, Figure 4-6).

These results show that the difference in tree mortality compared to more dynamic branchfall that is currently ignored by DGVMs mathematical approximations (Xu et al., 2007) is not the sole simplification that could be the cause for model outcome uncertainty. When comparing the first four years of BIFoR (Norby et al., 2024) and first four years of EucFACE (Jiang et al., 2020ab), enhanced C input through photosynthesis will not lead to increased NPP_{branch} for every mature forest. Leaving the question of where the surplus of C goes after enhanced assimilation (Ellsworth et al., 2017) for EucFACE is still unanswered. But by combining the treatment effects on BIFoR FACE's oak woodland enhanced photosynthesis (Gardner et al., 2020), NPP_{stem+branch} increase (Norby et al., 2024) and the indication for positive feedback of eCO₂ by increasing branch support for leaf structures (Chapter 2), the accuracy for temperate forest projections of DGVMs (Ciais et al., 2013) might be improved. The C output flux through branchfall cannot be utilized for all forest projections as merely an additional flux with a

different but static residence time. These results show that branches of different sizes and forests exposed to eCO₂ for different time periods generate different woody turnover rates, and thus woody residence time for branch compartments would need to be specified according to forest type, canopy structure and AGB_{branch} standing stock and potentially adjusted along with time that atmospheric CO₂ concentrations rising.

4.4.1 Branchfall, twig litterfall and wood turnover did not increase with previous woody NPP increase under eCO₂

In contrast to the first hypothesis, observations did not show an increase in branchfall or woody turnover through branchfall in the mature forest that previously showed woody NPP increase (Norby et al., 2024), while the mature forest where P limitation has inhibited enhanced woody NPP under treatment (Ellsworth et al., 2017; Jiang et al., 2020) did show increase in branchfall and woody turnover instead. When combining the results a pattern emerges. There is a significant increase in Oak leaf litterfall under eCO₂ while the difference in twig litterfall between treatments remain relatively small (Table 3-1). Additionally, there is a non-significant, but noticeable lower woody turnover of branches smaller than 3.00 cm in diameter under eCO₂ (Figure 4-7). An increase in branch density of similar sized branches in the upper canopy of the oaks was also observed (Figure 2-7). Together, these results could point to a branch growth increase in upper canopy under eCO₂ that has brought the system in these plots over carrying capacity, but this excess has not yet been corrected through mechanisms such as resource competition and mortality. This argumentation is in line with the first years of EucFACE twig litterfall data, showing a lower twig litterfall under eCO₂ until the fourth year where the eCO₂ litterfall caught up with the aCO₂ litterfall (Jian et al., 2022b).

That woody turnover of small branches did not increase under eCO₂ at BIFoR FACE while an increase in woody NPP in previous years was observed (Norby et al., 2024), might be a remnant from pre-fumigation plot characteristics or large scale branchfall events. Figure 4-2 shows that the deadwood mass at BIFoR FACE is larger under aCO₂, and that aCO₂ plots mean Oak ABG_{stem+branch} is higher (Table 3-1). If high damage event in the last caused extensive damage, and stochastically impacted eCO₂ plots more, carrying capacity was potentially reduced in these plots. In this case the influence of regrowth would have outweighed a CO₂ fertilization effect on growth and subsequent branchfall. The ramifications of such a pre-treatment effect could carry on well into treatment and measurement period of this investigation and can obscure treatment effects for multiple years, as was likely the case when at DUKE FACE eCO₂

treatment effect on litterfall was presumed to be obscured by overwhelming and random branchfall distribution (Lichter et al., 2008).

EucFACE has extensive liana growth and canopy dynamics were active over the years (Kim Calders, personal communications). Increased Liana growth could potentially push mature ecosystems back in succession stage (Körner 2004) and replace productivity capacity of canopy dominant trees with their own leaves to a 1 on 1 ratio (van der Heijden et al., 2013). Both of which would start with increasing mortality of late successional stage, canopy dominant trees. The higher EucFACE woody turnover in the small material under eCO₂ could be the result of a precursory branchfall spike before this liana induced mortality (Zuleta et al., 2023).

4.4.2 eCO₂ effect was not varied across canopy dominant and understory species

The expected outcome of a discernible difference in response to eCO₂ between species in contrasting canopy positions and with growth-mortality trade-off straits was not observed. In both forests it is the canopy dominant trees of eucalypt and oak made up most of the branchfall biomass (Figure 4-5, Figure 4-6, Table 4-1, Table 3-2) and the relative fraction of understory species contributing to total branchfall, and litter was not different between treatments. At BIFoR FACE both understory leaf litterfall ($p = 0.309$) and oak leaf litterfall were higher under eCO₂ ($p = 0.017$), including similar positive treatment effects of 1.1 to 1.3. Additionally, total branchfall for both species types was significantly lower under eCO₂ under eCO₂ ($p = 0.021$ and $p = 0.016$) with a negative treatment effect of 0.4 to 0.6. Understory wood NPP for 2021 and 2022 at BIFoR also showed no larger treatment effect (1.2 and 1.08) under eCO₂ compared to Oak NPP_{stem+branch} in the same years (1.106 and 1.164) (Norby et al., 2024). Together, these outcomes show that understory species did not take more advantage of eCO₂ compared to canopy dominant species at BIFoR in these years, unlike other research on this topic has predicted (Körner 2004) or observed in experiments with shade-grown individual species (Finzi et al., 2001), but aligns with others where fast and slow growing species did not differ in eCO₂ treatment response (Poorter & Navas 2003). The results of 2022 also show liana litterfall with a non-significant tendency of negative treatment effect, contradicting predicted enhancement under eCO₂ (Körner 2004; van der Heijde et al., 2013). Important to note is EucFACE does maintenance to keep Liana growth under control, which could obscure any impact on both branchfall as precursor for increased mortality (section 4.4.1) or a competition for photosynthetic capacity.

There was no noticeable difference in eCO₂ effect magnitude found between eucalyptus or understory branchfall. There was a minimal tendency towards positive treatment effect ($e/a = 1.1$ to 1.23) in total branchfall and < 1.50 cm diameter sizes of understory branchfall and a weak to moderate positive treatment effect ($e/a = 1.04$ to 3.3) for total branchfall and in sizes < 2.00 cm in diameter for Eucalypts. These results are in line with higher understory NPP under eCO₂ in second (2015) and third (2016) year observations at EucFACE. The NPP_{stem} and leaf litterfall of eucalyptus both start lower under eCO₂ in 2013 but vary in response direction over following years (Jiang et al., 2020b), thus no clear increase in response of understory versus overstory over prolonged exposure time was observed in EucFACE.

4.4.3 eCO₂ effect could be scaled with exposure time to eCO₂.

The final hypothesis of longer exposure to eCO₂ increasing the effect of increased woody turnover could not be disproven. While there is an apparent negative treatment effect (e/a ratio < 1) on branches of 2.00 cm diameter and larger, an apparent positive treatment effect ($e/a > 1$) was observed, including higher total leaf, bark, and twig litterfall at EucFACE after 10 years of exposure. Although the differences are not statistically significant, the tendency for positive treatment effect is consistent for all small sized branch and litterfall except lianas. While BIFoR FACE exposure of 4 years a similar tendency for positive effect in oak leaf litterfall, there is a weak negative treatment effect observed in the twig litter or any of the branches. When comparing the earliest years of eCO₂ exposure at EucFACE, the eucalyptus leaf and twig fractions of litter were consistently lower but for the fourth year when it became higher than or equal to aCO₂ respectively (Jiang et al., 2020b).

The absence of an enhancing treatment effect on woody turnover at BIFoR FACE could be indicative of the relative short eCO₂ exposure time. In first generation FACE experiment DukeFACE a positive eCO₂ treatment effect on total litter mass was found in the first 2 years, of which the second-year difference was significant (Finzi et al., 2001). Extended observations over nine years of CO₂ enrichment at this experiment concluded that initial significant disparities in litter deposition observed did not persist, but the yearly and total contributions remained higher than aCO₂ (Lichter et al., 2008). And when looking at a productivity study done at ORNL FACE, the positive treatment effect of 24% higher stand NPP in the first 5 years decreased after, interpreted as progressive nitrogen limitation (Norby et al., 2022). This suggests that while current exposure time at BIFoR FACE might not be enough to have increased branch

and litterfall to the point of a detectable treatment effect, continuation of exposure has the potential for this to be either reinforced or have this lack of treatment effect persist.

4.4.4 Bark makes up a large fraction of the total wood branchfall and follows the branch trend.

Bark observations made up ~ 30% of total samples observed on the transects at EucFACE, in line with observed 20% to 45% on eucalyptus forest floors (Grootemaat et al., 2017). The cumulative branchfall and bark litterfall are slightly higher in eCO₂ than in aCO₂ (Table 4-1), which is a continuation of previous years (Jiang et al., 2020b). Cumulative stem bark shedding did not show a consistent effect size throughout the year (Figure 4-7), with total stem bark lower under eCO₂. Earlier studies at EucFACE measured that increased photosynthesis in the eucalypts was enhanced by 19% in the first three years of fumigation, but phosphorus limitation caused the absence of enhanced stem growth (Crous et al., 2015; Ellsworth et al., 2017). Our results of bark shedding at the stem do not contradict these findings.

4.4.5 Limitations

The limited replicates of treatment plots at the FACE facility make the detection of treatment effects challenging, as natural variability is more influential in smaller studies. By comparing two FACE facilities, this chapter aims to observe any discernible eCO₂ treatment effect across the two mature forests with different canopy dominant species and exposure times, highlighting both the commonalities and differences. Both FACE facilities are high-intensity research sites placed within existing woodlands that are regularly visited by researchers, staff and, in some cases, wild animals. Although great care is taken to avoid installed equipment and measures are taken to keep wildlife like badgers at BIFoR and kangaroos at EucFACE discouraged from entering the research plots, there is still a chance that some of the samples recorded on the transects are not from branchfall, but from branch displacement. Such events might have also inflated the biomass, especially in the V decay class. In addition, the notation of decay classes is a non-exact measurement and might not be best used to compare such different climates, but it does provide a rough estimate of when branch death or branchfall occurred. The general standing deadwood in the aCO₂ plots at BIFoR is higher than aCO₂, but this is a very likely pre-treatment effect. It is still relevant to put the high aCO₂ branchfall into perspective; with only 6 plots in a forest, it shows how much the impact of dynamics in one plot impacts the mean observed effect size. This is further underlined in the variation between the dotted lines for the individual plots in Figures 4-5, 4-6 and 4-7.

The study was limited in its capacity to process to the detail of AGB into different compartments, e.g. eucalyptus AGB_{branch} , in the same way as was done for Oak AGB_{branch} as was done in the study for Chapter 3. Therefore, complete tree AGB was used in the denominator to calculate woody turnover for both species in this chapter. By using branchfall in the nominator for this calculation, the assumption is made that the observed branchfall is approximately equal to branch NPP, including both the biomass growth and replacement of dead branches. This inferred balance between growth and mortality within mature forest ecosystems long-term, and any change in branchfall being attributed to treatment differences, causes the impact of events leading to large canopy breakages, such as storms at BIFoR FACE, or the recent floodings at EucFACE to be disregarded. These disturbances often have prolonged recovery periods or delayed effects, making their influence and the interplay with eCO₂ treatment on canopy (re)growth and turnover more appropriately analysed over a multi-year timeline, which falls outside the scope of this study. In addition to the limitations in previous paragraph, the LIS method cannot exactly pinpoint the time of death of branch samples found crossing the transect lines and may include branches that have already died in the canopy prior to the 12 months of observations. In contrast, it can also fail to include branches that have died but have not detached from the tree yet, or have but are retained by other branches, understory or specifically in EucFACE forest, are ensnared by lianas. It is assumed that the proportion of missed branchfall and excess branchfall are approximately equal, though future studies could provide evidence to support or refute this.

It also needs to be acknowledged that the twigs in the litter traps were not measured in length or diameter, so the litter traps are not mutually exclusive in diameter size with the other classes. Only 2 plots were used for comparing litter bark and stembark traps, as at this point, it became clear that R5 would be turned off. This method is susceptible to aggravating the shedding by doing the inventory itself and only collecting a limited portion of the whole stem. It can certainly be improved by incorporating the total height of the stem and tagging with tape/paint so the origin of the bark can be tracked.

Other inflation of branchfall could have happened as Liana growth interventions took place during the observation year at EucFACE, which could have spiked both branches fall on the transects and in the litter traps. The supply chains for eCO₂ globally have become strained during the observation times at both EucFACE and BIFoR FACE, causing the facilities to reduce fumigation hours compared to the targets during the year (Hart et al., 2020) at EucFACE resulting in the permanent closure of one of the fumigated rings in December 2023. Although

an immediate impact on wood growth was not expected, this reduction might impact future research and comparability with earlier results.

Although EucFACE and BIFoR FACE have a varying ecosystems and soil status (Norby et al., 2016), it was outside the scope of this study to investigate in detail how events in previous years have potentially impacted branch dynamics. The relative short measurement period within this chapter is also relevant for interpreting the bark flux since using one month of transect observation data to determine bark volume as a function of length and, subsequently, weight for a whole year is a limited dataset on which to base a relationship. However, bark-fall in g m^{-2} from transect (Figure 4-5) and bark litter fraction (Table 4-1, Figure 4-7) are in the same 70-90 g m^{-2} range and show a similar small effect size under eCO_2 .

AGB of Eucalypts included leaves where AGB of oaks doesn't, however, author has found that at EucFACE a larger portion of branchfall throughout the month is including leaves still attached to the samples, where this was less the case at BIFoR. Making that using total AGB including leaves for EucFACE is not incomparable with the observed branchfall and that using total $\text{AGB}_{\text{stem+branch+leaves}}$ instead of solely $\text{AGB}_{\text{branch}}$ is still relevant to understand the stand dynamics, especially since branchfall included leaves often at EucFACE.

4.5 Conclusion and future works

In this chapter, the aim was to assess if eCO_2 impacts branchfall, litterfall and woody turnover through branchfall in two second generation FACE experiments with similar treatment concentrations, but varying species composition, treatment exposure times and previous productivity responses. The investigation included a comparison of eCO_2 response between species in the two positions of canopy dominance and understory and if branchfall and woody turnover varied between branch sizes. This study was also undertaken to fill an evidence gap and provide observational data of branchfall in these mature forests exposed to eCO_2 so that dynamic global vegetation models can increase accuracy of future forest response to increasing CO_2 concentrations in the atmosphere. The overall aim of the chapter in providing observational data on branchfall was achieved, although outcomes were not always in line with expectations. In the mature oak woodland of BIFoR FACE a weak and non-significant but negative treatment effect was observed for branchfall and twig litterfall as well as woody turnover through the smallest branch sizes after 4 years of treatment, despite previously published increases in woody NPP. Instead at EucFACE, the Eucalypt branchfall up to and woody turnover of the smallest sizes showed a non-significant, positive treatment effect after 10 years of fumigation. Without an earlier observed productivity increase in productivity

(section 4.4.1). To gather more robust data that can be used to support or deny the multiple explanations for these results at BIFoR and at EucFACE, this investigation will need to continue over several years. Analysis of a long-term dataset would reduce the potential obscurement of treatment effect due to stochastic branchfall events in the current 12-month observation period and would better highlight any impact of other environmental stressors such as floods and droughts with potentially delayed or long-lasting effects on both productivity and mortality. Continued observations on bark shedding of both stem and branches, re-evaluation on capturing methods and improve on them to be able trace back to tree compartment bark originates from would be worthwhile. The canopy positions at both BIFoR FACE and EucFACE were not associated with a difference in treatment effect size, while this was expected. A direct comparison NPP_{branch} and NPP_{leaves} and branch and litterfall of both canopy positions over multiple years, preferably including pre-treatment data, should be carried out. Such a future study should also investigate the impact of liana growth on branchfall under eCO_2 and if the projected ecosystem scale impact on increase productivity and mortality of understory or liana's will outcompete slow-growing species and eventually decrease net C gain in these forests over time. The forest with the longer exposure time did show a weak but positive treatment effect in the smaller branches compared to the slight negative treatment effect in larger diameters and in shorter exposure time the treatment effect remains, weakly, negative for all size classes. The precise woody turnover per size class remains to be elucidated at EucFACE, for which observations on standing branch biomass in the canopy would be the first step to take.

Chapter 5

Synthesis and conclusions

5.1 Forest ecosystem carbon fluxes and the role of woody growth and turnover

Understanding how tree strategies regarding wood growth and turnover affect forest responses to elevated CO₂ (eCO₂) is essential to improving long-term predictions of forest carbon (C) cycling. Human emissions of greenhouse gasses impact the global net ecosystem productivity by increasing the C availability for plants. Forest are currently important C sinks that capture more C from the atmosphere than that they emit back, by using the post-photosynthesis C components for growing branches, leaves and reproductive tissues (Net Primary Production, NPP). Trees have the capacity to lock C in these tissues or transport to other C pools in forest ecosystems for years, decades or longer. But if the global forest C sink remains in the where atmospheric CO₂ concentrations continue to rise is uncertain (Ciais et al., 2013; Friedlingstein et al., 2022). Chapter 1 describes the challenges faced in describing and predicting accurate form and function of tree woody compartments (King & Loucks, 1978; Lehnebach et al., 2018) and how increased C availability has impacted mechanisms of growth on plant and tree level observed in controlled environments. Enhanced C assimilation, increased water use efficiency and biomass growth under eCO₂ treatment have been well documented in seedlings and individual trees (Ainsworth & Long, 2005, Mndele et al., 2020). When the surplus of C available for growth is invested in leaves and woody tissues supporting leaves, even more C becomes available leading to positive feedback, e.g. CO₂ fertilization effect (CFE) (Walker et al., 2019). The collective outcomes of in-field Free Air Carbon Enrichment (FACE) experiments done in young forest stands point out that the strength and persistence of this CFE is varied on temporal and geographic scales (McGrath & Lobell, 2013). The young monoculture mesic-temperate forest of these first-generation FACE experiments represent but a fraction of the diversity global forests, while the mature forests are arguably more important in determining global forest long-term carbon (C) storage, as they contain larger trees that have accumulated more C in both living biomass and death wood on the forest floor over time (Burrascano et al., 2013).

However, the complex mechanisms that drive the within forest ecosystem C cycles, e.g. the rate and ratio in which productivity of different components happens after C assimilation but

before the components are decomposed, causing C to be returned to the atmosphere, remain poorly understood and so is the impact eCO₂ has on these mechanisms. Litterfall is the largest pathway of nutrient transfer between different biomass pools, and subsequent C pool, from living vegetation to microbes to soils and back to vegetation (Finzi et al., 2008). Branchfall is another central flux and is also dynamic, with less frequent abscission from the canopy compared to litter but with more regular intervals than tree stem death occurrences. Both the litter and branchfall fluxes impact the productivity of forest stands, e.g. the input C flux, by subtracting from net photosynthesis capacity. Litter and branchfall also impact the C output flux by increasing substrate available for decomposition. It is therefore critical to investigate the impact of eCO₂ on these fluxes and study the potential drivers enhancing or reducing these fluxes. Chapter 3 introduction describes the variation in current literature in observation methods used in field-experiments to capture these fluxes. A large-scale observation method is comparing the before and after of the flux occurrence in the canopy, i.e. by quantifying canopy damage through aerial remote sensing (Zuleta et al., 2023, Simonetti et al., 2023). The most in-field observations methods are collections of the outcome of the fluxes, i.e. through collections in litter traps and surveys with line intersect sampling (Pook et al., 1997; Woldendorp et al., 2004; Korboulewsky et al., 2021). Transect length, orientation and minimal size inclusion thresholds are often site and research aim specific. This poses challenges for comparison between different forests. How eCO₂ affects the timing and magnitude of these bi-directional fluxes is crucial for understanding whether the CFE occurs and persists in forest ecosystems. To address these questions more in field-observations are required in a wide range of forest ecosystems, that have passed the exponential growth phase and where the biomass is at a carrying capacity so that net changes in fluxes can be disentangles. Chapter 4 introduction describes that a comparable eCO₂ enhancement of photosynthesis in two mature forests with FACE experiments can have varying outcomes in growth responses due to limitation of other nutrients (Ellsworth et al., 2017, Jiang et al., 2020a, Norby et al., 2024). The impact of eCO₂ on the intermediate and bi-directional flux of branchfall was not yet systematically monitored, and litterfall collections yet to be compared between the sites.

At the centre of the uncertainty in projections of future forest responses to eCO₂ lies the simplification of these complex ecosystem. Biomass pools and fluxes are captured by mathematical approximations by dynamic global vegetation models (DMVS) and typically summarized in a single biomass pool with a constant residence time, causing up to 30% of inter-model variation (Xue et al., 2017). The absence of enough observational data of the net

branch and litterfall fluxes within mature forests ecosystems exposed to eCO₂ is a key knowledge gap. Notwithstanding these uncertainties, DGVMs tend to predict a shift in allocation towards wood (De Kauwe et al., 2014; Walker et al., 2015), but accurate quantifications of where additionally assimilated C is allocated to and how long it remains in these compartments in forest ecosystems are missing. The second-generation FACE experiments provide a unique opportunity to fill this gap by measuring biomass growth and fractions of biomass loss from forest stands under eCO₂. The key findings in each chapter can inform more realistic parameterisations of internal C cycling for DMVGs projections.

5.2 Key findings

The aim of this thesis was to understand whether eCO₂ affects branchfall and litterfall or not, and if so, why mechanisms might drive to increase or decrease wood growth and wood loss. This thesis investigated if and how eCO₂ affects branch distribution in the canopy and woody turnover of different sizes, defined as fraction of total branch biomass or aboveground biomass lost through branch and litterfall over time. The research took place at two second-generation FACE experiments in mature forest ecosystems: EucFACE and BIFoR FACE. Below are the key findings from each research chapter.

Chapter 2 showed that small branch biomass distribution in canopy-dominant oaks changed under eCO₂, and the observed pattern of this occurring by increase in branch density instead was in line with the hypothesis that this process is driven by light foraging. Chapter 3 results did not support the expected outcome of eCO₂ showing a positive treatment effect on twig litterfall and smaller sized branchfall in similar magnitude to previously observed increase in leaf litter and preliminary stem and branch growth increase. Instead, a negative treatment effect in the smaller branch sizes was observed. A non-significant but lower total branchfall in both dominant and understory under eCO₂ was observed, in addition to a lower woody turnover the smallest branch size. In chapter 4, contrary to expectations, there was a weak positive treatment effect under eCO₂ in smaller sized branchfall and branch turnover at in the semi-dry eucalyptus forest of EucFACE. Surprisingly, because no increase in productivity was observed accredited to the P limitation during 10 years of fumigation. In contrast, the oak woodland at BIFoR FACE that showed positive treatment effect on productivity during 4 years of fumigation, did not show positive treatment effect on branchfall or woody turnover. The hypothesis that exposure time is important in determining treatment effect size could not be invalidated, but the expected positive treatment response and higher magnitude of response of understory compared to canopy dominant was not observed.

5.3 Implications of collective outcomes

The outcomes of Chapters 2 and 3 show that eCO₂ impact on productivity cannot be used to identify or project the enhancement of turnover woody material in oak-dominated woodlands. The observed increase in branch density in Chapter 2 was not associated with higher twig or small branch turnover in Chapter 3. There is an increased turnover of oak and understory leaves ($p = 0.017$ & $p = 0.302$ respectively) and combined with previous observations of enhanced photosynthesis (33%) (Gardner et al., 2022) and observed increase in woody NPP (Norby et al., 2024) it could be concluded that mature oak woodland response to eCO₂ is in increased NPP for overstory leaf (Pritchard et al., 1999), but delayed in wood turnover. The increased within-canopy distribution of leaf mass per area after 12 years of eCO₂ treatment in ORNL FACE (Norby et al., 2022) supports the hypothesis of the eCO₂ effect being driven by light foraging and detected in the smaller diameter sizes first. This interpretation is consistent with findings from the longer-running EucFACE experiment in Chapter 4, where the turnover of branch, litter and bark is enhanced under eCO₂ in the semi-dry eucalyptus forest exposed to eCO₂ for over 10 years. These outcomes suggest that the NPP response is not or is yet to be indicative of the long-term steady-state that might be achieved in these forests under extended eCO₂ treatment, hindering the extrapolation of future mortality or branchfall responses.

Increased NPP of trees directly reduces tree's lifespan (Brienen et al., 2020) and which brought forth the hypothesis that branchfall and twig-litter would follow a similar pattern. Yet collectively, the chapter outcomes show that a surplus to the assumed carrying capacity reached in steady-state ecosystems, the observed NPP response to eCO₂ is not or not yet indicative enough to extrapolate accurate future mortality or branchfall. In fact, the increase in fine branchfall, twig litter, bark litter and overstory leaf litter after 10 years eCO₂ at EucFACE point away from NPP as indicator since no stem growth NPP response has been observed previously. Jiang et al., 2020 reported a slight positive NPP response to eCO₂ of which 75% was driven by the understory but was not followed by an equivalent understory biomass increment and therefor suggested the possibility of a higher understory biomass turnover to account for these results. The observed similarity in turnover treatment effect between eucalypt and understory stayed consistent from the earlier years till now, the dominant eucalyptus trees will have consistently lost more biomass under eCO₂ compared to ambient. Eucalyptus is widely assumed to exhibit high branch and bark production and turnover as part of an evolutionary strategy to encourage bushfires, which these trees normally survive and enjoy a competitive advantage in post-fire community recovery. Figure 4-7 shows that eucalypts lose 1 to 1.5 % of

total biomass through branchfall annually, whereas oaks are just lost ~ 0.1 %. The oaks in Chapter 2 seem to direct additional available C toward smaller branches without an increased turnover rate, but at EucFACE, there are no observations indicating a similar allocation pattern under eCO₂. In the end, it is the longevity of stem and branch biomass of trees that dictate an important fraction of the climate change mitigation potential of forests (Körner, 2017). If the eCO₂ effect in mature eucalyptus forests remains consistently unbalanced, with more biomasses lost than produced, it will put the efficiency of our existing mitigation policies into further question.

5.4 Reflection on methods, assumptions and limitations

These chapters use novel approaches to quantify branch biomass distribution and branchfall. In both TLS and allometry-derived biomass, there is a risk of overestimation of biomass due to overfitting of cylinders (Demol et al., 2022; Hackenberg et al., 2015). This warrants a cautious interpretation of absolute volume numbers; however taking this risk into account, the deductions taken from observed treatment effects remain unaltered. Any systematic bias that is present, is present in both the numerator and the denominator in this ratio-comparison between treatments (section 2.4.4). The results in these chapters provide insight for eCO₂ impact on within ecosystem fluxes of branch growth, branchfall and litterfall in two mature forests. The ability to generalize to global forest responses is limited, as this thesis refers to only two representative plots. These plots do provide the only opportunity to gather observations of a mature forest stand in the current day, while facing conditions that future forests will face. DGVMs tend to predict a shift in allocation towards wood (De Kauwe et al., 2014; Walker et al., 2015), but the surplus of C after enhanced photosynthetic activity takes place remains not completely accounted for. It is these research plots that can contribute to filling in this gap, even when that means trying to disentangle one impact or flux in an ecosystem with many processes and responses happening at the same time, of which some positive and some negative. Additionally, the compounding variability due to other factors such as local microenvironmental differences between plots, or caused by variation in weather, hydrology can impact or completely obscure treatment effects. The method of observing the branchfall and litterfall in a mature forest ecosystem eliminates at least some compounding impact of i.e. exponential growth phases eCO₂ treatment effect. Putting the outcome of the branchfall flux in the nominator, instead of the net productivity and replacement of dead branches, causes some processes to be ignored or overlooked in this thesis (section 3.4.4). The results from FACE experiments, like in this thesis, are prone to incorrectly accepting the null

hypothesis of no difference or Type II errors. This can lead to small-sized but persistent treatment effects to become not as quickly shared with the wider research community and under-acknowledged in academia's "significance" driven publication landscape. Investigating if CO₂ impacts two relevant within ecosystem fluxes of woody C and determine to which direction, enhancement or reduction, this impact drives these fluxes is still worth reporting, even when statistical significance is not achieved. By continuing the observations and gathering more timepoints both statistical power and the scope to include a wider range of branchfall events increases.

5.5 Future perspectives

This thesis set out to understand how tree strategies in wood growth and turnover shape the forest responses to elevated CO₂, moving from branch distribution in the canopy level to generalized ecosystem implications. Future studies on this topic should continue to quantify the within ecosystem fluxes, especially focusing on woody tissues and particularly with long-term exposure data to assess whether the impact of eCO₂ discussed in this thesis are sustained over time. One natural progression of this work is repeating the terrestrial laser scanning campaigns across multiple years, to see if the increased density of branches in the upper canopy at BIFoR FACE is persistent.

Future studies should account for even more temporal variation and environmental conditions that better reflect the diversity in global forest ecosystems. This can be done adding observations from the Amazon FACE to current comparison between BIFoR FACE and EucFACE the geographical range and temporal variation of exposure times range can be increased. A comprehensive review of the impact of eCO₂ on branch distribution, branchfall and litterfall at all sites and at different exposure times is recommended. Ultimately, the work presented in this thesis provides a starting point. From branch to forest to globe, further research is essential to expand our understanding of how the continuing rise of CO₂ concentrations in the atmosphere will impact forests contribution to global C dynamics, now and in the future.

Appendix A: Supplementary Material

Chapter 2:

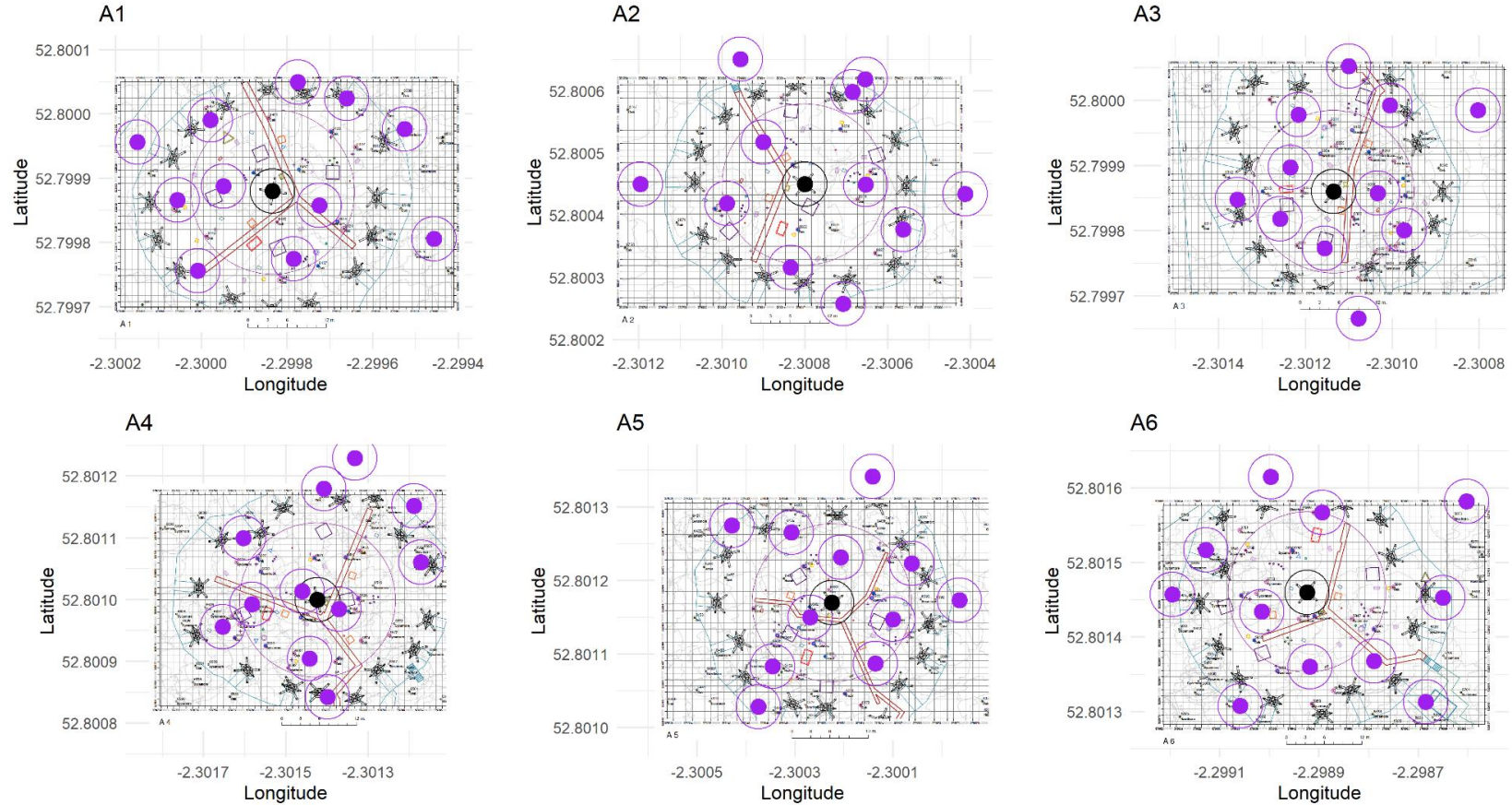


Figure A-1 Top view map of each BIFoR FACE plot. Black points indicate plot centre tower coordinates, red lines mark infrastructure walkways, and purple points show RIEGL V400i scan locations. As 180° and 90° scans were taken at the same positions, averaged coordinates and transparent rings represent approximate scan patterns within plot infrastructure.



Figure A-2 Photographs of Fallen Canopy section A) Side view section. B) Tagging of branches and determining the “height” of branch bifurcations along the stem. C) Measuring the diameters of smaller branches with a calliper and tape measurement for branch length

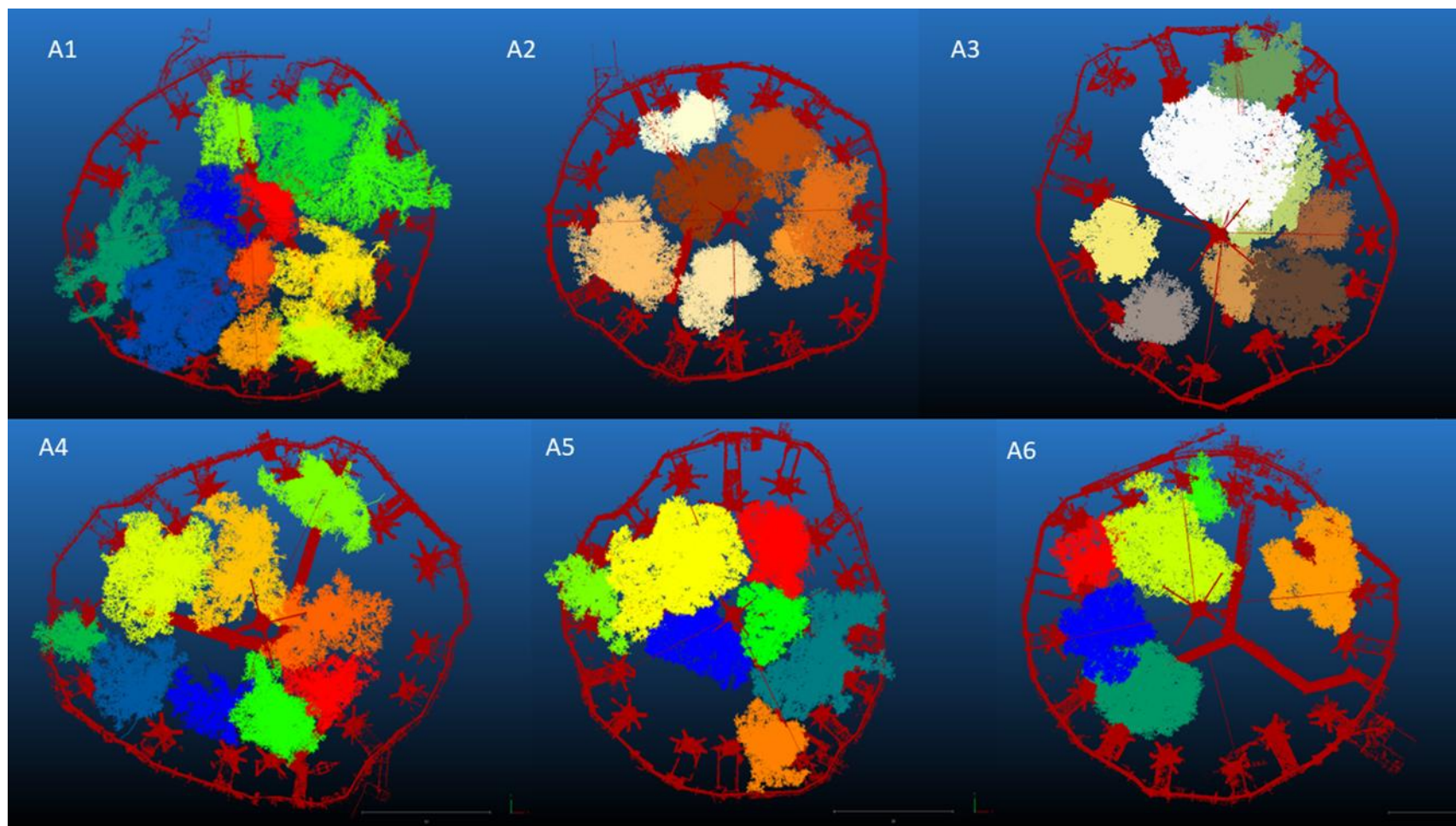


Figure A-3 Top view of isolated target trees and infrastructure at BIFoR FACE. Trees that did not pass quality checks are omitted from this figure. Images generated with Cloud Compare.

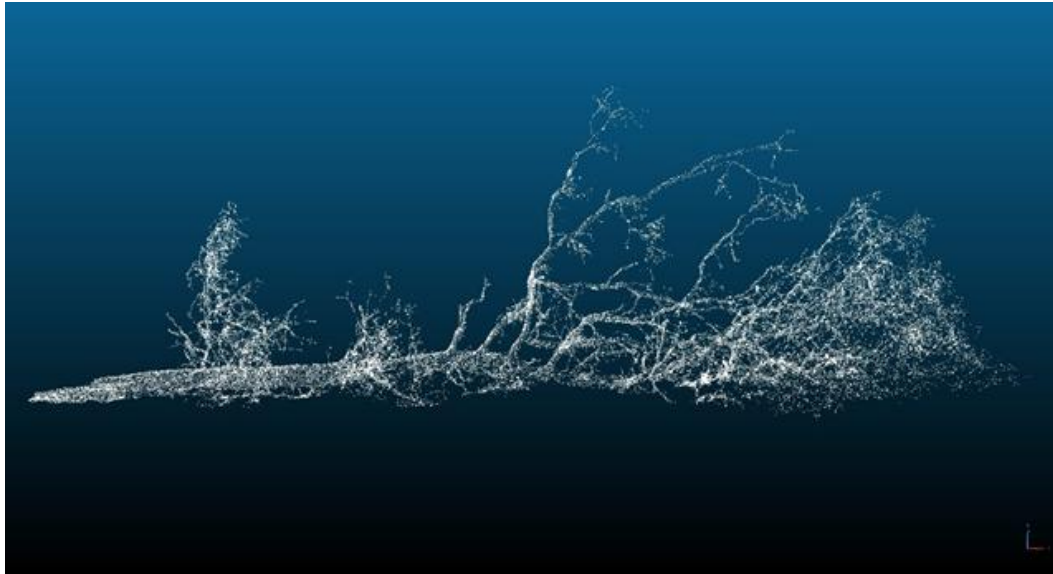


Figure A-4 Side view of the point cloud of the Fallen Canopy section in CloudCompare before it is reoriented to mimic a standing tree

Table A-1 Rundata output from the best optQSM-generated model per tree at BIFoR FACE. PatchDiam1, PatchDiam2min, PathDiam2max, BallRad1, and BallRad2 are the smallest segments used to segment the point clouds. Units are in m.

Tree_ID	PatchDiam1	PatchDiam2Min	PatchDiam2Max	BallRad1	BallRad2
Plot_A1_Tree_8432_rundata	0.04444	0.02222	0.03434	0.0484	0.0374
Plot_A1_Tree_8433_rundata	0.04040	0.02222	0.03232	0.0440	0.0352
Plot_A1_Tree_8434_rundata	0.03838	0.02222	0.03232	0.0418	0.0352
Plot_A1_Tree_8437_rundata	0.04242	0.02222	0.03232	0.0462	0.0352
Plot_A1_Tree_8444_rundata	0.03636	0.02222	0.02828	0.0396	0.0308
Plot_A1_Tree_8445_rundata	0.03232	0.02222	0.02626	0.0352	0.0286
Plot_A1_Tree_8446_rundata	0.04242	0.02222	0.03434	0.0462	0.0374
Plot_A1_Tree_8457_rundata	0.04444	0.02222	0.03434	0.0484	0.0374
Plot_A1_Tree_8465_rundata	0.03434	0.02424	0.02828	0.0374	0.0308
Plot_A1_Tree_8467_rundata	0.03636	0.02222	0.02828	0.0396	0.0308
Plot_A1_Tree_8468_rundata	0.03434	0.02222	0.02828	0.0374	0.0308
Plot_A2_Tree_8668_rundata	0.03636	0.02222	0.03030	0.0396	0.0330
Plot_A2_Tree_8673_rundata	0.03838	0.02222	0.03030	0.0418	0.0330
Plot_A2_Tree_8674_rundata	0.03232	0.02222	0.02626	0.0352	0.0286
Plot_A2_Tree_8675_rundata	0.04040	0.02222	0.03232	0.0440	0.0352
Plot_A2_Tree_8676_rundata	0.04242	0.02222	0.03232	0.0462	0.0352
Plot_A2_Tree_8689_rundata	0.04040	0.02222	0.03232	0.0440	0.0352
Plot_A2_Tree_8749_rundata	0.04848	0.02222	0.03636	0.0528	0.0396
Plot_A3_Tree_8300_rundata	0.03838	0.02222	0.03030	0.0418	0.0330
Plot_A3_Tree_8301_rundata	0.04444	0.02222	0.03636	0.0484	0.0396
Plot_A3_Tree_8313_rundata	0.04242	0.02222	0.03434	0.0462	0.0374
Plot_A3_Tree_8343_rundata	0.04444	0.02222	0.03636	0.0484	0.0396
Plot_A3_Tree_8345_rundata	0.03030	0.02222	0.02626	0.0330	0.0286
Plot_A3_Tree_8351_rundata	0.04040	0.02222	0.03232	0.0440	0.0352
Plot_A3_Tree_8357_rundata	0.04848	0.02222	0.03838	0.0528	0.0418
Plot_A3_Tree_9301_rundata	0.05252	0.02222	0.04040	0.0572	0.0440
Plot_A4_Tree_6516_rundata	0.04444	0.02222	0.03434	0.0484	0.0374

Tree_ID	PatchDiam1	PatchDiam2Min	PatchDiam2Max	BallRad1	BallRad2
Plot_A4_Tree_6518_rundata	0.04646	0.02222	0.03434	0.0506	0.0374
Plot_A4_Tree_6520_rundata	0.04444	0.02424	0.03434	0.0484	0.0374
Plot_A4_Tree_6574_rundata	0.04444	0.02222	0.03434	0.0484	0.0374
Plot_A4_Tree_6580_rundata	0.05050	0.02222	0.03838	0.0550	0.0418
Plot_A4_Tree_6581_rundata	0.04040	0.01212	0.03232	0.0440	0.0352
Plot_A4_Tree_6621_rundata	0.04242	0.02222	0.03434	0.0462	0.0374
Plot_A4_Tree_6622_rundata	0.04646	0.02222	0.03434	0.0506	0.0374
Plot_A4_Tree_6626_rundata	0.04848	0.02222	0.03636	0.0528	0.0396
Plot_A4_Tree_6632_rundata	0.04646	0.02222	0.03636	0.0506	0.0396
Plot_A5_Tree_6357_rundata	0.03838	0.02424	0.03030	0.0418	0.0330
Plot_A5_Tree_6373_rundata	0.04040	0.02222	0.03232	0.0440	0.0352
Plot_A5_Tree_6382_rundata	0.03636	0.02222	0.03030	0.0396	0.0330
Plot_A5_Tree_6384_rundata	0.04646	0.02222	0.03838	0.0506	0.0418
Plot_A5_Tree_6387_rundata	0.04444	0.02222	0.03434	0.0484	0.0374
Plot_A5_Tree_6398_rundata	0.04040	0.01010	0.03232	0.0440	0.0352
Plot_A5_Tree_6406_rundata	0.04646	0.02222	0.03636	0.0506	0.0396
Plot_A6_Tree_3684_rundata	0.03030	0.02222	0.02626	0.0330	0.0286
Plot_A6_Tree_3750_rundata	0.03232	0.02222	0.02626	0.0352	0.0286
Plot_A6_Tree_3752_rundata	0.03838	0.02222	0.03232	0.0418	0.0352
Plot_A6_Tree_3755_rundata	0.03232	0.01818	0.02626	0.0352	0.0286
Plot_A6_Tree_5844_rundata	0.03636	0.01212	0.03030	0.0396	0.0330
Plot_A6_Tree_5850_rundata	0.03838	0.02222	0.03232	0.0418	0.0352
Plot_FC_Tree_1_rundata	0.04444	0.02222	0.03232	0.0484	0.0352

inputs from the best QSM generated among 30 per tree

Table A-2 Comparison of mean and standard deviation of total volume (in m³) across the optQSM-generated models (n = 30) and the treeQSM-generated models (m = 5) per tree.

Plot	TreeID	Mean Total Volume (m ³) optqsm	σ optqsm	Mean Total Volume (m ³) treeqsm	σ treeqsm
A1	8432	13.4182110	0.22933125	15.124802	0.43659705
A1	8433	10.9685225	0.27756870	12.135892	0.30197049
A1	8434	10.0446473	0.28801946	13.016005	1.17839270
A1	8437	7.8846558	0.31940553	9.338190	0.31914017
A1	8444	3.3689593	0.02326569	3.947650	0.10352778
A1	8445	3.2498648	0.21534896	4.748693	0.23493694
A1	8446	13.9450025	0.09214408	16.590428	0.60491650
A1	8457	11.5721042	0.15890120	12.889310	0.55169330
A1	8465	4.3499953	0.39350080	5.244979	0.52299133
A1	8467	4.1304053	0.26213614	5.256955	0.70367322
A1	8468	4.2139332	0.45442994	4.573651	0.30517862
A2	8668	6.9905940	0.28041122	8.383058	0.62081409
A2	8673	9.4730780	0.15243941	10.861728	0.78459009
A2	8674	3.9326895	0.11885603	4.568811	0.01632782
A2	8675	8.2132782	0.54814108	9.803812	0.83216315
A2	8676	7.1299881	0.11652667	8.493243	0.24891631
A2	8689	6.1531072	0.22354836	7.010768	0.19209338
A2	8749	16.8001287	0.18564220	14.784936	0.78468988
A3	8300	5.1005215	0.10405840	6.456366	0.12923047
A3	8301	3.5875633	0.04948732	4.525146	0.04476141
A3	8313	5.3127515	0.09908235	6.665366	0.24414049
A3	8343	9.3916614	0.22224537	10.574244	0.73295392
A3	8345	3.6959683	0.10634944	4.842133	0.56067560
A3	8351	5.8554044	0.03300385	6.742970	0.09193362
A3	8357	6.4164840	0.10898296	7.558581	0.38200858
A3	9301	16.9979347	0.27026718	18.601437	0.37365182
A4	6516	7.4895586	0.13763868	8.107938	0.26332758

Plot	TreeID	Mean Total Volume (m ³) optqsm	σ optqsm	Mean Total Volume (m ³) treeqsm	σ treeqsm
A4	6518	5.5156688	0.05625793	5.599097	0.04083730
A4	6520	10.5990681	0.13589299	12.341689	0.36864465
A4	6574	5.3674768	0.06359088	5.768057	0.10234758
A4	6580	6.5315050	0.32717558	7.775222	0.43772589
A4	6581	3.7886386	0.12312490	3.468929	0.20962418
A4	6621	10.9268396	0.14897465	12.117135	1.15448450
A4	6622	11.5627701	0.37807863	13.852933	0.59796216
A4	6626	2.4937836	0.20361710	2.855739	0.06491990
A4	6632	7.7750742	0.14021328	8.258980	0.69068524
A5	6373	6.3377446	0.35559487	7.851923	0.17630353
A5	6382	8.5769707	0.04730595	9.431699	0.04268141
A5	6384	8.2302205	0.17222214	9.958007	0.47722009
A5	6387	13.9013036	0.25074178	15.043205	0.52804504
A5	6398	6.1791854	0.36749583	9.933834	0.26012735
A6	3684	2.4459064	0.04510017	2.749307	0.22906682
A6	3750	4.6127766	0.91768709	4.703007	0.37487851
A6	3752	9.0813361	0.10493505	10.943064	0.12885403
A6	3755	8.0165623	0.13219307	9.263604	0.44268338
A6	5844	6.8015269	0.29913680	9.445643	0.77209210
A6	5850	7.7228437	0.10762916	9.376701	0.16714235
FC	FC_1	0.9895876	0.09042154	1.139946	0.05648928
Comparison of Mean Total Volume (m ³) and Standard Deviation between Optqsm and Treeqsm. N optqsm = 30, N treeQSM = 5					

Table A-3 The difference in total volume in m3 between the final QSM from optQSM and the final QSM from treeQSM.

Plot	TreeID	Mean Total Volume (m ³) optqsm	σ optqsm	Mean Total Volume (m ³) treeqsm	σ treeqsm
A1	8432	13.4182110	0.22933125	15.124802	0.43659705
A1	8433	10.9685225	0.27756870	12.135892	0.30197049
A1	8434	10.0446473	0.28801946	13.016005	1.17839270
A1	8437	7.8846558	0.31940553	9.338190	0.31914017
A1	8444	3.3689593	0.02326569	3.947650	0.10352778
A1	8445	3.2498648	0.21534896	4.748693	0.23493694
A1	8446	13.9450025	0.09214408	16.590428	0.60491650
A1	8457	11.5721042	0.15890120	12.889310	0.55169330
A1	8465	4.3499953	0.39350080	5.244979	0.52299133
A1	8467	4.1304053	0.26213614	5.256955	0.70367322
A1	8468	4.2139332	0.45442994	4.573651	0.30517862
A2	8668	6.9905940	0.28041122	8.383058	0.62081409
A2	8673	9.4730780	0.15243941	10.861728	0.78459009
A2	8674	3.9326895	0.11885603	4.568811	0.01632782
A2	8675	8.2132782	0.54814108	9.803812	0.83216315
A2	8676	7.1299881	0.11652667	8.493243	0.24891631
A2	8689	6.1531072	0.22354836	7.010768	0.19209338
A2	8749	16.8001287	0.18564220	14.784936	0.78468988
A3	8300	5.1005215	0.10405840	6.456366	0.12923047
A3	8301	3.5875633	0.04948732	4.525146	0.04476141
A3	8313	5.3127515	0.09908235	6.665366	0.24414049
A3	8343	9.3916614	0.22224537	10.574244	0.73295392
A3	8345	3.6959683	0.10634944	4.842133	0.56067560
A3	8351	5.8554044	0.03300385	6.742970	0.09193362
A3	8357	6.4164840	0.10898296	7.558581	0.38200858
A3	9301	16.9979347	0.27026718	18.601437	0.37365182
A4	6516	7.4895586	0.13763868	8.107938	0.26332758

Plot	TreeID	Mean Total Volume (m ³) optqsm	σ optqsm	Mean Total Volume (m ³) treeqsm	σ treeqsm
A4	6518	5.5156688	0.05625793	5.599097	0.04083730
A4	6520	10.5990681	0.13589299	12.341689	0.36864465
A4	6574	5.3674768	0.06359088	5.768057	0.10234758
A4	6580	6.5315050	0.32717558	7.775222	0.43772589
A4	6581	3.7886386	0.12312490	3.468929	0.20962418
A4	6621	10.9268396	0.14897465	12.117135	1.15448450
A4	6622	11.5627701	0.37807863	13.852933	0.59796216
A4	6626	2.4937836	0.20361710	2.855739	0.06491990
A4	6632	7.7750742	0.14021328	8.258980	0.69068524
A5	6373	6.3377446	0.35559487	7.851923	0.17630353
A5	6382	8.5769707	0.04730595	9.431699	0.04268141
A5	6384	8.2302205	0.17222214	9.958007	0.47722009
A5	6387	13.9013036	0.25074178	15.043205	0.52804504
A5	6398	6.1791854	0.36749583	9.933834	0.26012735
A6	3684	2.4459064	0.04510017	2.749307	0.22906682
A6	3750	4.6127766	0.91768709	4.703007	0.37487851
A6	3752	9.0813361	0.10493505	10.943064	0.12885403
A6	3755	8.0165623	0.13219307	9.263604	0.44268338
A6	5844	6.8015269	0.29913680	9.445643	0.77209210
A6	5850	7.7228437	0.10762916	9.376701	0.16714235
FC	FC_1	0.9895876	0.09042154	1.139946	0.05648928

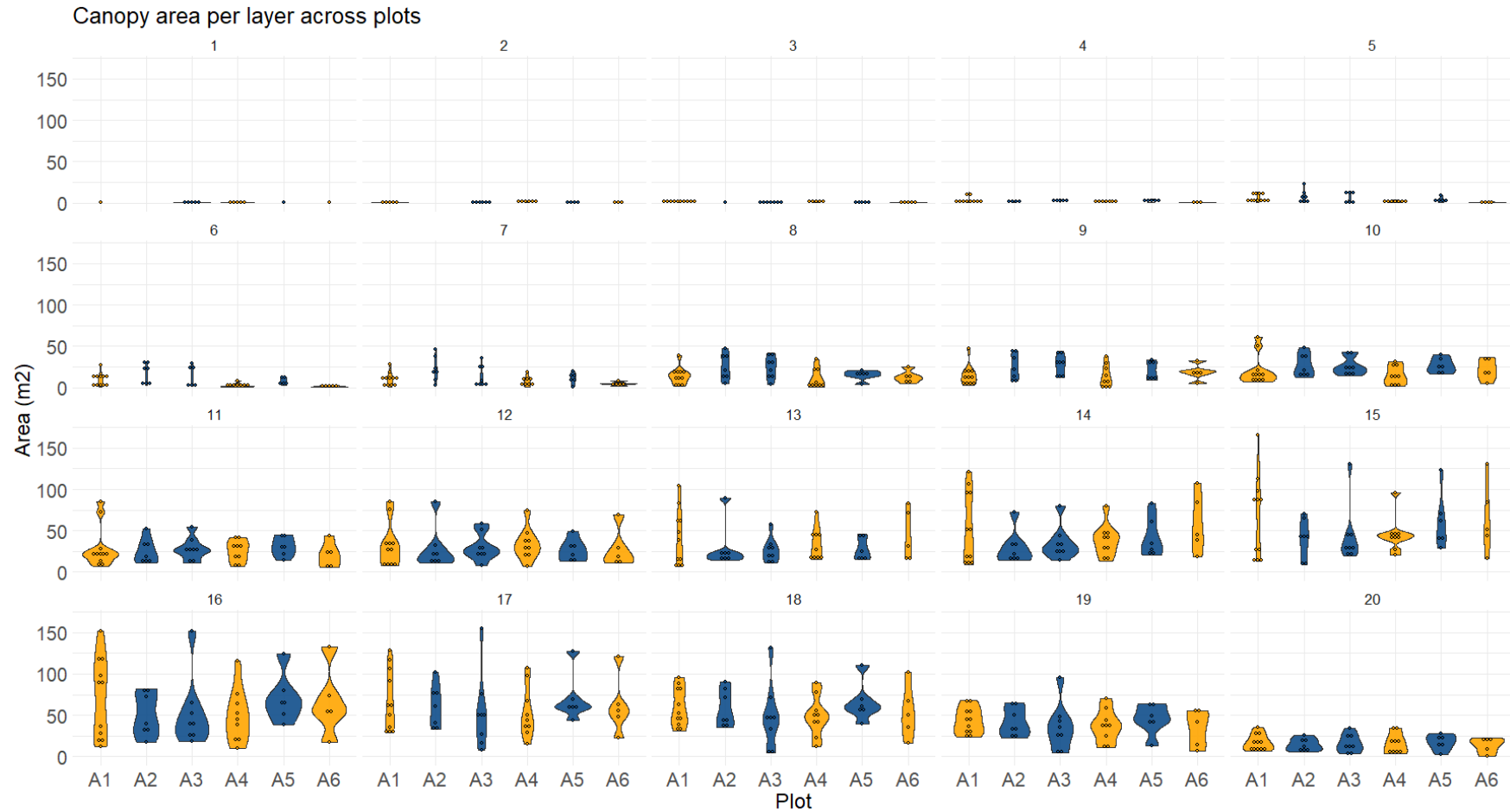


Figure A-5 Violin and dot plot of canopy projected area per height layer per plot. 1 is stem, 20 is top of the canopy. These numbers are pre-scaling. The dots within the violin plots reflect the number of QSM trees from each plot, with $nA1 = 11$, $nA2 = 7$, $nA3 = 8$, $nA4 = 9$, $nA5 = 6$, $nA6 = 5$.

Chapter 3:

$$\text{Upper area} = \frac{\text{Ellipse area}}{\text{Circle area}} = \frac{\frac{\pi}{2} * T(T + l)}{\frac{\pi}{2} * T^2} \quad (\text{A-1})$$

$$\text{Upper shaded area} = \frac{\pi}{2} (T(T + l) - T^2) = \frac{\pi}{2} * T * l \quad (\text{A-2})$$

$$\text{Lower area} = \frac{\text{Ellipse area}}{\text{Circle area}} = \frac{\frac{\pi}{2} * T(T + l)}{\frac{\pi}{2} * T^2} \quad (\text{A-3})$$

$$\text{Lower shaded area} = \frac{\pi}{2} (T(T + l) - T^2) = \frac{\pi}{2} * T * l \quad (\text{A-4})$$

$$\text{Total shaded area} = 2 \frac{\pi}{2} * T * l = \pi * T * l \quad (\text{A-5})$$

$$\text{Probability} = \frac{\text{shaded area}}{\text{plot area}} = \frac{\pi * T * l}{S} \quad (\text{A-6})$$

Where branch length l is in cm, transect radius T is in cm and plot area S in cm^2 .

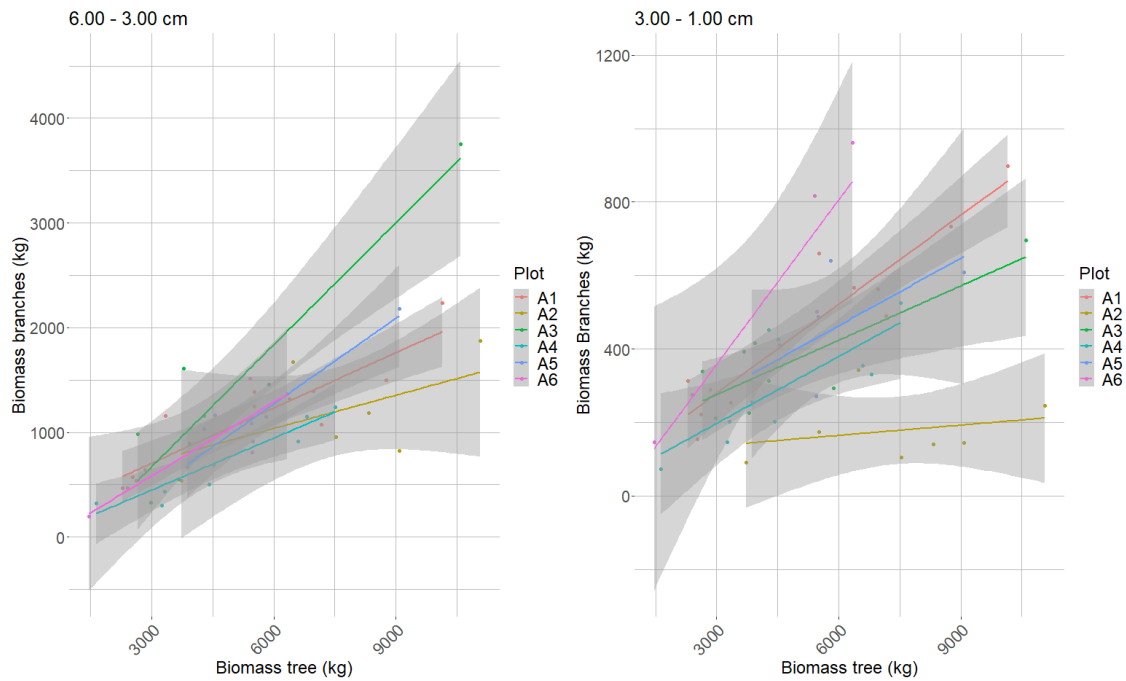


Figure A-6 Linear relations to estimate biomass in the 6.00 -3.00 and 3.00-1.00 cm diameter classes of the oak canopy from the total tree biomass per plot.

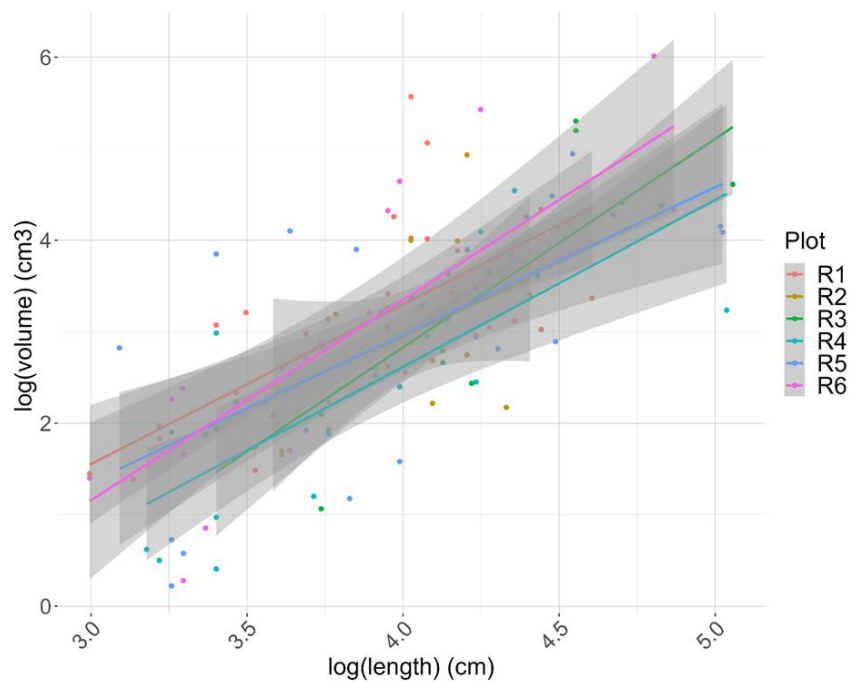


Figure A-7 Linear relations to estimate bark volume based on bark length per plot

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