Exploring the response of lianas to elevated atmospheric carbon dioxide (CO_2) in a mature Australian forest remnant.

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Abstract

Atmospheric CO_2 is rising globally and is set to increase by up to 50% over the next 50 years. Elevated atmospheric CO_2 has direct effects on vegetation as well as indirect effects through changing climates. Consequently, it is a global research priority to understand the effects of elevated atmospheric CO_2 so that we may better forecast how the earth's ecosystems may be affected by climate change.

Forests are responsible for the largest terrestrial uptake of atmospheric CO_2. Thus, much of the research efforts into ecosystem response to elevated atmospheric CO_2 has focused on trees and their role in forests. Consequently, this high impact research has excluded other woody forest plants such as lianas (woody vines), which are becoming increasingly more dominant in forests across the globe.

Lianas are growing in biomass, and diversity, and are proliferating in many of the world's forests, yet remain an underrepresented plant functional group in science. As structural parasites, and strong competitors, of trees, lianas negatively impact the fecundity, growth, and survival of host trees. In turn lianas negatively impact the ability of forests to absorb and sequester carbon, which may lead to long term changes to the carbon balance of forests.

Much of our knowledge of lianas is biased towards the neo-tropics, however liana species have been found worldwide. Similarly, the responses of lianas to elevated atmospheric CO_2 is still poorly understood and biased towards evidence from small scale experiments, which have been either short term or have focused on the experimental manipulation of juvenile lianas. This has led to a key knowledge gap into how canopy reaching lianas respond to long term increases in atmospheric CO_2.

There are few experimental sites capable of testing the effects of elevated atmospheric CO_2 on vegetation. However, the EucFACE facility in Australia is a large-scale Free Air Carbon Enrichment (FACE) facility that hosts a locally abundant liana, *Parsonsia straminea* in the *Eucalyptus tereticornis* woodland, offering a unique opportunity to explore: i) how these lianas respond to elevated atmospheric CO_2; and ii) to contrast these responses to the dominant tree species.

This thesis applies a novel remote sensing approach to retrospectively examine the effects of elevated atmospheric CO_2 on lianas and their hosts. This is achieved using Terrestrial Laser Scanning (TLS) surveys to examine increases in liana load, using a novel imaging analysis to examine canopy responses with a simplistic greenness ratio, and exploring the hyperspectral response of lianas and trees and relating the response to possible chemical changes.

At the EucFACE forest, lianas were found to be increasing in stature, measured as the height which lianas could be detected (LAH), and liana load, or proportion of trees hosting lianas, throughout the experiment. Increases in LAH and liana load were similar in ambient and elevated CO_2 treatments and were similarly constrained by a multiyear drought between 2018 and 2020. Lianas showed a pronounced increase in greenness to elevated atmospheric CO_2 while the dominant trees were found to be insensitive to CO_2 regime. Canopy greenness response to elevated CO_2 was greatest during seasonal water limitation but was constrained by the multiyear drought in both treatments. Leaf responses to elevated atmospheric CO_2 were examined with hyperspectral spectroscopy, finding that lianas had a pronounced response to elevated CO_2 conditions compared to that of trees, but that the response was limited to the visible and red-edge spectra. These lianas presented a spectral response that indicates increasing leaf chlorophyll concentrations in response to elevated CO_2 conditions, which contrasts with prior responses of woody plants in elevated atmospheric CO_2.

These results indicate that: a) liana proliferation is insensitive to elevated CO_2 conditions, b) lianas are likely more secure against seasonal droughts in elevated CO_2 conditions, c) lianas are more responsive to elevated atmospheric CO_2 than co-occurring trees, and d) liana greenness, and likely productivity, is constrained by long term drought regardless of CO_2 treatment. Thus, it is likely that the liana *Parsonsia straminea* is advantaged by elevated atmospheric CO_2 in short term periods of water limitation, whereas *Eucalyptus*

tereticornis appears to show signs related to plant stress when exposed to elevated atmospheric CO_2.

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Chapter 1. Thesis introduction

Globally concentrations of atmospheric carbon dioxide (CO_2) are rising (Ciais et al., 2009; Friedlingstein et al., 2022). Elevated atmospheric CO_2 has direct effects on vegetation (Körner and Arnone, 1992; Ainsworth and Long, 2021) as well as causing changes to the climate, thus affecting the patterns and processes of plant communities (Hättenschwiler and Körner, 2003; Vogado et al., 2022). The advent of free-air carbon dioxide enrichment (FACE) facilities, allows studies of the effects of CO_2 in more natural environments than those found in growth chamber experiments (Norby et al., 1999, 2005; Belote et al., 2004). Much of the research from forest FACE sites has concentrated on the trees located therein, and in Australasian forests up to 90% of aboveground carbon is stored as wood (Hopmans et al., 1993; Norby et al., 2016). Limited research has gone into the response of other woody forest organisms, some of whom have the capacity to negatively influence the carbon balance of forests (van der Heijden et al., 2013, 2015). Therefore, my research will be examining lianas (woody climbers) in an Australasian forest FACE facility and comparing their response(s) to that of the dominant trees.

Lianas are a functional group of climbing woody plants (Schnitzer and Bongers, 2002; Rowe and Speck, 2005). While liana research has advanced considerably in recent decades, lianas remain critically understudied. Supporting lianas comes at a cost to the host tree(s) as lianas compete not only for below ground resources, such as nutrients and moisture, but also for light as the leaf deployment of lianas is above those of their hosts (Visser et al., 2018a; Meunier et al., 2020).

The competition between lianas and trees is therefore intense, often more so than tree-tree competition (Tobin et al., 2012; Álvarez-Cansino et al., 2015). Competition for resources from lianas negatively affect the fecundity (Kainer et al., 2006; Nabe-Nielsen et al., 2009; García León et al., 2018), survival (Phillips et al., 2005; Ingwell et al., 2010; Reis et al., 2020) and growth of host trees (van der Heijden and Phillips, 2009; Ingwell et al., 2010; Schnitzer et al., 2014). These impact of lianas on the forests and their hosts reduces the carbon stored and sequestered in forests (van der Heijden et al., 2013, 2015;

Brienen et al., 2015). However, due to having a large leaf area compared to their wood, lianas do not compensate for the displacement of carbon dense tree stems (van der Heijden et al., 2013; Schnitzer et al., 2014; Brienen et al., 2015; van der Heijden et al., 2015).

Lianas are increasing in neo-tropical, the Asian tropics and temperate forests (Londré and Schnitzer, 2006; Schnitzer et al., 2011; Schnitzer and Bongers, 2011; Chandler et al., 2021b), though the trend in the African paleo-tropics remains unclear (Schnitzer and Bongers, 2011; Bongers et al., 2020). The proliferation of lianas may therefore have further impacted on the global carbon balance and therefore impact on future climate change. However, the drivers of the observed increase in liana biomass and abundance are still unknown, though several potential mechanisms have been put forward, amongst which is the increase in atmospheric CO_2 concentrations.

Previous studies have shown that at the individual plant level there is evidence that elevated CO_2 conditions can increase the biomass (Granados and Körner, 2002; Mohan et al., 2006) and stem length of lianas (Granados and Körner, 2002) in controlled conditions. While CO_2 appears to facilitate increased growth in juvenile lianas, comparative studies with conspecific trees have shown that the effects of CO_2 favour neither lifeform over the other in growth chambers (Marvin et al., 2015). As such it is currently poorly understood how lianas exposed to elevated atmospheric CO_2 respond in field conditions.

Field testing of the effects of CO_2 on lianas in forests is rare, however there has been an expansion of forest Free Air Carbon Enrichment (FACE) facilities in recent decades (Norby et al., 2016). Free air carbon enrichment experiments allow for manipulation of atmospheric CO_2 within pre-existing or artificial ecosystems (McLeod and Long, 1999; Norby et al., 2016). This allows researchers the opportunity to observe whole ecosystem responses to elevated CO_2 conditions, which thus far has not been replicable with smaller experiments such as growth chambers or bench experiments (Hendrey et al., 1993; McLeod and Long, 1999). While most are situated far from the liana abundant forests of the tropics (Norby et al., 2016), the only Australian forest FACE site, EucFACE, hosts the local liana species *Parsonsia straminea* (Muell). *P. straminea* is a locally abundant liana, found along the eastern seaboard of Australia from the temperate, sub-tropical region around the Sydney basin north to the rainforests of Queensland. As such this liana and its colonisation of EucFACE allows a unique opportunity to observe the response of lianas to elevated CO_2 conditions in-situ.

As field-based data were not available, an alternative method was needed to assess whether the lianas were responsive to elevated CO_2 concentrations. Routine remote sensing measurements at EucFACE are a part of the operational setup. This then allows me to use emergent remote sensing technologies as a vehicle to understanding the response of *P. straminea* and *Eucalyptus tereticornis,* the dominant tree, to elevated atmospheric CO_2. The structure of this thesis is such that each experimental chapter will be zooming in on the lianas and in chapters 5 and 6 comparing with *E. tereticornis* (Figure 1.1).

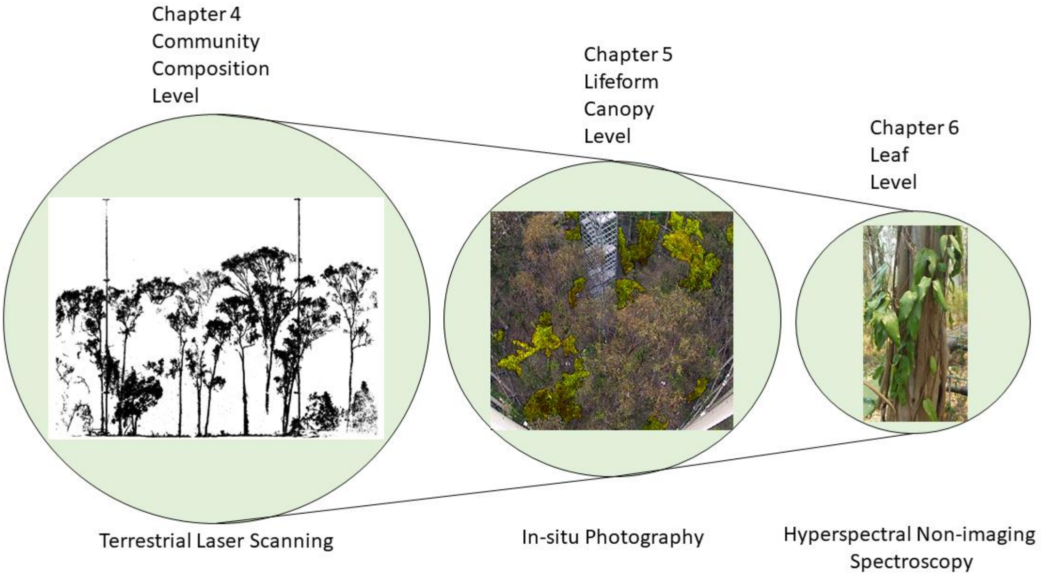


Figure 1. 1 Graphical representation of the changing focus throughout the thesis, from community level to canopy then to individual leaf level.

1.1. Chapter aims and objectives

The first experimental chapter (chapter 4) draws on advances in Terrestrial Laser Scanning (TLS) to study the proliferation of lianas within the forest community present at EucFACE. This chapter aims to determine whether lianas are increasing at EucFACE and whether this increase is driven by elevated CO_2 concentrations. I used TLS surveys taken at irregular intervals over a 10-year time period to census the proportion of eucalyptus trees that host lianas and the changes in height of liana-infestation on the tree stem, to determine whether there were differences in the proportion of trees hosting lianas and liana attained height in woodlands subjected to ambient or elevated CO_2 conditions.

My second experimental chapter (chapter 5) compares the canopy greenness response of trees and lianas in ambient and elevated CO_2 conditions using in-situ photography for an 8-year time period (2014-2022). This chapter builds upon prior work utilising similar off the shelf photographic equipment (Waite et al., 2019; Chandler et al., 2021a), where lianas and trees are shown to be spectrally separable. I have used RGB images from the top of the canopy at a fine temporal resolution (weekly), to test whether and how elevated atmospheric CO_2 changes lifeform greenness responses to both seasonal and climatic changes. With this chapter I ask whether CO_2: i) causes change in the optical response of lianas, ii) affects the optical differences between lianas and trees, and iii) changes the canopy response of lianas and trees to seasonal or severe drought.

My final chapter (chapter 6) focusses on the leaf level responses of both lianas and trees to elevated CO_2 conditions. Utilising hyperspectral non-imaging spectroscopy from, I aim to assess whether CO_2: i) causes change in the visible spectral response of lianas, ii) affects the spectral differences between lianas and trees, i.e. do lianas and trees become more or less similar, and iii) changes canopy response to seasonal or severe drought and relate any changes in the spectral response to changes in leaf chemistry.

Chapter 2. Literature Review

2.1 Carbon dioxide

Atmospheric carbon dioxide (CO_2) has been rapidly increasing over the last century from ~300ppm in 1900 to ~420ppm at present (Keeling et al., 1976; Friedlingstein et al., 2022). The global increase in CO_2 has been driven by rapid industrialisation combined with widespread land cover change, such as deforestation, across the globe (Friedlingstein et al., 2014, 2022; Peters et al., 2019). CO_2 absorbs and emits infrared radiation in the lower atmosphere, trapping energy radiated from the environment in the atmosphere (Myhre et al., 2017). Thus increased atmospheric CO_2 is responsible, in conjunction with other chemical emissions, for atmospheric warming (Hansen et al., 1981; Haywood and Boucher, 2000). Global warming further alters climatic patterns across the world, such as increasing the severity of dry seasons, intensifying rainfall events, and altering atmospheric airflow patterns (Hansen et al., 1981, 1997).

Terrestrial plants, through the process of photosynthesis, uptake atmospheric CO_2. Plants therefore have the potential to mitigate the increase in atmospheric CO_2 by increasing rates of photosynthesis thereby potentially allowing for greater plant growth due to increased production of carbohydrates (Keutgen et al., 1997; Norby et al., 1999; Keutgen and Chen, 2001). There is a large body of evidence for this carbon fertilisation effect from greenhouse studies, especially from species used in agriculture (Poorter, 1993; De Gelder et al., 2012; Hidaka et al., 2022). Typically studies have found that in high concentrations of CO_2 plants respond with increasing stem and leaf biomass (Avila et al., 2020; Hidaka et al., 2022), increased fruit yield (van der Kooi et al., 2016; Hidaka et al., 2022), and decreased foliar macronutrient concentrations (Keutgen et al., 1997; Keutgen and Chen, 2001). However, these physiological responses to elevated CO_2 are species dependant (Poorter et al., 1997; Jablonski et al., 2002; De Gelder et al., 2012; van der Kooi et al., 2016) and can be limited by factors such as water or nutrient availability (De Gelder et al., 2012; van der Kooi et al., 2016; Hidaka et al., 2022). Furthermore, in herbaceous (non-woody) plants there is evidence that photosynthetic pathway influences plant level responses to elevated CO_2 with C_3 pathway typically showing greater increases in growth to elevated CO_2 compared to C_4 pathway crop plants (Poorter, 1993; van der Kooi et al., 2016; Wu et al., 2019).

Studying the response of woody plants to elevated CO_2 presents a challenge due to their size (Norby et al., 1999) and requires increasingly expansive infrastructure (Norby et al., 1999). Growth chambers, or the larger whole tree chamber (WTC), can be used to isolate an individual tree for atmospheric gas injection and range from being a chamber placed directly over a portion of a plant to modify the local environment (sensu Zotz et al., 2006) to either open or closed topped structures that hold whole trees (Horton and Foley, 1961). These systems tend to test CO_2 concentrations much higher than atmosphere, for example in one of the few studies focusing on lianas, Oki at al. (2013), subjected portions of lianas to ~800ppm CO_2. In contrast other studies have ranged between 200 – 800ppm above ambient CO_2 (Körner and Arnone, 1992; Granados and Körner, 2002; Zotz et al., 2006; Körner et al., 2007). Despite all these applications having provided useful information on the response of woody plants to elevated CO2 conditions, they aren't able capable of fully capturing the dynamics of a full ecosystem (Horton and Foley, 1961; Hendrey et al., 1993; Norby et al., 1999).

Free air carbon enrichment (FACE) studies are designed to capture whole ecosystem responses, rather than singular plant responses, to elevated CO_2 and allows tracking of the effects of CO_2 during environmental events such as drought or flooding, to increases in atmospheric CO_2. and typically require large scale infrastructure to do so (Hendrey et al., 1993; McLeod and Long, 1999). Although they can vary in their construction (Ainsworth and Long, 2021), most follow a similar make up and use a series of elevated pylons to inject pressurised CO_2 gas into the canopy or sub canopy of a forest, typically at lower concentrations than those found in greenhouse studies (Norby et al., 1999; Allen et al., 2020). FACE experiments are costly and therefore spatially limited, with only EucFACE in Australia, AmazonFACE in the Brazilian Amazon basin, and BiFOR in the United Kingdom currently running and several others in North America having shut down in the 2010s (Norby et al., 2016).

2.2 Lianas as a lifeform

Lianas (woody climbers) are a polyphyletic group of climbing plants that rely on trees to provide structural support to reach the forest canopy, which allows lianas to deploy leaves into the canopy with little investment in woody tissue (Gerwing, 2004; Schnitzer and Bongers, 2011; Soffiatti et al., 2022b). Unlike (hemi) epiphytic plants, lianas retain a root stock throughout their life cycle (Schnitzer and Bongers, 2002). Lianas have evolved independently multiple times over the course of history, resulting in over 130 plant families now including at least one liana species (Putz, 1984a; Gentry, 1991; Schnitzer and Bongers, 2002).

2.2.1 Liana physiology

The independent evolution of the climbing growth form has led to a diversity in functional and mechanistic traits within the liana grouping, many of which characteristically differ from co-occurring tree species. As lianas do not require the ability support themselves as they mature, they present a different structural functionality compared to their host trees (Gerwing, 2004; Isnard and Silk, 2009; Soffiatti et al., 2022b). For example, by relying on trees for structural support, lianas can devote more resources to leaf production. Lianas can therefore contribute up to 30% of the total leaf area while only accounting for 5% of woody stems biomass (van der Heijden et al., 2013). To be able to transport water to their relatively large canopies, lianas have had to develop an efficient vascular architecture for transporting water to the canopy (Rowe et al., 2004; Soffiatti et al., 2022b). Lianas usually have larger xylem vessels than tree species (Gartner et al., 1990; Rowe et al., 2004) although there is often compartmentalisation of within the xylem bundles to increase pressure of vertical water transport (Rowe et al., 2004; Ewers et al., 2015; Soffiatti et al., 2022b). This results in lianas typically having a higher sap flux density than host trees, especially when water availability is high (Chen et al., 2015; van der Sande et al., 2019).

These adaptations also increase the hydraulic conductivity of lianas during the dry season (van der Sande et al., 2019) allowing lianas to take advantage of increased light availability and allowing lianas to continue growing during periods where co-occurring trees are dormant (van der Sande et al., 2013; Schnitzer and van der Heijden, 2019; Smith-Martin et al., 2019).

Lianas further differ from trees in stem pliability (Rowe and Speck, 1996; Rowe et al., 2004). Increased pliability of liana stems decreases the risk of mechanical injury from falling from host trees or from uncontrolled movement due to windstorms (Rowe and Speck, 1996, 2005; Ewers et al., 2015; Soffiatti et al., 2022a). Stem pliability is achieved through lower concentrations cellulose in the flexible wood of lianas, while simultaneously the concentration of hemicellulose is greater than that of co-occurring trees (Hoffmann et al., 2003; Rowe et al., 2004). These adaptations, collectively referred to as lianoid wood, are triggered when liana stems transition from self-supporting to wholly dependent on host trees for support (Rowe and Speck, 1996; Soffiatti et al., 2022a). This transition from stiff to flexible wood appears to be hard-wired into lianas, with evidence suggesting that there are diameter and length controls prompting the development of lianoid wood (Soffiatti et al., 2022a).

Lianas can be brought down from the forest canopy when host trees fall. This does not mean the end for a liana however. Fallen liana stems are capable of resprouting when in contact with the ground (Alvira et al., 2004; Gerwing, 2006) leading to high density clonal regrowth in treefall gaps (Ledo and Schnitzer, 2014; Rocha et al., 2020). Recent studies suggest that resprouting of lianas is positively linked to the severity of canopy fall, in manipulative experiments lianas which suffered the greatest damage doubled the number of clonal sprouts than those with minimal or no damage (Rocha et al., 2020).

Classically liana root systems have been suggested as some of the deepest root systems within tropical forests (Putz, 1984a; Chen et al., 2015). The hypothesis for root system differentiation is that unlike tree root systems, lianas are free of the constraints of self-supporting growth and therefore do not need structural root systems (Ewers et al., 2015).

This would potentially allow investment into fine root structure that can reach deeper water sources than those of co-occurring tree species (Andrade et al., 2005; Chen et al., 2015). However recent research into liana biomass allocation has found, in contrast, that lianas did not root to depths greater than those of co-occurring trees (De Deurwaerder et al., 2018; Smith-Martin et al., 2020). Smith-Martin et al., (2020) note that rooting patterns and subsequent biomass allocation, differs between juvenile and adult lianas, with juvenile lianas typically allocating more biomass to leaves and stem than to roots. De Deurwaerder et al., (2018) found that lianas can maintain an active root system in shallow soil layers which allows for faster uptake of dry season precipitation and thus decreases direct resource competition with co-occurring trees.

Lianas deploy their leaves directly through the canopy, in many cases displacing or over topping the leaves of host trees directly competing for and intercepting light in upper and middle canopy layers (Schnitzer and Bongers, 2002; Rodríguez-Ronderos et al., 2016; García León et al., 2018). Within liana leaves concentrations of chlorophyll can vary by site conditions, Sanchez-Azofeifa et al. (2009) found that lianas growing in dryer conditions had lower chlorophyll concentrations. Comparative to host trees, lianas have a higher concentration of foliar phosphorous and nitrogen particularly in periods of drought (Kazda and Salzer, 2000; Cai et al., 2008). Thus, lianas can rapidly create new leaves and photosynthetic tissues, increasing leaf biomass faster than co-occurring trees (Kazda and Salzer, 2000). Liana leaves typically have greater water content than co-occurring tree species, combined with greater cavity space within the mesophyll of the leaves (Sánchez-Azofeifa and Castro-Esau, 2006) which allows for increased photosynthetic capacity due to greater gas diffusion through the photosynthetic pigments (Zhang et al., 2016).

2.2.2 Liana influence on forest fauna

Connection between tree canopies is limited in liana-free forests, in part due to the canopy shyness phenomena, where tree growth into adjacent canopies is limited (Putz et al., 1984; Adams et al., 2017; Markham and Fernández Otárola, 2020). As such this can lead to forest trees becoming biological islands, a phenomena increased when trees are emergent from the canopy (Odegaard, 2000; Adams et al., 2017, 2019). This can limit the dispersal of arboreal animals who are incapable of flight (Arroyo-Rodríguez et al., 2014; Powell et al., 2011). Due to lianas being capable of lateral growth between and within tree canopies, lianas can create interconnected webs within the forest canopy facilitating dispersal of non-flying animals (Yanoviak and Schnitzer, 2013; Arroyo-Rodríguez et al., 2014). Lianas also serve as valuable food sources for herbivorous animals (Arroyo-Rodríguez et al., 2014; Odell et al., 2019). Tangles of lianas have been shown to increase the diversity of arboreal arthropods, thus also maintaining the diversity of insectivorous birds (Michel et al., 2014; Odell et al., 2019; Schnitzer et al., 2020).

2.3. Competitive effects of lianas

2.3.1. Mechanisms of competition

Lianas compete intensely with their host trees for essential resources both below ground for water and nutrients as well as above ground for light (Phillips et al., 2005; Schnitzer et al., 2005; Schnitzer, 2018; Marshall et al., 2020). As lianas place leaves directly over those of their hosts, aboveground competition between lianas and trees can be intense (Schnitzer et al., 2005). Lianas can also strongly compete belowground cause of mortality and stunted biomass accumulation especially in juvenile trees (Schnitzer et al., 2005; Toledo-Aceves and Swaine, 2008; Meunier et al., 2020). In a study by Tobin et al., (2012) of mature trees, the removal of lianas increased sap flow in trees by ~8% in dry season conditions, which may in part be due to increased evaporative potential in the canopy due to liana die off or through reduced below ground competition for water resources. Similar results were presented in Alvarez-Cansino et al., (2015) showing there is a strong seasonality to the effects of lianas on tree sap flow. Despite the evidence of negative liana competition, the disentangling of the effects of above/below ground competition has yet to be fully realised for mature trees in the current literature.

2.3.2 Effects of liana competition on individual trees

Hosting lianas is not without risks for their hosts. For example, trees that are infested by lianas are often limited in their growth (Schnitzer et al., 2005, Alvarez-Cansino et al., 2015). Studies have indicated that when lianas are removed, diameter growth of trees increased up to 25% (Alvarez-Cansino et al., 2015). In a study by Dias et al., 2017 found that with liana competition, tree allometry responded to increased load with infested tree stems being shorter than those without lianas. Liana-induced effects upon tree growth increases with liana occupation in the tree crown (van der Heijden and Phillips, 2009; Dias et al., 2017).

Liana infestation also increases host tree mortality, with lianas accounting for up to 30% of large tree mortality in some areas (Phillips et al., 2005). Liana-induced mortality rates have been shown to increase as liana occupation increases, doubling the mortality rate compared to lower infestation levels (Ingwell et al., 2010). The direct cause of the death of host trees is likely to be due to a combination of effects derived from above and below ground competition as rooted liana density and basal area increases with canopy liana infestation (Ingwell et al., 2010).

Tree fecundity has been shown to be reduced through competition with lianas (Kainer et al., 2006; Nabe-Nielsen et al., 2009; García León et al., 2018; Visser et al., 2018b). There may be several mechanisms at work here, evidence suggests that liana infestation suppresses seed production in canopy trees, which reduces the number of viable saplings produced in the understory (Kainer et al., 2006, Nabe-Nielson et al., 2009). Furthermore, competition in the understory further suppresses sapling growth and increases juvenile mortality (Garcia-Leon et al., 2018, Visser et al., 2018). There is evidence to suggest that liana suppression of sapling establishment is higher for pioneer species than is normally reported, as lianas appear to disproportionally cause the mortality of faster growing, shade intolerant tree species (Visser et al., 2018b).

2.3.3 Implications of liana infestation on forests

Competition with lianas is not evenly distributed amongst tree species within the forest. Slower growing trees with higher wood densities were found to host lianas more often than those that are faster growing with lower wood densities (Putz, 1984; van der Heijden et al., 2008; Schnitzer and Carson, 2010). This has been interpreted that slower growing trees were more negatively affected by lianas than faster growing trees, however this is likely an effect of survivorship bias. As put forward by Visser et al. (2018b), faster growing trees were more adversely affected by lianas i.e. mortality was increased. However, the surviving faster growing trees had escaped being infested whereas, slower growing trees were capable of tolerating infestation (Visser et al., 2018b). At similar basal areas, faster growing trees were found to be more at risk of mechanical damage from lianas, altering the vertical and species composition (Visser et al., 2018b). Therefore, liana infestation of slow growing tree species that can survive heavy liana loads may facilitate the infestation of fast growing neighbours (Visser et al., 2018b).

Liana proliferation can alter the dynamics of forests. As lianas regularly connect multiple tree canopies (Putz, 1984a), lianas can pull down multiple trees when a host tree falls. Thus, increasing liana abundance can accelerate forest gap creation. Forest gaps increase light availability in the understory which may in turn benefit both lianas and faster growing trees (Schnitzer et al., 2000; Schnitzer and Carson, 2010). While forest gaps can increase local species diversity (Schnitzer and Carson, 2010), lianas slow the regeneration process by reducing tree growth (Medina-Vega et al., 2022a). Stalled forest gaps, those with low canopy height with abundant lianas, reduce the carbon uptake of forests, as both the lianas and the preferentially selected pioneer trees are less carbon dense than slower growing, denser non-pioneer trees (Schnitzer et al., 2000, 2014; Schnitzer and Carson, 2010; van der Heijden et al., 2015).

High canopy forests are not immune to the effects of lianas. Due to their size, large lianas (>15cm dbh) are implicated in increasing the mortality risk for their host trees, either through competitive effects as discussed above, or due to the increasing crown liana load increasing the probability of a tree fall (Phillips et al., 2005). The selective pressure for large lianas to have large host trees is likely to increase the prevalence of smaller trees within tropical forests in areas where large liana infestation is a driver of tree mortality (Muller-Landau and Visser, 2018).

Due to the impact of lianas on the survival (Phillips et al., 2005), growth (Dias et al., 2017; Rodríguez et al., 2021; Medina-Vega et al., 2022a) and fecundity (Kainer et al., 2006; Nabe-Nielsen et al., 2009; García León et al., 2018) of their hosts, lianas can decrease the carbon storage and sequestration potential of forests (Schnitzer et al., 2014; van der Heijden et al., 2015). Due to their low investment in woody biomass, liana are unlikely to compensate for the tree biomass that they displace (van der Heijden et al., 2013). Additionally, lianas shift the allocation of above ground carbon stocks in forests from stems to leaves, reducing the return time of fixed carbon to atmospheric carbon due to high leaf litter turnover (van der Heijden et al., 2015; Akihiro et al., 2022). Within forest canopies, lianas have been reported to contribute to 40% of canopy biomass despite only contributing <5% of stem biomass (Phillips et al., 2005; van der Heijden and Phillips, 2009; van der Heijden et al., 2013).

2.4. Putative drivers of liana proliferation and growth

Liana biomass has been increasing across the neo-tropics (Phillips et al., 2002; Schnitzer and Bongers, 2011; Laurance et al., 2014; Sullivan et al., 2022) and temperate forests (Carrasco-Urra and Gianoli, 2009; Perring et al., 2020). There is however, evidence of contrasting patterns in the paleo-tropics (Schnitzer and Bongers, 2011; Bongers et al., 2020) although recent studies have found increases in the Asian tropics (Parthasarathy et al., 2015; Chandler et al., 2021b). As such it is yet unclear what the drivers of liana abundance are, although several putative mechanisms have been put forward (Schnitzer and Bongers, 2011). The increase in liana biomass has been linked to several drivers including environmental change, human activity, intensifying seasonality and elevated levels of atmospheric CO_2 (Schnitzer and Bongers, 2011; Schnitzer, 2018).

2.4.1 Elevated atmospheric CO_2

Global elevated CO_2 concentrations have increased by 100 ppm over the last 60 years (NOAA 2020). Elevated atmospheric CO_2 concentrations has been proposed as a driver for increases in plant biomass (Hogan et al., 1991; Körner et al., 2007; Castanho et al., 2016) and has also been suggested as a potential explanation for the rise in liana biomass (Phillips et al., 2002; Schnitzer and Bongers, 2011). Elevated CO_2 (eCO_2) concentrations have been shown to increase liana biomass in growth chamber studies (Granados and Körner, 2002; Marvin et al., 2015). For example, a study by Granados and Korner (2002) focused on the effects of CO_2 enrichment on juvenile tropical lianas under varying light regimes. They show that liana vigour and biomass increase under elevated CO_2, primarily by an increase in stem diameter, but that the effect is species dependant. The greater response of lianas to elevated CO_2 in low light conditions suggests elevated atmospheric CO_2 may affect lianas in the lower canopy or understory more strongly, however evidence from canopy lianas is limited, to the point of almost non-existent in the literature.

Current evidence from field studies shows that increased liana proliferation and growth in elevated CO_2 is linked to other climate factors (Manzanedo et al., 2018; Venter et al., 2022). The woody cacti climber *Pereskia aculeata* Miller (*Cactaceae*) increased in biomass, in elevated CO_2, water limitation reduced the rate of biomass accumulation to below that of well-watered, ambient CO_2 lianas (Venter et al., 2022). The same study also showed that lianas grown with adequate water supplies in eCO_2 had the lowest chlorophyll content, greatest C:N ratio and lower foliar nitrogen concentrations suggesting an increased photosynthetic efficiency when well-watered (Venter et al., 2022). Furthermore Venter et al. (2022) found that within the eCO_2 treatments, lianas that are water-limited are ~16% more efficient in water usage than those with abundant soil moisture.

Studies on temperate lianas have shown results analogous to the results shown in Granados and Korner (2002). For example, in two separate Free Air CO_2 Enrichment (FACE) experiments, lianas were shown to increase in biomass and vigour in low light conditions when exposed to elevated CO_2 conditions (Mohan et al., 2006; Zotz et al., 2006). Both of the studied species (*Hedera helix* and *Toxicodendron radicans*) were shown to exceed the size of control plants when in elevated CO_2 conditions with *H. helix* having a greater chance of reaching canopy height (Mohan et al., 2006; Zotz et al., 2006). Mohan et al. (2006) found that *T. radicans* growth outperformed that of other woody species leading to potential dominance shifts if left unchecked. Manzanedo et al. (2018) found that increasing basal area of a temperate liana (*Hedera helix*) strongly correlated with increasing CO_2 but was dependent upon temperature, using a dendrochronology and species distribution modelling approach. Manzanedo et al., (2018) found increasing temperatures decreased the potential for CO_2 fertilisation of *H. helix* (Manzanedo et al., 2018). Likewise co-occurring trees were negatively impacted by rising mean temperatures (Manzanedo et al., 2018). However, increasing monthly mean temperatures in this study were accompanied by increasing water stress, a condition likely to favour lianas over co-occurring trees (Manzanedo et al., 2018).

Although previous work showed that lianas respond to elevated CO_2 conditions, work by Marvin et al. (2015) showed that there is no difference in response of liana saplings to elevated CO_2 when compared to co-occurring tree saplings. This study further highlighted that individual species responded differently to elevated CO_2 concentrations, with the biomass of the liana *Stigmaphyllon lindenianum* increasing by 322%, but that of *Paullinia pinnata* decreasing by 19% (Marvin et al. 2015). These results are similar to those by Belote et al., (2004) on two co-occurring invasive lianas (*Lornicera japonica* and *Microstegium vimineum*) found that physiological responses to CO_2 enrichment differ between species and may be constrained by moisture availability.

However, all studies comparing the effects of lianas and trees to elevated CO_2 conditions were performed exclusively on seedlings or understory lianas and are therefore unlikely to represent the response of adult lianas to elevated CO_2 conditions. This is important because lianas and trees are highly similar in early ontogeny, when lianas are still often freestanding (Rowe and Speck, 1996; Smith-Martin et al., 2020). Additional research is therefore needed to investigate the response of adult lianas elevated CO_2 conditions. As lianas have a detrimental effect on forest carbon storage, it is imperative that we assess whether elevated CO_2 concentrations may be the dominant driver of the increase in liana biomass to aid our understanding how forests will respond to future conditions (Gallagher et al., 2010; van der Heijden et al., 2013; van der Heijden et al., 2015; van der Heijden et al., 2022).

2.4.2 Environmental drivers

Increases in liana biomass have been linked with environmental changes, such as intensification of dry seasons, reduced precipitation and rising disturbance (Phillips et al., 2002; Schnitzer and Carson, 2010; Schnitzer et al., 2011; Schnitzer and Bongers, 2011). Increased disparity between wet and dry seasons due to changing or decreasing rainfall is thought to be a driver of liana changes as lianas have been shown to increase in abundance and species diversity with decreasing rainfall and increasing temperature (Swaine and Grace, 2007; Parolari et al., 2020; Medina-Vega et al., 2021a; Schnitzer and Bongers, 2011). In seasonally dry forests, lianas appear capable of increased growth relative to co-occurring trees during periods with low rainfall/soil moisture availability (Schnitzer and van der Heijden, 2019; Medina-Vega et al., 2021b) potentially due to increased water-use efficiency and limited drought susceptibility in lianas (Cai et al., 2009; Chen et al., 2015; van der Sande et al., 2019). As many lianas are well adapted to grow in periods of drought, reduced rainfall and increases in the length of dry season allow lianas greater periods of growth compared to host trees (Schnitzer, 2005; DeWalt et al., 2010; Álvarez-Cansino et al., 2015; Schnitzer and van der Heijden, 2019; Medina-Vega et al., 2021a). Temperatures and drought occurrence are likely to increase in forests (Seidl et al., 2017; Sommerfeld et al., 2018), which could lead to greater liana abundance and diversity as predicted droughts increase in severity (Dale et al., 2001; Phillips et al., 2009; Gallagher et al., 2010; Álvarez-Cansino et al., 2015; Umaña et al., 2019).

The disturbance of forests by pests, disease, or abiotic factors, such as wind or fire, is an integral element of forested ecosystems under normal climatic and biological circumstances (Dale et al., 2001). Disturbance of forests has been shown to increase liana diversity (Ledo and Schnitzer, 2014; Campbell et al., 2018; Schnitzer et al., 2021) and biomass as lianas are capable of colonization and establishment in gaps left by forest disturbance at rates and density that often out compete co-occurring tree species (Gerwing and Vidal, 2002; Alvira et al., 2004; Schnitzer et al., 2011; Ledo and Schnitzer, 2014). Where lianas out compete co-occurring tree species in gaps this can lead to species regime shifts as well as potentially leading to forest desiccation due to increased solar radiation at lower canopy and ground layers (Cochrane and Laurance, 2008; Schnitzer et al., 2011; Addo-Fordjour et al., 2021). Mechanistically, increases of lianas where forest gaps are created could be due to the propensity of lianas towards clonal reproduction (Rocha et al., 2020; Schnitzer et al., 2021). Where lianas fall from canopy to forest floor up to 90% of liana stems can survive and regenerate within the gap (Putz, 1984a; Rocha et al., 2020). Increases of lianas within gaps can also be attributed to lianas being responsive to light regime changes, increasing in height, biomass and relative growth rate with increasing light (Cai et al., 2008; Yuan et al., 2016). It is therefore likely that disturbances which alter canopy structure or decrease tree leaf area may allow sufficient increases in light regime to allow liana proliferation despite the absence of large canopy gap creation.

2.4. Anthropogenic land use drivers

Anthropogenic land use changes in forests are increasing. Predominantly in the tropics, primary forests are de-forested for farming, cattle ranching and infrastructure and eventually abandoned when it becomes financially unsustainable (Foley et al., 2005; Willcock et al., 2016). Primary and secondary forests are under pressure for production of timber, both within legal frameworks and through illegal logging operations (Food and Agriculture Organisation of the United Nations, 2015). Disturbed primary forests are more likely to host greater numbers of liana saplings than disturbance free forests (Schnitzer et al., 2004; Sullivan et al., 2022).

Forests affected by selective logging have greater canopy openness (Asner et al., 2006), which allows understory lianas greater access to higher light conditions, which as with natural gap creation is likely to promote greater relative growth in lianas (Cai et al., 2008; Yuan et al., 2016; Sullivan et al., 2022). Similarly where land is being abandoned and reverting to secondary forest lianas are likely to proliferate, as lianas take advantage of both the light regime and the heterogeneous vertical profile of these forests, i.e. where forest canopies contain an array of different tree heights and sizes, lianas are capable of moving between hosts vertically thus proliferating through the canopy and further slowing forest succession (Estrada-Villegas et al., 2020). Similarly forest fragmentation has been shown to lead to higher relative liana biomass, likely through the same processes of increased light availability as well as increased trellis availability (Reis et al., 2020; Addo-Fordjour et al., 2021).

Forests disturbed by human actions often harbour greater diversity of lianas which have a reproductive advantage over co-occurring trees (Gerwing and Vidal, 2002). It is unlikely that human activity will decrease in forests due to the value of goods derived from these natural resources, thus it is likely that as humans continue to exploit forests lianas will continue to be advantaged by anthropogenic forest disruption.

2.5 Remote sensing

2.5.1 Remote sensing of forest properties

The simplest definition of remote sensing is the gathering of data on a target without the need for direct interaction with the target (Schowengert, 2007). The resultant remotely sensed data are becoming more prevalent as a data source in forest ecology and is derived from a myriad of technologies on different platforms including; satellites, occupied or unoccupied airborne vehicles and hand-held or static (Lechner et al., 2020). Each of these platforms have an array of sensor types. Broadly speaking remotely sensed data is made up of data that has been captured at a range of resolution types (spatial, spectral and temporal), which allows for fast and accurate capture of vegetation properties and changes to them within vegetative assemblies (Disney, 2016; Lechner et al., 2020; Fassnacht et al., 2024). Space borne platforms (satellites) such as Landsat have spatial resolutions (i.e., pixel sizes) of 900m^2 and up (USGS 2020), although newer platforms such as the Planetlabs Skysat constellation are capable of <1m^2 resolution (Planetlabs 2020), while sensors upon UAVs are capable of even higher resolution ~10mm^2 pixel depending on flight altitude (Colomina and Molina, 2014; Waite et al., 2019; Zambrano et al., 2022). Remote sensing platforms can be broken down into two broad categories: active and passive (Schowengert, 2007). Active systems utilise an on-board source of electromagnetic radiation, e.g. laser emitters or radar systems, whereas passive systems operate through the measurement of reflected or emitted electromagnetic radiation alone, e.g. photographic imaging sensors or thermal sensors. This thesis will utilise both using in-situ imaging (passive), field spectroscopy (active due to use of a leaf clip with integrated light source) and terrestrial laser scanning (active) to allow multi-spatial and temporal analysis of liana infestation.

Remote sensing in forest ecology and forest management has typically been used to provide data on the spatial extent and dynamics of forests, forest type and species assemblage, and biophysical and biochemical properties of forests (Boyd and Danson, 2005). Remote sensing allows for the user to collect data at a range of temporal, spatial and radiometric scales, and as such have a myriad of platform options that can cover the remote sensing of vegetation metrics (Nijland et al., 2014; Bolton et al., 2018; Lechner et al., 2020). In recent years there has been a trend towards the use of satellite or unoccupied aerial vehicles (UAVs) for the monitoring of forest health and assemblages (Boyd and Danson, 2005; Torresan et al., 2017; Waite et al., 2019). There is however the need to consider how applicable both the resulting data and platform type are to the study. While satellite derived data can provide routinely forecast returns over a study target, these data can be limited in spatial resolution (Boyd and Danson, 2005; Chandler et al., 2021a) which could limit the detection of physically small assemblages within the forest canopy. Similarly, there are limits placed upon the use of UAVs, despite their small size and relative ease of deployment, the use of UAVs is restricted by aviation laws limiting deployment to areas away from regular aircraft traffic. This thesis places another limitation on the use of aerial remote sensing, the lianas at EucFACE were not present within the canopy at the start of the experiment, and by 2022 were present within but not necessarily atop, the forest canopy. This limits the utility of data derived from UAVs and satellite as neither source provides an adequate view of below canopy structures.

In forest ecology, the application of remote sensing has been increasing rapidly as data can be gathered at scales larger than those achievable by field measurement alone (Barrett et al., 2016; Fassnacht et al., 2024). At global and landscape scales, remote sensing data has been used to map and monitor changes to global or country-wide forest cover (Hansen et al., 2013; White et al., 2017; Kangas et al., 2018; Breidenbach et al., 2022). These forest cover studies provide useful insight into both the inventory of trees within a forest, but also can be used to predict the growth and carbon dynamics of forests (Kangas et al., 2018; Breidenbach et al., 2022). Increasingly multi-temporal studies are being enacted to further quantify how changes to forest cover are being enacted upon landscape and countrywide scales, drawing from freely available datasets, such as Landsat, and from commercially derived products, such as the National Tree Map from Bluesky International (Breidenbach et al., 2022, Bluesky International 2024).

Perhaps the most widespread use of remote sensing in forestry is in inventory management, typically through the use of aerial photography (Fassnacht et al., 2024). These data have been used for a range of forestry needs, including stem surveying, tree health assessment, tree species composition, and tree pest identification (Asner and Martin, 2009; Holopainen et al., 2015; Torresan et al., 2017; Zambrano et al., 2022). Aerial photography has a long history in these use cases, traditionally requiring trained photo-interpreters to identify and delineate canopies (Berveglieri et al., 2016; Fassnacht et al., 2024). Efforts towards automating both canopy delineation and species composition have found that using simple red, green, blue (RGB) imagery remains challenging (Fassnacht et al., 2016) but with an experienced operator, simple imagery is sufficient for measuring canopy area and by extension liana infestation of tree crowns (Waite et al., 2019).

Forest structure at a local, i.e. per forest, scale affects how and where forests store carbon (Pan et al., 2013; Stovall et al., 2018). As forests can be highly complex and varied in vegetative structure, quantifying forest structure has been a persistent challenge for researchers. Relatively recent advances in aerial laser scanning (ALS) have increased understanding of forest structural properties through the use of vegetation structure indices (Holopainen et al., 2015; Valbuena et al., 2016, 2017; Terryn et al., 2022a). These indices allow for assessment of the vertical profile of forests, i.e. where branching or leaf structures develop (Holopainen et al., 2015; Valbuena et al., 2017), which could include non-tree vegetative structures and as such could be used to identify liana influence on forest structures (Terryn et al., 2022a). In combination with terrestrial laser scanning (TLS) these ALS data can be used to create 3-dimensional digital forest twins, from these it is possible to investigate tree scale structural development, such as branching angle or biomass distribution (Lovell et al., 2014; Coops et al., 2021; Terryn et al., 2022a). These structural metrics can indicate the influence of external factors upon the development of trees, including the influence of lianas (Krishna Moorthy et al., 2018).

At an individual tree up to a local plot scale, remote sensing is typically deployed to assess structure or tree health (Calders et al., 2014; Reid et al., 2016; Bianchi et al., 2017; Dell et al., 2019). Tree structural measurement from ground based remote sensors has typically imitated those of field based measurement, e.g. diameter at breast height (DBH) and height (Disney, 2019) although recent work has focused on the application of full tree geometric modelling to improve biomass estimates (Calders et al., 2015; Gonzalez de Tanago et al., 2018; Luck et al., 2020; Terryn et al., 2022a). Tree health is a major concern for forest managers and ecology across the globe, thus detection of the signs and symptoms of pests and disease, is a growing facet of remote sensing. Applications to monitor tree health can be found at multiple scales and multiple technological approaches. At individual canopy or sub-plot scales it has been shown that crown fractal structures, i.e. how branches develop, of trees can be indicative of response to disease in simple imagery (Murray et al., 2018). Simple imagery from a variety of sources has been used to identify patterns of mortality and tree health status in multi-temporal studies (Stone et al., 2001; Michez et al., 2016; White et al., 2017; Dell et al., 2019; Huang et al., 2019).

The use of remote sensing technologies in liana ecology has mostly been limited to mapping of liana infestation (e.g. Castro-Esau et al., 2004; Foster et al., 2008; Waite et al., 2019; Chandler et al., 2021b). While most of the sensor and platform combinations shown within Figure 2.4 could be used in part of the analysis of the lianas at EucFACE, this study will make use of ground based or *in-situ* sensors due to issues with over-flight access for drones and limitations with pixel size relating to space- and air-borne sensors. As lianas are integrated into the canopy of trees viewing change in liana biomass needs very high spatial and temporal resolution data, thus making space borne and to an extent, airborne sensors impractical to be used as part of this study (Castro-Esau et al., 2004; Chandler et al., 2021b). The very high-resolution data captured using remote sensing in this thesis included: terrestrial laser scanning; terrestrial RGB sensors and leaf scale spectroscopy.

2.4.2 Terrestrial laser scanning

Terrestrial laser scanning (TLS) is an active millimetre spatial resolution remote sensing technology (Calders et al., 2014). This terrestrial scanning by way of lasers is a relatively recent development for data capture of vegetation at very high-resolution stemming from airborne laser scanning (ALS). The first dedicated systems being available in the late 1990s (Ullrich et al., 1999).

The use of TLS for forest monitoring is relatively recent, first being demonstrated in literature in the early 2000s (Hopkinson et al., 2004; Lovell et al., 2014). Earliest uses of this technology in forests was focused on deriving traditional forestry measurements, such as diameter at breast height (DBH) and tree height (Hopkinson et al., 2004). This eventually evolved into whole tree volumetric assessment for biomass estimation (Calders et al., 2015; Gonzalez de Tanago et al., 2018) while currently TLS data are being used for habitat assessment (Ashcroft et al., 2014), monitoring successional vegetation regime change (Cuni-Sanchez et al., 2016), investigation of branch architecture (Lau et al., 2018) and in quantifying wild fire fuel loads, i.e. brush wood, on forest floors (Chen et al., 2016). These uses for TLS data are a result of the high data resolution (Newnham et al., 2015) which allows for the discrimination and classification of fine structures, such as leaves, stems and shoots.. TLS data can be combined with traditional airborne LiDAR and photogrammetry to increase accuracy of canopy models (Lau et al., 2018) and provide further insight into canopy architecture (Lovell et al., 2014) and its influence on forests such as greenness metrics (LaRue et al., 2018), canopy cover (Lovell et al., 2014) and forest timber volume (Henning and Radtke, 2006).

Early systems relied on "time of flight" calculations to measure the distance between the scanner and a reflective target (Newnham et al., 2015) whereas the more modern RIEGL VZ400 and 400i (RIEGL, Austria) used in chapter 3 are waveform, time of flight recording instruments (Pirotti et al., 2013). These waveform recording instruments, also known as multiple return time-of-flight instruments, allow for the recording of range (equation 1), reflection and roughness of point targets (Jutzi and Stilla, 2005) rather than solely the range.

$$R_i = V_g/2 \times (t_i - t_{ref}) \qquad \textit{Equation 1.}$$

The return equation from the VZ-400, used to calculate range (R) to targets. The flight time of the return echo (t_i) is used to calculate the range of individual targets, where V_g is the speed of light (about 3×108 m/s) and t_{ref} is the timestamp of laser pulse emission. V_g is defined as c_0/n_g, where c_0 is the speed of light in vacuum and the factor n_g addresses the group velocity index of refraction (Calders et al., 2017).

These multiple time of flight instruments provide the "gold standard" of TLS returns, as the discrete pulse laser systems produce a low signal to noise ratio (SNR) (Newnham et al., 2012, 2015; Calders et al., 2020). While time of flight instruments tend to be bulky and expensive, the higher powered instruments such as the Riegl VZ400i used in this thesis, are capable of reaching out to ranges of ~800m in ideal conditions (Bienert et al., 2018; Calders et al., 2020). Within forests, particularly those with dense understories, these ranges are reduced somewhat, down to a theoretical maximum of ~150m when accounting for the reflectance of vegetation (Calders et al., 2020). Other sensors such as the phase-shift type, which uses a continuous laser beam, have been evaluated for use in forests (Newnham et al., 2012). While these sensor configurations offer high-resolution data and generally lower carrying weights, due to the continuous beam emitters generally have a lower signal to noise ratio to time of flight machines (Newnham et al., 2012, 2015). It has been suggested however that due to the light weight of these sensors, that these machines would be advantageous in remote or difficult terrain with the caveat that data generated would require significant filtering to reduce noise (Newnham et al., 2012; Stovall et al., 2018).

Terrestrial laser scanning presents some unique opportunities for monitoring forest canopies, and by extension lianas. Several studies have used TLS with some success in non-destructively extracting the liana biomass of experimental forests in Nouragues, French Guiana and Gigante Peninsula, Panama (Krishna Moorthy et al., 2018, 2019, 2020). In a study of an Australian rainforest researchers were able to identify liana stems within their TLS point clouds, although the study did not focus on lianas but required that liana stems were removed from the point cloud to avoid influencing tree measurements (Terryn et al., 2022b). Prior studies using TLS to identify lianas also derived structural parameters such as branching angle, branching order and stem slenderness to examine how lianas proliferate throughout forest canopies and furthering the links between plant structure and function (Krishna Moorthy et al., 2020). While these measure would be valuable to examine the lianas of EucFACE within this thesis, these prior studies were examining lianas, which presented much larger stems than those studied here, by fitting traditional cylinder based models to the liana (Krishna Moorthy et al., 2018, 2020). Cylinder fitted models may not be appropriate in situations where liana stems are particularly small, for example in the case of canopy lianas, Moorthy et al. (2020) found that where stems of lianas were >2cm diameter they became less distinct from host tree branches. This leads to two problems for using TLS where a) the identification of lianas using a computer vision aided extraction tool was in incomplete (Krishna Moorthy et al., 2019) and b) that lianas with narrow stems can still deploy a large leaf biomass within or over the host trees canopy which would go unreported if TLS based models cannot trace the stem. This later issue is similar to issues found with particularly dense interwoven tree canopies or the tops of conifer stems where point clouds are simply too dense to be distinctly shaped as either stem or foliage (Saarinen et al., 2017, 2019; Krishna Moorthy et al., 2019; Calders et al., 2020). As TLS data has already been collected at EucFACE for the years 2012, 2015, 2018, 2020, and 2022, and were already fixed in resolution and coverage these data were utilised as a retroactive structural survey of lianas rather than attempting to fit cylinder models to these rather narrow lianas.

2.5.3 In-situ imaging

Photographic sensors have been used in remote sensing since the inception of the field (Moore, 1979). Some of the earliest examples being the use of cameras on hot air balloons in the mid-19th century (Colomina and Molina, 2014). Thus photographic based remote sensing is a relatively well understood and widely adopted mode of observing phenomena affecting the natural world (Klosterman et al., 2014).

In-situ photographic sensors allows for collection of very high spatial and temporal data, which in turn allows for continual, and potentially automated, monitoring of phenology and plant health (Migliavacca et al., 2011; Morris et al., 2013). In-situ sensors allow for collection of data at temporal intervals not matched by satellite or air-borne sensors, and can offer a less resource intensive method of data collection than continual field campaigns (Richardson et al., 2009). As such there has been a large effort made to increase the deployment of in-situ photographic sensors although most of this effort has been in the global north (Richardson, 2019).

One of the largest continuous deployments of in-situ cameras is the PhenoCam network, a primarily North American network of camera sites across multiple biomes (Brown et al., 2016; Richardson et al., 2018a). The PhenoCam network is a large scale example of how in-situ photography can be used at a large scale (reviewed in Richardson, 2019). Primarily used to track changes in phenological cycles, such as the increasingly early arctic green up (Andresen et al., 2018), it has also been used to detect successional changes in spruce dominated forests post disturbance (Matiu et al., 2017), test the influence of warming climate on peatlands (Richardson et al., 2018b), and the influence of elevated atmospheric CO_2 on mountain grasslands (Joseph et al., 2022). Automation of photographic analysis has allowed for decadal time series analysis of plant phenology and canopy health (Klosterman et al., 2014; Matiu et al., 2017; Richardson, 2019).

While phenology of plants is the most readily apparent metric derived from in-situ photography, studies have adopted the technologies to calculate canopy cover or leaf area index (LAI) of the vegetated target (Chianucci and Cutini, 2012; Duursma et al., 2016; Alivernini et al., 2018; Chianucci, 2020), as well as for individual plant health assessment (Nijland et al., 2014; Reid et al., 2016). This has been primarily through the use of vegetation indexes which are closely related to, and often linked to similar satellite derived vegetation indices (Reid et al., 2016; Richardson, 2019; Luo et al., 2022).

The equipment requirements for repeatable, consistent RGB photographic data is limited in resource requirements, due to the affordability, functionality, and wide availability of suitable digital camera platforms (Sonnentag et al., 2012). These data are typically stored as JPEG files which, while a compressed format, are more easily stored and read than files such as the RAW file type (Richardson et al., 2018a; Richardson, 2019). There has been concern over the calibration of these data however, as commercially available cameras are rarely calibrated for the degree of spectral accuracy as would be found in a purpose built multi- or hyperspectral imaging unit (Karcher and Richardson, 2003; Sonnentag et al., 2012). There are also concerns as the illumination sensitivity of commercial grade cameras, some of which do not respond linearly to changes of brightness within images (Richardson et al., 2018a). These concerns can however be overcome by the use of indices such as the GCC or its counterpart the red chromatic coordinate (RCC) which are both illumination insensitive but are also drawn from the individual red/green/blue channels of an RGB image rather than the additive display (Sonnentag et al., 2012; Richardson et al., 2018a). As these indices can be used locate lianas (Waite et al., 2019; Chandler et al., 2021b) and to quantitatively assess the influence of climatic and biotic influences (Nijland et al., 2014; Reid et al., 2016, Joseph et al., 2022), it is possible to adapt the methodologies developed as part of the PhenoCam network to test how both the tree and liana canopies respond to elevated atmospheric CO_2 in multiple climatic conditions (Joseph et al., 2022).

2.5.4 Field spectroscopy

Spectral reflectance of plant leaves is intrinsically linked to leaf-scale chemical and structural composition; studies have shown strong linkages between reflectance in the visible spectrum and photosynthetic tissues (Curran, 1989; Pacheco-Labrador et al., 2014; Wujeska-Klause et al., 2019a; Morley et al., 2020) as well as linkages between red-edge and near infra-red (NIR) reflectance and leaf chemical processes (Curran et al., 1991; Stone et al., 2001). Hyperspectral sensors typically operate with a spectral resolution of 3-10nm across the range 340-2500nm, although some instruments sacrifice spectral range for resolution e.g. the Ocean optics QE (Ocean Insight, Florida) has a spectral range of 645-810nm with a resolution of 0.2nm. Such instruments have been frequently used in the capture of foliar chemistry, with handheld hyperspectral sensors affording non-destructive data capture. As well as providing an inventory of foliar chemicals within a leaf sample (Curran 1989), the use of hyperspectral remote sensing has been demonstrated to detect plant stressors. Typically, stressed vegetation show increased reflectance in the red wavelengths, with changes in both the position and strength of reflectance at the red-edge, where the visible red and near infra-red (NIR) wavelengths meet (~780nm) (Dawson and Curran; Curran et al., 1991; Ustin et al., 2009).

Studies utilising hyperspectral remote sensing rarely report on the singular wavelengths that are associated with a given chemical or biological compound. This is due to multiple scattering across similar wavelengths, i.e. reflectance or the inverse absorbance associated with a particular chemical property are spread across multiple similar wavelengths (Curran, 1989). As such, using spectra to determine foliar chemical content and thus processes that determine their concentration usually requires further processing (Dawson and Curran; Curran, 1989). As such, there have been numerous indices and derivative processes shown in literature to have linkages to either leaf chemical content and/or concentrations (Gitelson et al., 2002; Kimura et al., 2004).

In a study by Yoder and Pettigrew-Crosby (1995) into nitrogen and chlorophyll content at canopy and leaf scales, a derivative approach was used to identify differences in leaf spectra. This study used first-difference spectra (approximating first derivatives). This was calculated from the difference between the values at each wavelength, divided by the range of wavelengths for raw reflectance, log reflectance and inverse log reflectance (Yoder and Pettigrew-Crosby, 1995). Using correlative analysis it was found that raw reflectance correlation was strongest with chlorophyll in visible wavelengths (around 720 and 750nm) a result similarly found for log reflectance and first-difference transformations (Yoder and Pettigrew-Crosby, 1995). The authors stated however that when using these spectral transformations to create a predictive model of chlorophyll that the first-difference transformation had “much better predictions” than either raw or log reflectance on model predictive behaviour (Yoder and Pettigrew-Crosby, 1995).

Band depth analysis is another technique that has been developed for predictive modelling and analysis of leaf chemical composition (Kokaly and Clark, 1999). Using the relative depth of absorbance features, this technique allows for comparative analysis of spectral features associated with chemical composition (Kokaly and Clark, 1999). A study into the effects of radiation on pines in Belarus used the band depth normalised by area (BDNA) methodology found there were significant differences in wavelengths associated with photosynthetic compounds, lignin, cellulose and water caused by bio-accumulation to radiocaesium (^{137}Cs) concluding that radioactivity impacted the structure of needles on older trees (Boyd et al., 2006).

Vegetation indices for use in spectral studies have been classed into three categories; 1) intrinsic indices, calculated from reflectance with no external corrective factors e.g. red-

NIR index, normalized differential vegetation index (NDVI). 2) soil-line indices, those that remove the effect of a soil background e.g. soil adjusted vegetation index (SAVI). 3) atmospheric corrected indices, those that correct for atmospheric absorption and scattering (Rondeaux et al., 1996; Daughtry et al., 2000; Gitelson et al., 2002; Kimura et al., 2004; Raymond Hunt et al., 2011). Of these indices only intrinsic indices will be used as part of this thesis, as I use a contact probe to collect spectral measurements, this removes the influence of background and atmosphere.

This thesis uses the ASD Fieldspec pro spectrometer (Malvern Panalytical, UK) to gather spectral data. These spectrometers record in a resolution of 3-10nm across the range 350-2500nm, with sensor cross over features at 1400 and 2100nm. ASD spectrometers use proprietary software to interpolate spectra with a resulting 1nm resolution for users. I deployed a contact probe with a leaf clip with integrated light source for spectra sampling as this allows direct measurement of spectra without the influence of atmospheric scattering, background reflectance or changing illumination. The leaf clip contains a small Spectralon disk (Spectralon, USA) for calibration between measurements.

Hyperspectral remotely sensed data captured in this way should therefore allow observation how leaf chemistry responds to elevated atmospheric CO_2. In a study in the neo-tropics Oki et al. (2013) found that the hyperspectral reflectance of 3 lianas and 4 co-occurring trees changed when the leaves were exposed to elevated CO_2 conditions for 90 days. This study demonstrated that most of the species studied showed decreases in indices such as NDVI which are normally concurrent with biological or abiotic stressors (Oki et al., 2013).

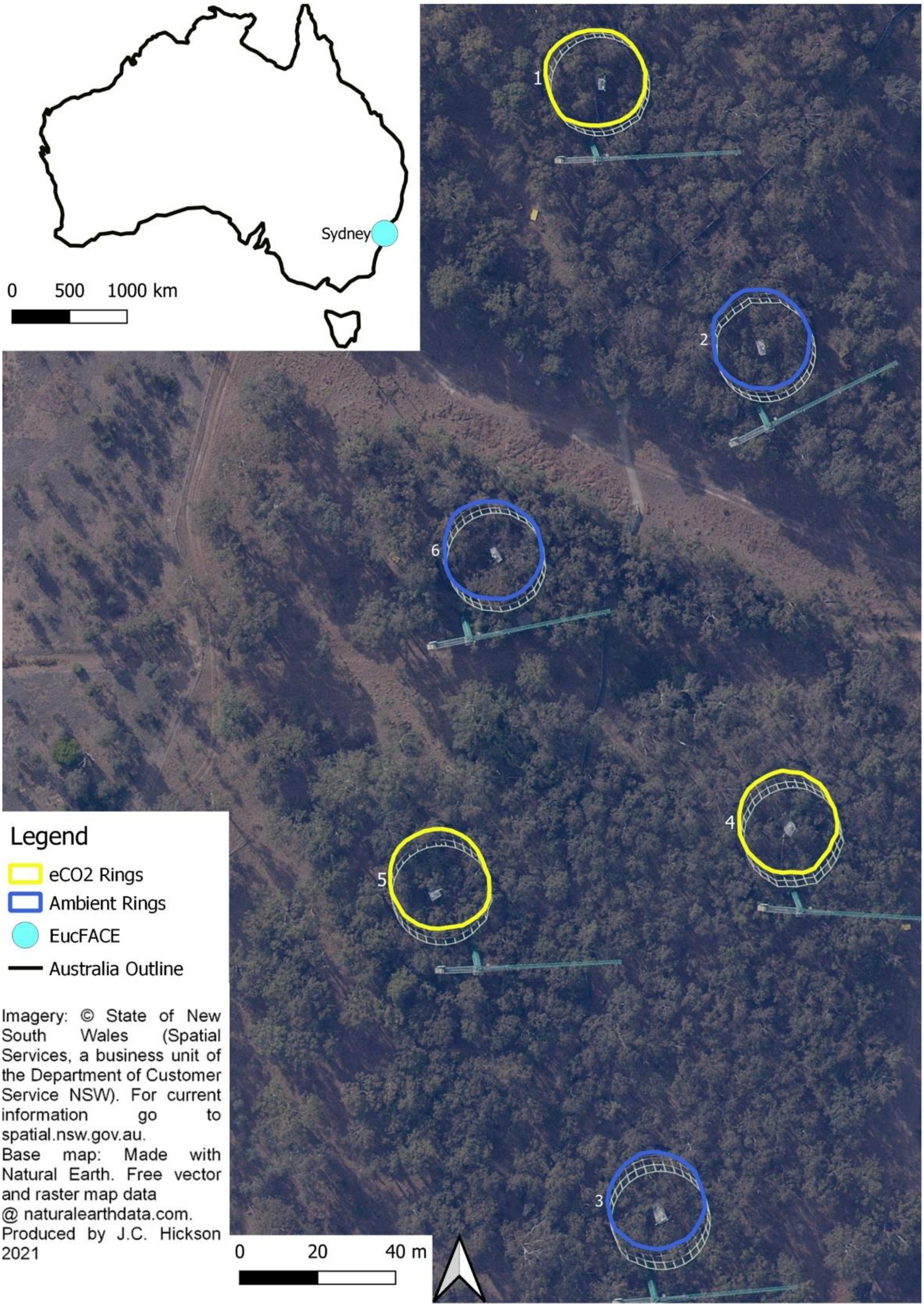
Chapter 3. Study site, species, and structure

3.1. EucFACE

The study site is the Eucalypt Free Air CO_2 Enrichment (EucFACE) experiment, which was established in December 2012 and consists of 6 experimental gas injection plots within a mature *Eucalyptus* dominated woodland located within a 167ha remnant of the Cumberland Plain woodland (Figure 3.1) (Ellsworth et al., 2017b). Cumberland plain woodland, which once stretched across much of the Sydney basin, is a critically endangered savannah like woodland (Threatened Species Scientific Committee, 2009), which is now limited to the western suburbs of Sydney, estimated to have covered ~ 125449ha (Tozer, 2003), currently around 6% remains (Tozer et al., 2010). Typically, woodlands in the Cumberland plain are dominated by *Eucalyptus tereticornis* or *Eucalyptus moluccana* trees with scattered shrubs and C3 and C4 grasses. The EucFACE experiment is surrounded by savannah-like grasslands with sparse *Eucalyptus* trees indicating the fragmentation of the remnant forests. The EucFACE site is bisected by a fire clearway around a series of high-voltage pylons, separating rings 1 and 2 from the other rings by ~20m of open grassland. When the site is subjected to high volumes of rainfall, an ephemeral stream is known to form between rings 5 and 6 which flows westwards towards the Hawkesbury River.

The climate at EucFACE is categorised as temperate-subtropical. It is therefore a predominantly dry site receiving up to 800mm of precipitation per year with mean annual temperature of 17.5 °C (Ellsworth et al., 2017b), moisture availability follows a semi-seasonal pattern with soil water content regularly falling as low as $0.03m^3m^{-3}$ during summer (Duursma et al., 2016; Ellsworth et al., 2017a). The site is known to be nutrient poor, primarily phosphorus (P) limited (Crous et al., 2015) with a loamy sand (>75% sand) soil at the surface which transitions to a sandy clay loam (>30% silt and clay) soil ca. 50-300cm depth (Duursma et al., 2016). Ground-water depth is between 12.6-12.9m below surface (Crous et al., 2015; Duursma et al., 2016; Gimeno et al., 2016).

The Eucalypt Free Air CO_2 Enrichment (EucFACE) experiment uses six 25-m-diameter circular plots to release concentrations of carbon dioxide (CO_2) into the enclosed Cumberland Plain woodland. These circular plots (referred to as 'rings') are constructed with a cylindrical frame of 32 vent pipes and extend 28 m high (Figure 2.3). The experiment began in September 2012, with three of the six rings (numbered 1, 4, and 5) providing a gradual CO_2 enrichment at a rate of 30 $\mu mol\ mol^{-1}\ month^{-1}$ above ambient CO_2 concentrations to the enclosed woodland. Enrichment was gradually increased until early 2013 where the max enrichment of elevated atmospheric CO_2 (eCO_2) was reached (550 $\mu mol\ mol^{-1}$) (Duursma et al., 2016; Ellsworth et al., 2017b). The remaining three rings (numbered 2, 3, and 6) are control plots and have received ambient atmospheric CO_2 (~400 $\mu mol\ mol^{-1}$) since the commencement of the experiment (Duursma et al., 2016; Ellsworth et al., 2017b).



Imagery: © State of New South Wales (Spatial Services, a business unit of the Department of Customer Service NSW). For current information go to spatial.nsw.gov.au.
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Figure 3. 1 Aerial view of EucFACE showing the experimental rings highlighted in blue (ambient CO_2*) and yellow (elevated* CO_2*).*

Figure 3. 2 EucFACE experimental ring. One of the 6 ring structures delivering CO_2 through 28m tall vertical vent pipes. Ring structure is 25m diameter with a permanent observation tower in the centre of the ring.

The site is predominantly covered by *Eucalyptus tereticornis* and it one of the only FACE sites that includes climbing and canopy dwelling lianas (*Parsonsia straminea)*. Lianas are abundantly present at EucFACE, the presence of lianas amongst the rings however is not uniform and one of the rings has been liana-free (ring 1, eCO_2) since the onset of the experiment. However, although the abundance of lianas has been increased since the inception of the EucFACE experiment (B. Medlyn pers. comms.), none of the high-impact research emerging from EucFACE has focussed on lianas. The EucFACE experiment therefore presents a unique opportunity to establish the first mechanistic understanding of the response of adult lianas to elevated atmospheric CO_2. EucFACE is a world class research facility and with a suite of data being collected as standard (Table 3.1). For example, photographic data of the woodland canopy is taken at three-times daily intervals using in-situ security cameras (Morris et al., 2013)(Morris et al., 2013)(Morris et al., 2013)(Morris et al., 2013)(Morris et al., 2013) located in the superstructure of the experimental rings. Several Terrestrial Laser Scanning surveys have also been conducted five times between 2012 and 2022.

Table 3. 1 Data Availability at EucFACE for use in this thesis. Other data is generated and available from relevant authors.

Data type	**Data source**	**Usability**
Terrestrial Laser Scanning	Scheduled scanning by K. Calders. (2012, 2015, 2018, 2020, 2022)	Used in thesis
Photographic imaging	Daily photography in all rings. (2014-2022)	Used in thesis
Rainfall data	Daily readings from rainfall gauges. (2012-onwards)	Not used due to sensor issues
Soil moisture data	Daily readings from automated probes. (2012-onwards)	Used in thesis
Leaf litter data	Periodic leaf litter data from in-situ leaf traps.	Not used
Weather data (rainfall, UV exposure, wind speed)	Daily data from Flux tower and from Australian Meteorological data.	Meteorological data used
Tree diameter/spatial measurements	Periodic diameter measurements and spatial data from establishment of experiment.	Spatial data used to verify location of trees in TLS data

3.2. Parsonsia straminea

The liana present at the EucFACE is *Parsonsia straminea* (R.Br.) F.Muell. (Apocynaceae). Native to the eastern seaboard of Australia, *P. straminea* is a root climbing liana with some stem twinning, capable of reaching the canopy of host trees (Figure 3.3). The leaves of *P. straminea* are dimorphic, with adult leaves elliptic to oblong-ovate, 4–24 cm long, 1.5–8 cm wide, with glaucous undersides and a yellow-green top surface. Juvenile leaves are 1-5cm long, thin with purple lower surface with similar yellow-green top (National Herbarium of NSW, 2012). *P. straminea*'s native range extends from Northern Queensland to Southern New South Wales with rare occurrences in Tasmania (Atlas of Living Australia). *P. straminea* is predominantly found in rainforests and along forest margins where fires are rare (Zich et al., 2020). There is observational evidence that *P. straminea* may be tolerant to flooding as this species has been found in woodlands occasionally inundated by salt- and freshwater (Grieger et al., 2019).

Figure 3. 3 Parsonsia straminea on a Eucalyptus tereticornis at EucFACE at different infestation stages. Panel a) Vines climbing a young Eucalyptus tree, largest stem at left of image has partially detached from tree trunk. Foliage is attached to stems <1 cm diameter reaching ~6m on host trunk. Panel b) Liana overtopping dead Eucalyptus tree within ring 5. Multiple stems create a dense tangle reaching the top of the broken trunk.

3.3 Eucalyptus tereticornis

The EucFACE forest is primarily a monoculture of *Eucalyptus tereticornis* Sm. (Myrtaceae). *E. tereticornis* is native to the eastern seaboard of Australia, following a roughly similar distribution to *P. straminea* (Atlas of Living Australia). Capable of reaching 50m with smooth, white or greyish bark, which sheds in large flakes (Fig.3.4a) (National Herbarium of NSW, 2012). Adult leaves are narrow-lanceolate or lanceolate, 10–20 cm long, 1–3 cm wide, dull green, juvenile leaves are broader to ovate, and dull blue green (National Herbarium of NSW, 2012). Widespread in wet and dry forests, *E. tereticornis* tolerates a range of soil fertility but thrives in higher fertility areas (National Herbarium of NSW, 2012).

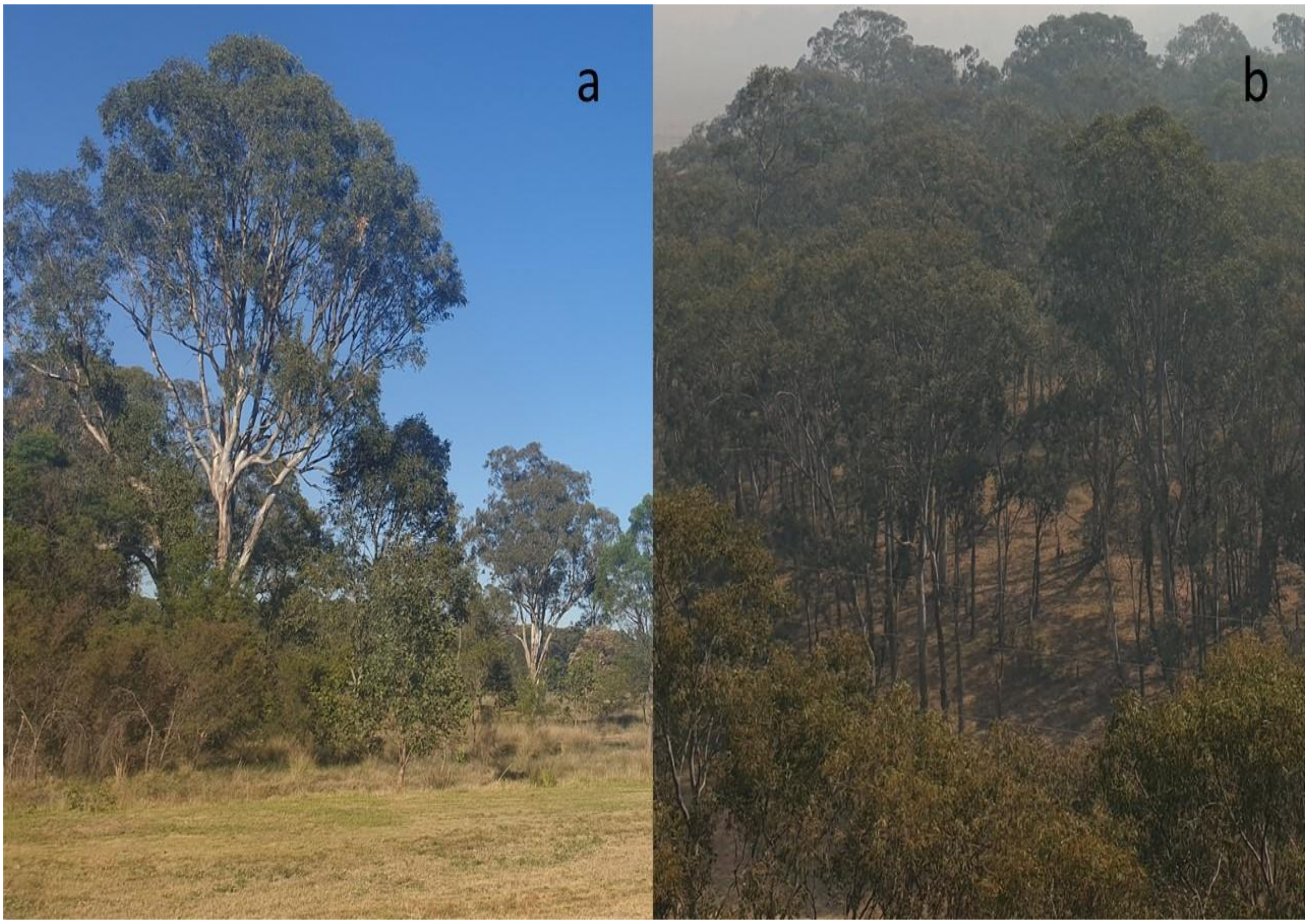

Figure 3. 4 Eucalyptus tereticornis at EucFACE Panel a) Mature individuals ~40m tall at edge of EucFACE site. Panel b) View of Eucalyptus tereticornis canopy from above. Image taken from canopy access crane. Both images taken during drought conditions in November 2019.

3.4 Thesis structure

This thesis is presented as a hybrid thesis, where chapters 4, 5, and 6 are presented in a paper format. Chapter 4 was originally formulated as an article for a Frontiers in Forestry special issue and follows the formatting guidelines of Frontiers journals. Chapters 5 and 6 similarly follow the formatting of chapter 4 but so far have not been submitted for journal editing. Each chapter is presented to fulfil the overarching aims of this thesis, which is to elucidate whether the liana *Parsonsia straminea* responds to elevated atmospheric CO_2 and whether the response(s) contrast those of *Eucalyptus tereticornis*.

Chapter 4. Elevated atmospheric carbon dioxide does not affect liana infestation in a mature eucalypt woodland using a novel structural measurement from low resolution terrestrial laser scanning.

4.1 Abstract

Lianas are increasing in many of the world's forests. Currently the drivers of liana proliferation are still unclear, but elevated atmospheric carbon dioxide (CO_2) has been proposed as a potential driver for this increase. I present findings from the Eucalyptus Free Air Carbon Experiment (EucFACE) in Australia where lianas are present. Using temporally explicit Terrestrial Laser Scanning (TLS) as a rapid measurement tool, I investigated whether liana infestation has increased in response to elevated atmospheric CO_2 over a 10-year period (2012-2022). I studied whether the proportion of trees supporting lianas and the vertical change in height of liana presence on the tree stem has increased over time in response to CO_2 treatment. My results show that the proportion of trees hosting lianas had increased to a similar extent in both the control and elevated CO_2 treatments. Furthermore, I found that the changes in the height on the tree stem that lianas attain was similarly in both treatments. The increase in lianas may therefore be driven by site wide disturbance and periods of water limitation rather than elevated levels of atmospheric CO_2. Liana proliferation and LAH increase was constrained during the period of drought between 2018 and 2020, in both treatments, suggesting that the response of lianas to long term drought is not mediated by elevated atmospheric CO_2.

4.2 Introduction

Elevated atmospheric CO_2 (eCO_2) has been shown to promote growth in plants (Gamage et al., 2018; Norby et al., 1999), increase photosynthetic rates (Körner et al., 2007), and increase water use efficiency (Keenan et al., 2013). This has prompted the "CO_2 fertilization" hypothesis (Ciais et al., 2009), which argues that elevated concentrations of atmospheric CO_2 increases photosynthesis and thus the growth of plants, and may help explain how forests can help mitigate the effects of climate change (Walker et al., 2019). Considerable effort has thus focused on understanding how forest ecosystems are responding to elevated CO_2 conditions (Norby et al., 1999, 2016). One important component of forests are lianas (woody vines), which are an abundant lifeform in many forests worldwide (Perring et al., 2020; Putz, 1983; Schnitzer and Bongers, 2002). Lianas have been increasing in biomass and abundance relative to trees across some Neotropical and temperate forests (Perring et al., 2020; Phillips et al., 2002; Schnitzer and Bongers, 2011), although currently there is limited evidence of liana proliferation in the Paleotropics (Bongers et al., 2020; Wright et al., 2015; Caballé and Martin, 2001; Thomas et al., 2015). Amongst other putative mechanisms, the increases in atmospheric CO_2 have been offered as a potential explanation for the observed liana increase (Schnitzer and Bongers, 2011).

Elevated CO_2 concentrations have been found to have a fertilising effect on the growth of juvenile liana stems and leaf biomass of both temperate and tropical liana species (Belote et al., 2004; Condon et al., 1992; Granados and Körner, 2002; Hättenschwiler and Körner, 2003; Körner and Arnone, 1992; Marvin et al., 2015; Mohan et al., 2006; Zotz et al., 2006). For example, Hättenschwiler and Körner (2003) found that liana stems grown in elevated CO_2 conditions were up to 137% longer and increased two-fold in biomass compared to those grown in ambient conditions. Mohan et al. (2006) reported a similar result in field conditions and found that average annual growth of lianas in elevated atmospheric CO_2 was 149% greater than in ambient conditions. Additionally, growth chamber studies have indicated that there may be an interaction effect between CO_2 fertilisation and light (Granados and Körner, 2002; Zotz et al., 2006). These studies showed that growth of tropical liana saplings was greatest in low-light conditions, similar to those found the forest understory (Granados and Körner, 2002; Marvin et al., 2015), with liana stems in elevated atmospheric CO_2 and low light conditions growing up to 60% longer compared to those grown in ambient conditions (Granados and Körner, 2002). Similarly, temperate lianas seedlings exposed to elevated atmospheric CO_2 were also capable of faster growth rates than co-occurring trees and were more likely to reach the forest canopy (Zotz et al., 2006).

Though the above indicates that liana saplings and seedlings seem to positively respond to CO_2 enrichment, it is still unclear whether lianas respond more strongly to elevated conditions compared to trees and whether this may therefore be the dominant driver of liana proliferation in parts of the world. For example, in a growth chamber study, Marvin et al. (2015) compared the growth of seedlings of 12 tropical liana species to that of 10 tropical tree species. This study found that, although growth of lianas increased under elevated CO_2 conditions, there was no difference in the average response between liana and tree seedlings.

Although many studies have looked at the effect of elevated CO_2 conditions on liana seedlings and saplings (Granados and Körner, 2002; Marvin et al., 2015; Zotz et al., 2006), little research has focussed on the effects on climbing and crown dwelling lianas. Lianas move from being largely self-supporting, to relying on structural support from trees during their ontogeny (Gerwing, 2004; Letcher and Chazdon, 2012; Rowe et al., 2004; Rowe and Speck, 2005; Smith-Martin et al., 2020). As lianas mature, they diverge from trees in their functional traits (Gallagher et al., 2011; Gallagher and Leishman, 2012), developing greater hydraulic efficiency (van der Sande et al., 2019; Medina-Vega et al., 2021a), higher leaf mass area (Gallagher et al., 2011; Medina-Vega et al., 2021a) and less nutrient intensive leaf deployment (Gallagher and Leishman, 2012; Medina-Vega et al., 2021), and have been shown to becoming better in acquiring resources than trees in seasonal forests (Buckton et al., 2019; Medina-Vega et al., 2021a). As such, older lianas tend to invest less into structural tissue and more into stem elongation and rapid leaf development than trees (Cai et al., 2007; Paul and Yavitt, 2011; Schnitzer and Bongers, 2002). Consequently, due to ontogenetic changes in both biomass allocation and functional traits, liana responses to elevated atmospheric CO_2 may therefore also differ between self-supporting juveniles and those that are structurally supported (i.e. those that have started to climb or are already crown-dwelling). Assessing the effect of liana that are structurally supported to elevated CO_2 conditions is therefore important to establish whether rising atmospheric CO_2 concentration could contribute to the recent observed liana proliferation (cf. Schnitzer and Bongers, 2011), at least in some parts of the world.

Studying the effects of elevated atmospheric CO_2 on climbing lianas is complicated as growth chamber experiments are not feasible since they would require at least a proxy of a forest canopy. Free Air CO_2 Enrichment (FACE) experiments, which elevate local CO_2 concentrations by injecting CO_2 into open cylinders within a forest, are used to assess the responses of ecosystems to elevated CO_2 conditions (Norby et al., 1999, 2016). Most of these experiments do not contain lianas (Norby et al., 2016), however, in the Eucalypt Free Air CO_2 Enrichment (EucFACE) experiment in Australia (Duursma et al., 2016; Gimeno et al., 2016) established climbing and crown-dwelling lianas are present. This provides a unique opportunity to assess the effect of elevated CO_2 conditions on liana growth and infestation dynamics in an established ecosystem over time.

While lianas are capable of surviving within the forest understory, lianas are predominantly light demanding (Gerwing, 2004; Rowe et al., 2004). As lianas rely upon the support of forest trees to reach more favourable conditions changes in the number of trees hosting lianas would therefore indicate how forest liana infestations develop over time (Phillips et al., 2005; Wright et al., 2015). Evidence presented by Ingwell et al. (2010) showed that the proportion of trees carrying lianas increased by 65% over a forty-year census period. Similarly, Wright et al. (2010) used the same measure to show a decline in liana presence in the canopy. An increase the proportion of trees hosting lianas can be indicative of a combination of increased liana recruitment and liana growth (Rowe et al., 2004; Cai et al., 2007). Rapid increase of the proportion of trees supporting lianas, in elevated atmospheric CO_2, would indicate that lianas can become a more dominant feature of forests in a CO_2 rich world. Secondly, quantifying how the presence of lianas on the tree trunks has progressed over time, i.e. by measuring the hieght of the liana infestation on the trunk, can be used to infer whether the severity of infestations are increasing in response to CO_2 treatment. Evidence from studies of temperate lianas have shown that sub-canopy liana stems attained greater heights, i.e. lengthened, upon their host trees, though this trend was not significant between CO_2 treatments (Zotz et al., 2006).

Monitoring lianas manually is time and labour intensive (van der Heijden et al., 2010). Ground based liana monitoring, while capable of accurately recording liana stem measurements, is limited by visibility when censusing lianas within dense forest canopies (Waite et al., 2019). Consequently there has been a drive towards the use of remotely sensed data for liana monitoring (Castro-Esau et al., 2004; Asner and Martin, 2008; Waite et al., 2019; van der Heijden et al., 2022). While satellite or aircraft-borne sensor systems can provide remotely sensed data on forest canopies and the lianas that reside there (Waite et al., 2019; Chandler et al., 2021a), ground based systems can provide data that is more suited to the study of lianas that reside within or below the canopy (Krishna Moorthy et al., 2018). Terrestrial laser scanning (TLS) generates a three dimensional digital recreation of forest structure (Disney, 2019) allowing for characterisation of vegetation profiles (Ashcroft et al., 2014), estimation of volume and mass of vegetation (Disney et al., 2018; Momo Takoudjou et al., 2018; Terryn et al., 2022a), and quantifying forest structure and architecture (Burt et al., 2013; Donager et al., 2018; Lau et al., 2018). TLS has thus been used to detect liana impacts on forest structure in tropical forests (Krishna Moorthy et al., 2018; Jiménez-Méndez et al., 2024). While it is well known that lianas are capable of rapidly colonising forests (Barry et al., 2015; Schnitzer et al., 2021) it is still poorly understood whether this speed of this response is driven by rising atmospheric CO_2. Similarly little work has gone into the structural development of liana infestation in field studies, primarily due to difficulties in accessing lianas as they ascend host trees, while 3D scanning can allow for navigation within and below the canopy in ways not possible in the field. Therefore, multi-temporal TLS datasets could facilitate tracking of how liana infestations develop in high CO_2 environments in lieu of high intensity field campaigns, using the 3D digital structure to census and quantify whether lianas respond to elevated CO_2 concentrations.

We therefore used information from repeated Terrestrial Laser Scanning surveys at five time points from 2012 to 2022, as a rapid survey technique to address two major aims. These are to assess whether changes in i) the proportion of trees supporting lianas and ii) the progression of trunk infestation of lianas over time was driven by elevated CO_2 conditions across the EucFACE experiment.

4.2. Methods

4.2.1 Study area

For full study site description see chapter 3

4.2.2 Liana data collection using Terrestrial Laser Scanning

Although regular tree measurements were taken as part of the data collection protocol at EucFACE, regular field measurements of lianas spanning the entire period of the experiment were not available. However, each of the six EucFACE rings were surveyed using Terrestrial Laser scanning (TLS) at five-time stamps - October 2012, May 2015, August 2018, March 2020, and February 2022 spanning the duration of the experiment. TLS is a ground based adaptation and extension of conventional LiDAR (Light Detection And Ranging) techniques (Watt and Donoghue, 2005; Telling et al., 2017) and has advanced structural measurement in vegetation (Calders et al., 2020). These data allow for three dimensional representations of forest structure (Newnham et al., 2015), which enables monitoring and sampling of traditional forestry metrics such as tree stem diameter and stem height, as well as modelling of canopy structure and biomass measurements (Burt et al., 2013; Calders et al., 2020; Gonzalez de Tanago et al., 2018; Krishna Moorthy et al., 2020; Momo Takoudjou et al., 2018; Newnham et al., 2015). Previous work using TLS has shown that lianas are both identifiable and measurable in the data captured from tropical forests (Krishna Moorthy et al., 2018; Krishna Moorthy et al., 2020), and I therefore use the TLS data to assess the proportion of tree supporting lianas and the liana attained height.

A RIEGL VZ400 terrestrial laser scanner was used to survey vegetation, which is a multiple return time-of-flight based scanner using a narrow infrared laser beam of wavelength 1550 nm and a beam divergence of 0.35 mrad, (Calders et al., 2015; Krishna Moorthy et al., 2018; Krishna Moorthy et al., 2020). Multiple scans of subjects from different scan positions are necessary to allow full 3D representation of vegetative structure and to limit occlusion when generating forests as geometric models (Newnham et al., 2012; Newnham et al., 2015). The rings were scanned from two separate positions at roughly 180° across the ring and keeping scan locations consistent across sampling periods.

Two initial scanning positions were chosen to avoid any ground based experimental infrastructure, e.g. leaf traps, and ground vegetation which at the initiation of the experiment was sparse and of low stature (Crous et al., 2015). Scans were originally commissioned to provide a rapid modelling of the tree biomass at EucFACE rather than a detailed structural survey. Scans from these limited positions therefore generate a sufficiently dense point cloud to allow geometric modelling of the trees using classic cylinder fitting (Calders et al., 2014), but are prone to occlusion of the lower tree trunk. This creates a “dark side” of trunks where lianas or tree trunk geometry, such as buttressing, are obfuscated. This could lower the detection efficacy of low lying or juvenile lianas within these scans which could lower the overall infestation detection accuracy.

The scans were spatially registered within the Riegl software and by manually manipulating the scans (sensu Calders et al., 2014; Lichti et al., 2019) to align them with the large permanent fibre-composite superstructure in each of the EucFACE rings. After co-registration, all ground vegetation, <2m tall, was manually segmented and removed from the point cloud in CloudCompare using the segmentation tools (CloudCompare, 2021) to ensure a clear view of the tree stems.

To remove ground vegetation, the initial point cloud was sliced at 2m height, all points within the resulting cloud that did not present as either tree trunk or adjacent lianas was then manually segmented out of the cloud. The lianas present a distinctive vegetative structure, all foliage within ~50cm of a tree trunk was visually inspected for lianescent structure before segmenting out or inclusion (Fig. 4.1). Similarly, the superstructure was removed from the point cloud by manual segmentation. This created a multipart point cloud made up of basal tree stems and tree canopies, this was then merged in CloudCompare leaving a point cloud of only trees with co-occurring lianas where they were present.

Thereafter, individual trees, including any co-occurring lianas, were extracted from the imagery using the segmentation tools in CloudCompare and matched tree stems to previous stem location maps produced during earlier studies at EucFACE (Data from Ellsworth et al., 2017). Manual segmentation involved identifying vegetative structures and removal of non-conforming structures by hand. Manual segmentation of each tree typically took an average of 3 hours per tree depending on canopy shyness, more complex canopies (where branches cross other trees or around superstructures) could take up to two days to fully extract from the original point cloud.

Where tree canopies intersected or were joined by lianas were segmented at a fixed point throughout the temporal series. Multi-stemmed trees or trees for which canopies were indistinguishable were segmented as one entity. Trees were extracted individually based upon tree maps, originally created to track tree diameter (DBH) (c.f. Ellsworth et al. 2017). Tree stems below 10cm DBH are excluded as these are less likely to be canopy trees. For each living tree ≥10 cm DBH, I used the TLS data to determine whether lianas were present on the tree stem. For each tree, I identified the highest clearly observable liana stem or leaf tissue along the main stem and calculated the distance along the tree stem from the ground to the highest point of liana infestation in meters, as a measure of liana attained height (LAH; Fig. 4.1). I focussed on lianas climbing on tree stems as the efficacy of TLS data for liana detection was affected by canopy occlusion, thus decreasing the likelihood of rendering fine liana structures within tree canopies. Where lianas were unobservable in their entirety due to occlusion by trees or other foliage the entire tree was excluded from analysis.

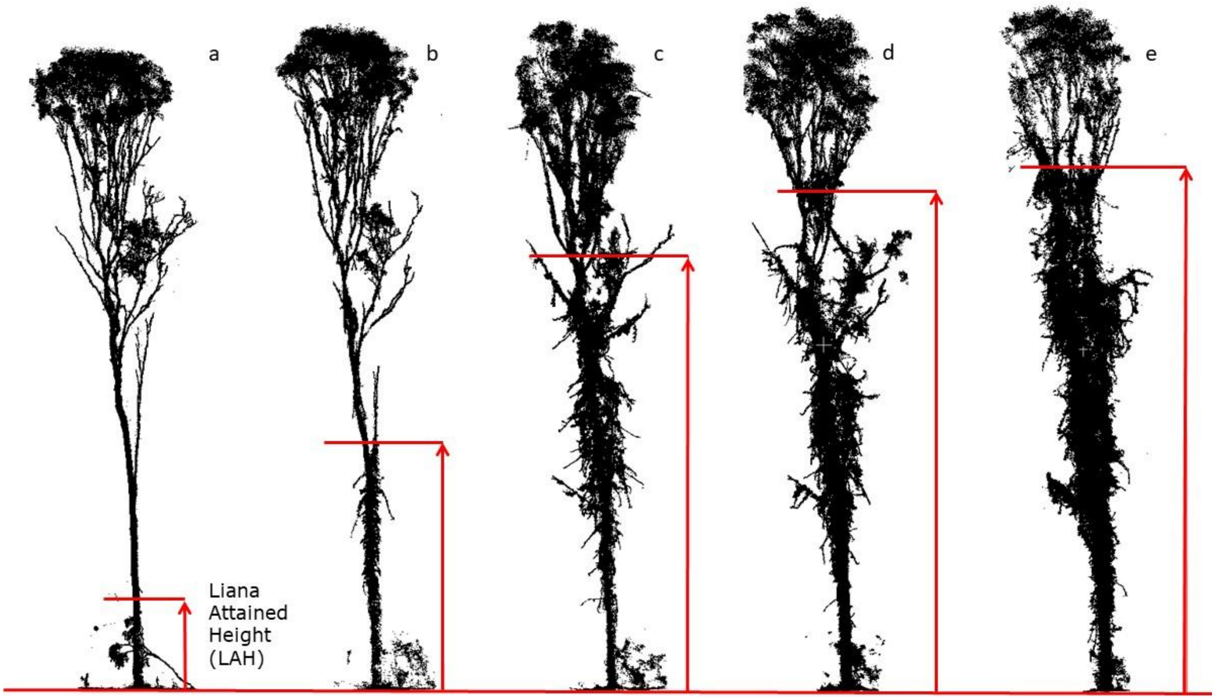

Figure 4. 1 An example of a progression of liana attained height for one single tree (#515) across 5 TLS surveys in a) 2012, b) 2015, c) 2018, d) 2020, and e) 2022. Red arrows show the vertical distance between the forest floor and the highest point on the tree stem where lianas were present as an indication of the progression of liana infestation over time.

4.2.3 Liana field survey

To validate the extracted liana data from the TLS scans (Fig. 4.1), I carried out a field survey of all climbing lianas in November 2019, ~4 months before the TLS survey in 2020. For each of the trees present in the six rings at EucFACE, I recorded whether the tree supported lianas on the stem and/or in the canopy. I used these data to determine whether the proportion of extracted trees matches those manually recorded with lianas.

4.2.4 Data analysis

To assess whether elevated CO_2 (eCO_2) conditions are driving a change in the proportion of trees supporting lianas over time, I used a mixed effects binomial (log) regression, which allows for both random and fixed effects (Gelman and Hill, 2007; Gardener, 2017.). I used treatment (either ambient or eCO_2) and the year of the TLS survey as fixed effects and the EucFACE ring as well as individual trees nested within the rings as separate random effects. These random effects account for the repeated measures of these data as well as allowing me to account for between ring variability in site factors. Models were also fitted with an interaction term between treatment and year. However, this was found to perform less well than those fitted without the interaction term (AIC= 393.9 vs AIC= 390.9 for models with and without the interaction term included).

To determine how the LAH differed between TLS surveys, I calculated change in absolute LAH per treatment. For each tree, I calculated the difference in LAH between surveys. To assess whether the change in LAH between survey periods was driven by elevated CO_2 conditions, I used a Multi factor ANOVA using year of TLS census, Treatment, the first recorded LAH per individual in 2012 as factors and a nested random effect of individual tree within experimental ring to account for repeated measures. I included first recorded LAH of a liana to assess whether initial survey height affected response to CO_2 treatment. To determine whether changes in LAH varies over time, I used post-hoc least square means tests to conduct pairwise analysis where the ANOVA was significant. All analyses were performed in R (R Core Team 2021) using the *nlme4* and *mgcv* (Wood, 2011) packages.

4.3 Results

My results show the proportion of trees supporting lianas was not evenly spread between rings within treatment at the beginning of the experimental treatment in 2012. Ring 1, receiving eCO_2 treatment, did not contain lianas prior to the beginning of the study and has remained liana-free for the duration of the study. The most heavily infested rings, 5 and 6, at the start of the experiment remained the rings with the most intense infestation (Table 4.1). Furthermore, on average, a higher proportion of trees hosted lianas in the ambient rings (36%-73% from 2012 to 2022) compared to trees in the rings fertilized by CO_2 (25 to 49% from 2012 to 2022; Table 4.1). The results from the TLS survey in 2020 showed that 66% and 41% of trees hosted lianas in the ambient and eCO_2 rings respectively, similar to the results from the field census (65% and 38% for ambient and eCO_2 rings respectively), which was conducted 4 months before the TLS census (Supporting information Table 1). From this it was concluded that visual examination of the TLS survey is within 5% of the manual census methods, and is thus a close enough margin of error when compared to the margin of error between human observers in other studies (Waite et al., 2019).

Liana infestation increased significantly over time ($P<0.001$ for all years. Table 4.1). The average percentage of trees supporting lianas increased 1.94 and 2.02-fold from 2012 to 2022 in eCO_2 and ambient conditions, respectively. This increase was mainly driven by the survey period from 2012 to 2015, when trees hosting lianas increased 1.54 and 1.45-fold increases on average in ambient and eCO_2 conditions, respectively. However, treatment effect was not found to be significant ($P=0.12$), indicating that the increase in the proportion of trees hosting lianas was not driven by elevated CO_2 (Fig. 4.2).

Table 4. 1 Percentage of trees supporting lianas where the tree has survived to the 2022 TLS survey. Trees which were occluded in the TLS data or died prior to or during the study are omitted. Trees included in this were both those verified by the field survey and trees which had been infested between the 2019 field survey and the 2020 TLS census.

Ring	% of trees supporting lianas 2012	% of trees supporting lianas 2015	% of trees supporting lianas 2018	% of trees supporting lianas 2020	% of trees supporting lianas 2022
1	0	0	0	0	0
4	15.38	20.51	23.68	29.72	55.55
5	59.37	87.5	95.23	95.23	90
eCO_2 mean	24.91	36	39.64	41.65	48.51
se	0.177	0.264	0.286	0.281	0.262
2	10.7	7.14	12	27.27	36.36
3	15.62	61.29	70	72.41	89.65
6	80.95	94.73	100	100	91.66
ambient mean	35.76	60.66	60.66	66.56	72.56
se	0.226	0.255	0.258	0.211	0.181

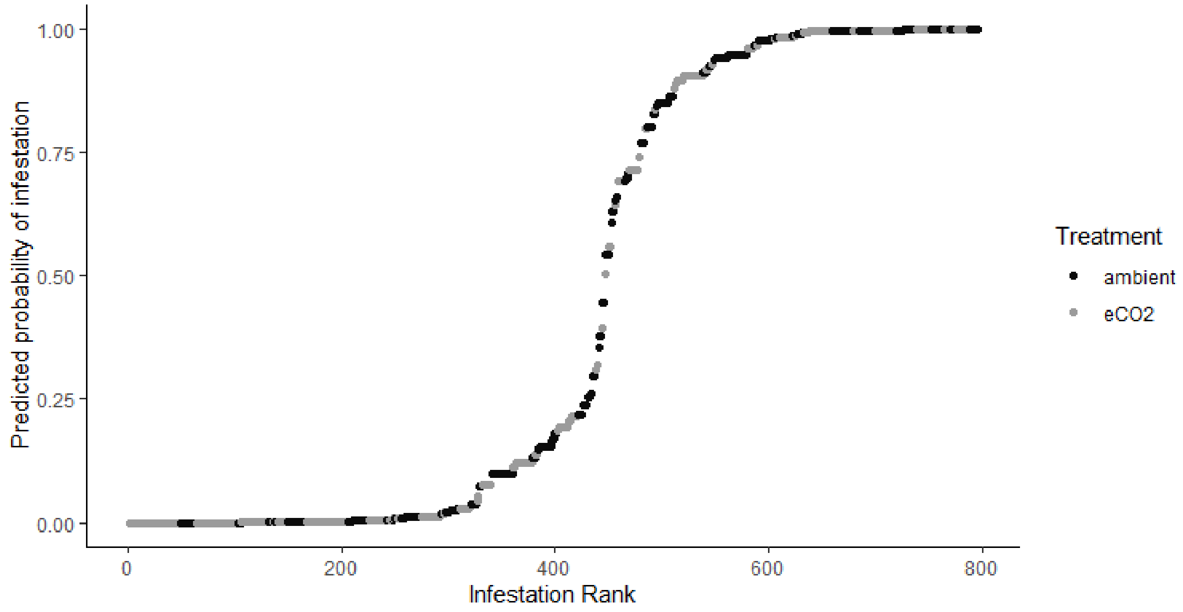

Figure 4. 2 Predicted infestation of EucFACE. Points indicate single trees rank by likelihood of infestation. Ambient conditions denoted by black points, eCO₂ conditions denoted by grey points. Curvilinear relationship shows both treatments equally likely to host lianas.

Liana attained height (LAH) increased in all rings (except ring 1) throughout the census period (Fig. 4.3). Mean LAH increased from 1.05m in 2012 to 6.64m in 2022 and 1.09m in 2012 to 4.74m in 2022, in ambient and eCO₂ conditions respectively (Table 3.2). LAH was highly variable within treatment (Fig. 4.3), with both rings 5 and 6 (eCO₂ and ambient respectively) both having the greatest increases in LAH over time and with most lianas in these rings reaching the crown where they could not be tracked anymore using the TLS data. Lianas in rings 2 and 4 (ambient and eCO₂ respectively) remained relatively low on host tree stems throughout the study. Ring 3 (ambient treatment), which showed the greatest increase in trees supporting lianas (Table 4.1), showed correspondingly great increases in absolute LAH from 0.24m LAH in 2012 to 7.35m LAH in 2022 (Table 4.2).

Table 4. 2 Mean LAH and standard errors per treatment.

	2012		2015		2018		2020		2022	
Treatment	Mean LAH (m)	se	Mean LAH (m)	se	Mean LAH (m)	se	Mean LAH (m)	se	Mean LAH (m)	se
eCO_2	1.09	0.228	2.13	0.34	2.91	0.503	3.4	0.578	4.74	0.658
ambient	1.05	0.245	2.5	0.391	4.27	0.576	4.83	0.634	6.64	0.707

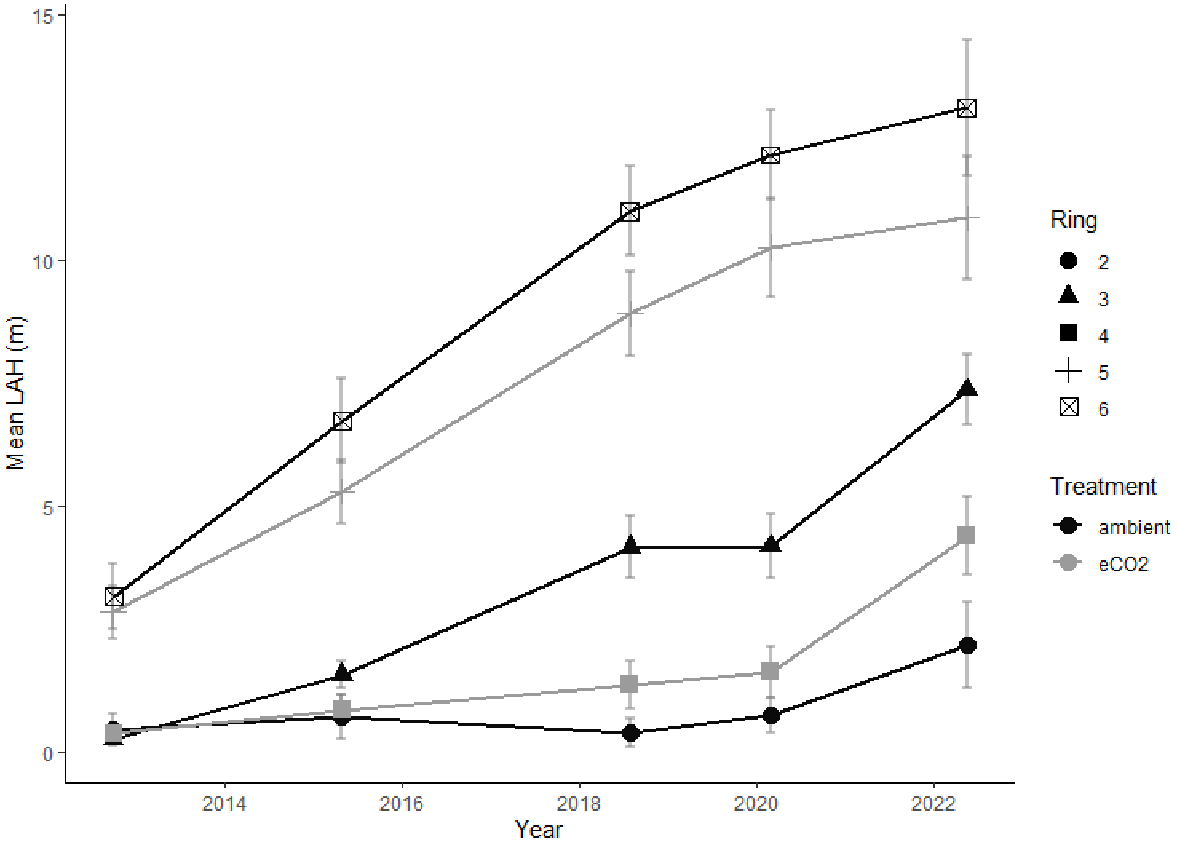

Figure 4. 3 Mean liana attained height (LAH). LAH is calculated as the highest observable point of a liana upon its host tree measured in meters. Mean LAH is shown per ring (points) (Ring2=octagon, Ring3=triangle, Ring4=square, Ring5=cross, Ring6=hatched square), grouped per treatment (line) (ambient shown in black, eCO$_2$ *shown in grey). Standard error bars are shown for each mean.*

Despite the significant increases in LAH over the study period (ANOVA F-value = 78.8288, p=<0.001), elevated CO$_2$ levels were not responsible for the increases in LAH over time (ANOVA F-value = 0.9667, p= 0.32). The period with the lowest mean change in LAH was between 2018 and 2020 for both treatments (Fig. 4.4), coinciding with a protracted period of drought.

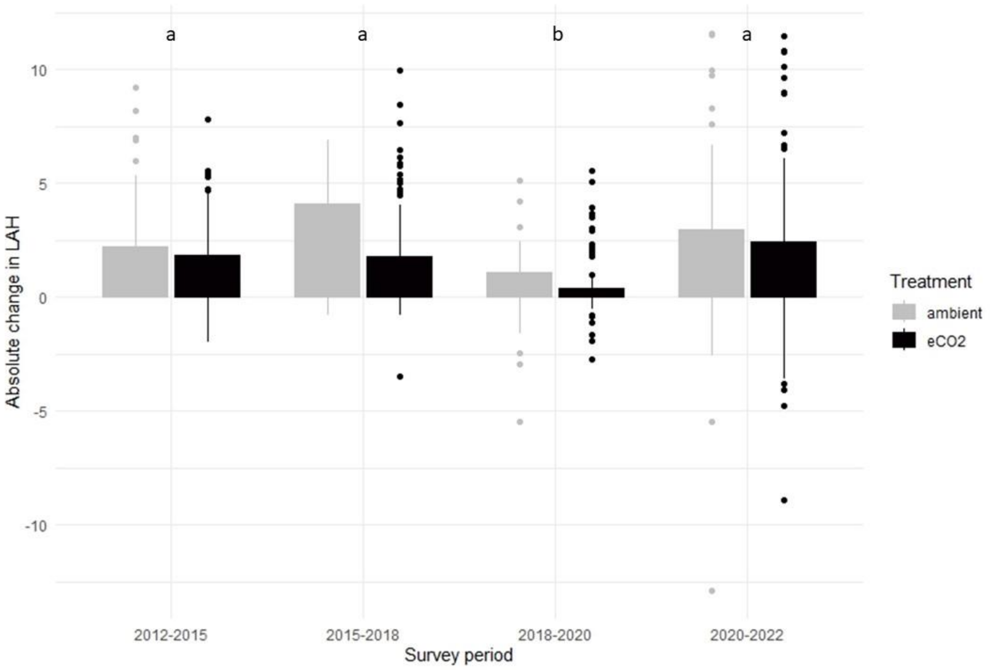

Figure 4. 4 Boxplot showing absolute change in liana attained height (LAH) between ambient and eCO$_2$ treatments for each of the survey periods. Significant (least squares means comparison, $p<0.05$) differences between survey periods shown with letters. No significant differences were found between treatments for any of the surveying periods.

4.4. Discussion

My results show that both the proportion of trees supporting lianas as well as the progression of liana infestation has increased over time. However, most significantly, these results show that this increase is not driven by elevated CO$_2$ conditions, as increases in trees supporting lianas and the height attained by lianas were found to a similar extent in both ambient and eCO$_2$ conditions (Fig. 3.3 and 3.4).

My results contradict the hypothesis that elevated CO$_2$ conditions may be driving increases in lianas. A potential explanation for these differences between my work and previous work is that previous studies primarily focussed on lianas in early ontological stages (Hättenschwiler & Körner, 2003; Zotz et al., 2006, Marvin et al., 2015, Granados & Körner, 2002), with none focussing on the proportion of trees supporting lianas or the height attained by lianas. Zotz et al. (2006) found that elevated atmospheric CO$_2$ stimulated the growth of juvenile temperate lianas within the forest understory more strongly than those found in the tree sub-canopy. From this evidence it is suggested that under elevated atmospheric CO_2 there would be increased proportions of forest trees infested by lianas (Zotz et al., 2006). While in this study the proportion of trees occupied has increased over time, I found there is no indication that infestation had increased in response to elevated CO_2.

Similarly, I found that liana attained height is unaffected by elevated atmospheric CO_2. Although evidence from a study on temperate lianas found that in elevated CO_2 conditions, sub-canopy lianas attained greater heights upon their host trees, though this trend was not significant (Zotz et al. 2006). Liana growth upwards may therefore be constrained more by local environmental factors than rather than by CO_2. Given that both treatments have low mean LAH, 4.74m and 6.64m in eCO_2 and ambient respectively, compared to canopy height of trees (18m+) is it is likely that LAH is limited by site-wide factors. The woodland at EucFACE is phosphorus limited (Ellsworth et al., 2017, Duursma et al., 2016), which has been shown to limit the growth of trees (Crous et al., 2015). As lianas appear to require greater concentrations of phosphorus than co-occurring trees (Collins et al., 2016), phosphorous limitation rather than CO_2 may be limiting their growth. This however is difficult to assess using the presently available data for two key reasons. Firstly, the TLS data were not of a sufficient resolution where I was able to geometrically model these lianas to assess CO_2 effects on allometry, and secondly any TLS measurements of lianas within tree canopies would be inherently biased towards larger liana stems, as smaller stems and foliage proved to be near indistinguishable.

The largest change in the proportion of trees hosting lianas between survey periods was from 2012 to 2015, which may be linked to on-site disturbances. During this period, a severe psyllid attack began in 2014 in ring 6 and extended to the rest of the site in 2015 (Ellsworth et al., 2017; Gherlenda et al., 2016). Psyllids, native defoliating insects, caused extensive canopy damage, which would have decreased canopy light interception, increasing light availability in the understory (Gherlenda et al., 2016). Lianas have acquisitive traits, such as phenotypic plasticity (Yuan et al., 2016), high specific leaf area (Collins et al., 2016) and greater hydraulic efficiency (van der Sande et al., 2019, De

Deurwaerder et al., 2018), which allows them,to capitulate on sudden changes in light availability by growing and vegetatively reproducing. This is further supported as the increment at which lianas attained height was greatest in the period following this canopy wide disturbance with LAH increment change decreasing in the period 3-5 years post psyllid disturbance (2015-2018).

Absolute change in liana attained height was lowest between 2018 and 2020 (Fig. 4.4), corresponding with a protracted period of drought on-site. While lianas are capable of growing during dry periods (Schnitzer and van der Heijden, 2019) and maintaining hydraulic security (Liu et al., 2022), through tighter stomatal control than trees (Chen et al., 2015), protracted droughts may cause sufficient water deficit that any potential fertilisation derived from eCO_2 are effectively negated. Furthermore post-drought (2020-2022) absolute change in LAH became negative, driven by lianas in rings 5 and 6 may have slipped into tree branch unions. Lianas can slip on host trees due to their weight surpassing their adhesive strength (Isnard et al., 2009; Dias et al., 2021), host tree limb drop (Putz, 1984a; Alvira et al., 2004), or from external influence from severe weather events (Soffiatti et al., 2022b). During the 2020-2022 period EucFACE was subjected to frequent saturation of ground water, with rings 5 and 6 regularly flooding. Following the protracted drought, the heavy rains and persistent inundation may have reduced the ability of some lianas to maintain their positions within the crowns of the trees.

The increasing liana proliferation and liana attained height found in the first 6 years of EucFACE could also be a product of disturbance prior to the establishment of the CO_2 injection rings. Schnitzer et al. (2021) found that lianas in the tropics proliferate in the wake of disturbance with lianas still being dominant within disturbed forests a decade after canopy gap creation. Canopy gaps remain few at EucFACE with a relatively homogeneous structure and tree height, despite this however there are distinct gaps within the forest structure where trees are supressed and perish. Lianas have been shown to thrive where gaps develop within forest structures (Schnitzer and Carson, 2010; Parthasarathy et al., 2014; Schnitzer et al., 2021). While every effort was made during construction to limit disturbance to the forest structure (Duursma et al., 2016; Norby et al., 2016), the addition of large semi-permanent structures may have caused enough mechanical disturbance to either soil or canopy, that lianas have proliferated.

The lianas at EucFACE are not distributed evenly between the experimental rings. Ring 1 (eCO_2) remained liana free in the TLS point cloud for the duration of the study, while liana infestation in ring 2 was only 10-36% throughout the study period. These rings are separated from the other four experimental rings by a clearway surrounding high voltage utility cabling. Spatially, lianas can be influenced by host tree, nutrient, and moisture availability (Cai et al., 2007; Blick and Burns, 2011; Mori et al., 2016) and also by seed mobility and clonal propagation through forest soils at a woodland scale (Ledo and Schnitzer, 2014; Michel et al., 2014). As the utility clearway has removed all woody vegetation, and therefore liana hosts, from a ~20m stretch within the woodland, this may have effectively limited the advance of lianas through the woodland. Nutrient availability at EucFACE is low but indicative of many native woodland systems in Australia (Tozer, 2003; Crous et al., 2015). However, nutrient limitation is distributed evenly across the site (Crous et al., 2015) and is therefore unlikely to be limiting the spatial distribution of the lianas.

Liana establishment, i.e. how long lianas have been present, may influence response to elevated atmospheric CO_2. There were only a few lianas, at the start of the experiment, with the majority not reaching the canopy of the trees that supported them (apart from in rings 5 and 6). Furthermore, although lianas in many of the rings reached the crowns of the trees that supported them in 2022, individual lianas stems were often still <2cm. These two factors may indicate that lianas may only recently have colonised the site. As liana abundance and biomass increase, liana-liana competition also increases which, as with trees, can result in self-thinning (Medina-Vega et al., In Prep; Westoby, 1981). More established liana populations may respond differently to CO_2 fertilisation as larger more mature lianas typically invest more into fruits and flowers, rather than rapid growth (Wright et al., 2015b) and therefore changing how lianas use available carbon.

Furthermore, larger lianas are more likely to extend between tree canopies (Putz, 1984b; Schnitzer et al., 2023) which increases the number of trees hosting lianas without directly increasing liana stem density or liana attained heights, as lateral growth of lianas would not increase liana attained height. The effects of elevated atmospheric CO_2 on liana stem density are still currently unclear, although as juvenile lianas increase in growth under elevated CO_2 conditions that liana stem density may also increase (Granados and Körner, 2002).

The key limitation arising in this chapter is the resolution of the data vs. the size of the lianas. The TLS data were collected and rendered at a 20mm resolution, which for structural and volumetric modelling of trees is a typically appropriate resolution (Calders et al., 2014; Newnham et al., 2015). However, as most of the lianas at EucFACE are <20mm diameter, this limits geometric accuracy when rendering liana stems with TLS scans (Krishna Moorthy et al., 2018) and prevents volumetric calculation of these lianas. These limitations meant that liana biomass dynamics as a response to elevated CO_2 concentrations could not be established. Furthermore, due to occlusion, from other woody material, and the narrow diameter of these lianas, detecting the stems of lianas within the canopy of trees proved difficult, which limits both the utility and accuracy of measurements of liana length. The distance between the ground and greatest height at which liana vegetative structures, such as leaves or stem tangles, could still be identified was therefore used. This liana attained height is an inherently conservative measure of liana progression as this was limited to advances on the tree stem only and not a measure of liana growth rate or biomass.

As it appears that lianas are not responding to eCO_2 either by increasing the proportion of trees hosting lianas or by increasing increments of change in LAH at EucFACE, further work is needed to elucidate whether lianas have any reaction to elevated atmospheric CO_2. Based upon previous studies at EucFACE it has been shown that *Eucalypts* respond to elevated CO_2 conditions by down regulating photosynthesis (Ellsworth et al., 2017a), i.e. reducing chlorophyll content but maintaining high photosynthetic rates (Ainsworth and

Rogers, 2007). However there has been no response of above ground tree diameter growth potentially due to phosphorus limitation (Ellsworth et al. 2017, Duursma et al. 2016).

Recent work into the carbon allocation of lianas shows that lianas invest carbon differently with changing ontogeny, i.e. when transitioning between freestanding to climbing growth stages (Smith-Martin et al., 2020), which may mean that their response to elevated atmospheric CO_2 may also differ between ontogenetic stages. Unlike trees which invest carbon in to self-supporting stems, structural parasitism allows lianas to invest relatively little into supportive stems, instead investing in efficient hydrological transport networks and creating large quantities of leaves (Putz, 1983; Parthasarathy et al., 2015; Rodríguez-Ronderos et al., 2016; Pathare et al., 2017). This may fundamentally influence how lianas use atmospheric carbon, as leaves are typically less carbon intensive investment than woody tissue (van der Heijden et al., 2015).

4.5. Conclusions

This study is the first to use terrestrial laser scanning to retrospectively explore the effects of elevated atmospheric CO_2 on the development of liana infestation. I found that liana infestation of trees has significantly increased from 2012 to 2022 across the EucFACE rings. However, increases in liana infestation did not result from exposure to elevated atmospheric CO_2, but could possibly track local disturbance. Lianas at EucFACE increased in the height at which they are located upon their hosts, but this is not influenced by the CO_2 regime. The results of this study do not rule out a response to elevated atmospheric CO_2 in the case of either the trees or the lianas at EucFACE, as leaf or canopy responses cannot be captured with data such as these. The strongest increases in both LAH and liana infestation occurred during periods of intense disturbance, disturbance is likely one of these drivers at EucFACE.

While the increase in lianas at EucFACE does not appear to be driven by elevated atmospheric CO_2, it is possible then that the effects of CO_2 upon lianas are seasonal rather than a long-term change in proliferation or height. It is currently unknown whether the lianas or trees at EucFACE respond differently to inter-seasonal or inter-annual changes differently when exposed to elevated atmospheric CO_2. As such there may be responses to elevated atmospheric CO_2 which are no detectable with TLS data, whether it be due to temporal coarseness or a response which is not expressed in the growth of woody plants. To this end my next chapter will use temporally dense imagery data to examine canopy response of these lianas and compare these with the response of trees.

Chapter 5: Optical response of *Parsonsia straminea* to elevated atmospheric CO_2 differs from co-occurring *Eucalyptus tereticornis*.

5.1 Chapter Abstract

Leaves are the gateway for CO_2 assimilation in plants, which means that response to elevated levels of CO_2 are most likely to be observed first in the greenness of leaves before any response may be detected in other plant organs. There is however evidence that limited soil moisture limits the response of plants to elevated atmospheric CO_2. The research presented in this chapter therefore aims to examine i) whether tree and liana canopies respond to elevated atmospheric CO_2 conditions and ii) whether the response is related to the availability of soil moisture over an eight-year period using a temporally frequent dataset of weekly RGB imagery. Using a simple greenness ratio, the green chromatic coordinate (GCC), the results show that lianas are responding to elevated atmospheric $CO_{2,}$ which is particularly prominent during periods of increased moisture availability when greenness of lianas increases. For trees, GCC is also increased in elevated CO_2 conditions but follows a more seasonal pattern indicating trees in elevated atmospheric CO_2 might be responding to increases in soil moisture faster than those in ambient CO_2 conditions. Liana GCC remains higher for longer than tree GCC after soil moisture decline, which is especially apparent in elevated atmospheric CO_2. These findings indicate that lianas are less affected than trees by decreases in soil moisture in both ambient and elevated CO_2 conditions. Unlike trees, lianas may therefore have a greater ability to ameliorate drought effects, such as declining productivity, on their leaves in elevated atmospheric CO_2 conditions, potentially then increasing the seasonal advantage reported in other studies. This could result in further intensification of liana biomass increase during dry periods, which in turn would result in increased liana competition on co-occurring trees. Ultimately then this may lead to lianas increasingly negatively affecting host trees and thus reducing the ability of forests to uptake carbon.

5.2 Introduction

Based upon my investigation utilising terrestrial laser scanning (TLS) (chapter 4), elevated CO_2 does not appear to be driving the observed long-term proliferation of the liana *Parsonsia straminea* at EucFACE. Although, it is possible that short term or inter-seasonal trends in the response of lianas and trees to elevated CO_2 have been overlooked due to the low temporal density of these data.

As leaves are the nexus between plants and atmospheric CO_2, it is possible that responses to elevated CO_2 will manifest within the leaves before being apparent elsewhere in the plants (Marvin et al., 2015). As leaves from woody vegetation turn over periodically, responses to elevated CO_2 may be masked in studies with relatively long re-surveying periods due to cyclical growth, maintenance and senescence of leaves, which alters the structure, and likely chemical composition, of canopies (Hikosaka et al., 1994; Hikosaka, 2005). Thus, short term or seasonally linked effects of elevated CO_2 may be represented in a canopy response before there is a detectable change in growth or species assemblages.

Studies of vegetation exposed to elevated CO_2 have shown strong interactions between soil moisture availability and leaf productivity (Volk et al., 2000; Belote et al., 2004; De Kauwe et al., 2021), as elevated CO_2 has been shown to increase water use efficiency, preventing the negative impacts of drying soils on leaf health (Gimeno et al., 2016; De Kauwe et al., 2021). Moreover, studies have found that the fertilising effects of CO_2, i.e. biomass accumulation and improved growth, are constrained by limited moisture availability, despite improved water use efficiency (Hovenden et al., 2019; Venter et al., 2022). The dominant trees of EucFACE (*Eucalyptus tereticornis*) follow the seasonal patterns of moisture availability in their phenology, with leaf flush normally following seasonal rainfall patterns, however leaf senescence was found to be delayed by elevated CO_2 (Duursma et al., 2016).

In comparative studies, lianas and trees have been shown to respond to water limitation differently, with lianas typically retaining greater leaf moisture, higher rates of photosynthesis and higher leaf area index (LAI) than co-occurring trees (Cai et al., 2009; Schnitzer and van der Heijden, 2019; Meunier et al., 2020). It may be then, due to these general adaptations, that lianas use elevated CO_2 differently to co-occurring trees, as lianas already possess efficient hydraulic networks capable of keeping leaves supplied with water during droughts (Heuzé et al., 2009; Ganthaler et al., 2019; Medina-Vega et al., 2021a). This in turn might suggest that lianas will present different leaf responses to their host trees when soil moisture is limited, which may further be different by the addition of CO_2, as it has been shown that, when grown under elevated CO_2 conditions lianas further increase their water use efficiency (Mohan et al., 2006; Venter et al., 2022).

While field experiments containing lianas have expanded in recent decades (Estrada-Villegas and Schnitzer, 2018; da Cunha Vargas et al., 2021), the occurrence of lianas in facilities capable of testing canopy responses to elevated CO_2 is severely limited. However, the EucFACE facility is one of the few CO_2 experimental sites that harbours a resident population of lianas (*Parsonsia straminea*). Furthermore, as is typical of the area in which this experimental forest resides, EucFACE follows a semi-seasonal pattern of moisture availability with soil water content regularly falling as low as $0.03m^3m^{-3}$ during summer (Duursma et al., 2016; Ellsworth et al., 2017a). The EucFACE site has seen several notable disturbances to the moisture regime since its creation in 2012 including drought between 2018 and 2020 and several periods of flooding in 2020 and 2021.

As response to external influences can happen rapidly within tree canopies (Duursma et al., 2016), thus testing canopy responses to elevated CO_2 requires temporally dense data, or intensive field monitoring. As the latter option requires intensive effort which cannot be applied retroactively, remote sensing offers several options at different levels of temporal density. Satellite or aerial remote sensing can offer relatively dense temporal data sets, with return rates measured in weeks to months (Lechner et al., 2020), however these data are limited in their utility where the target organism reside below the forest canopy. In-situ sensors can offer some remediation of this limitation (Richardson, 2019), with in-situ photographic sensors being both readily available and relatively easy to install to study both above and within canopy targets (Richardson et al., 2018a; Richardson, 2019). Typically these sensors consist of a consumer grade camera capturing images with red, green and blue (RGB) channels (Richardson et al., 2009; Sonnentag et al., 2012; Klosterman et al., 2014), from which it is possible to use simplistic (i.e. those with no external data included) vegetation indices, to track canopy phenology (Toomey et al., 2015; Richardson et al., 2018a), plant health (Reid et al., 2016), or response to soil water availability (Luo et al., 2022). It has been shown that lianas and trees can be optically distinct in simple red, green, blue (RGB) imagery (Marvin et al., 2016; Waite et al., 2019; Chandler et al., 2021b), therefore, delayed senescence of Eucalypt trees should be detectable with the use of remote sensing. Phenological studies utilising image based analysis, show that during leaf flush the greenness of tree canopies increases with leaf development until a seasonal peak and eventual senescence (Sonnentag et al., 2012; Richardson et al., 2018a; Luo et al., 2022).

Vegetation indices, such as the green chromatic coordinate (GCC) (Sonnentag et al., 2012), excess greenness (eGI) (Ide and Oguma, 2010), hue, saturation and brightness (HSB) (Karcher and Richardson, 2003), hue, saturation and intensity (HHI) (Carron and Lambert, 1994), have all been applied to RGB imagery for use in studies of forest canopy health and phenology. Vegetation indices transform the pixel values from the red, green or blue channels of an imagery to either highlight the influence of a single channel, e.g. eGI, or provide an empirical metric which can be used to determine differences between sensors or images (Morgan and Gergel, 2013).

Indices are subject to limitations from both the hardware selection, i.e. sensor bias (Ide and Oguma, 2010; Kior et al., 2024), the influence of shading or over-illumination (Sonnentag et al., 2012; Mishra et al., 2017), and external factors, such as those of cloud cover or precipitation on either foliage or lenses (Seidl et al., 2011; Sonnentag et al., 2012). Illumination of the EucFACE site is highly variable, with long periods of high solar irradiation loosely corresponding to the southern hemisphere summers (Wang et al., 2016), and can change rapidly during data capture. It is therefore necessary to use a vegetation index that is relatively insensitive to changes in illumination. GCC is relatively unaffected by illumination, especially when illumination changes rapidly. GCC therefore is a suitable empirical index to monitor canopy response of trees and lianas to elevated CO_2 from RGB imagery.

The EucFACE site has been recording daily imagery for all of the experiment rings since 2014, allowing me to explore 8 years of near-continuous data to examine i) how tree and liana canopies respond to elevated atmospheric CO_2 conditions and ii) whether the response is related to the availability of soil moisture. To achieve these aims the GCC has been used to determine the canopy response to elevated atmospheric CO_2 for both lianas and trees. Using GCC allows for comparisons between i) the response to CO_2 treatment per lifeform, ii) response to soil moisture per lifeform, iii) differences between lifeforms per CO_2 treatment, and iiii) whether differences between treatments and between lifeforms are influenced by soil moisture.

5.3 Methodology

5.3.1 Study site

For a full site description see chapter 3.

The EucFACE rings are 25m wide plots, surrounded by carbon-fibre infrastructure reaching 30m in height. These rings have an Axis Q6044-E PTZ (Axis communications AB.) security camera mounted on the northern aspect of the ring facing south. Cameras are aligned to cover ~70% of individual ring area, primarily the infrastructure and tree canopy. Four overlapping images are taken three times per day around noon in each ring with the operation taking ~30 seconds per ring. Acquiring images when the sun is at its zenith, and in rapid succession, limits shadows and differences in overall lighting quality. Pan/tilt settings are custom to each ring with ~5-15% image overlap at 1280x720 resolution, 96dpi.

Imagery was available for all rings from November 2014 with a data gap from March to September 2018 in rings 2:6. When data capture was restored, the camera in ring 4 was not centred on the ring correctly until January 2020. The study period spanned 417 weeks including these data gaps with ~ 35028 individual images generated per ring.

Table 5.1 Camera Pan-Tilt settings per ring. Image field of view 62.9° horizontal, 37° vertical. Images captured as JPEG file format.

Ring	Image label	Pan	Tilt	Resolution	DPI
1	Wide view left up	95.2507	-32.3877	1280x720	96
1	Wide view left down	94.8754	-60.2633		
1	Wide view right down	149.7511	-61.6918		
1	Wide view right up	150.1791	-29.2041		
2	Wide view left up	104.901	-26.8027		
2	Wide view left down	104.6921	-55.3993		
2	Wide view right down	161.1623	-59.7134		
2	Wide view right up	161.4346	-30.8582		
3	Wide view left up	94.3957	-36.6737		
3	Wide view left down	94.9189	-65.6399		
3	Wide view right down	157.6489	-65.6399		
3	Wide view right up	157.0958	-32.0108		
4	Wide view left up	-25.4281	-45.2557		
4	Wide view left down	-26.3014	-74.0808		
4	Wide view right down	25.8487	-69.3593		
4	Wide view right up	26.7515	-40.8855		
5	Wide view left up	-146.868	-31.3083		
5	Wide view left down	-148.332	-54.5373		
5	Wide view right down	-98.8624	-59.4114		
5	Wide view right up	-83.7886	-36.2121		
6	Wide view left up	-153.251	-35.2158		
6	Wide view left down	-137.709	-66.8623		
6	Wide view right down	-100.365	-66.8623		
6	Wide view right up	-94.4048	-30.8174		

5.3.2 Image analysis

The sensors used in this study are prone to over illumination (fig.5.1) during periods of intense solar irradiance, mostly during the Australian summertime. To avoid influence of image over-illumination and shadows, imagery was manually compared to a reference image with diffuse lighting (fig.5.1). Image series (4 individual images) that were closest in lighting to the reference image were then scrutinised for any optical aberrations or obstructions. When obstructions were found in one or more images, the series was excluded from the study. From the remaining image series, one series was selected per week to be processed into a panorama image.

Figure 5. 1 Example of images from EucFACE. Left hand image example of flattest light for use in image amalgamation. Right hand image too bright for use in analysis. Bright images suffer from shadow occlusion of understory vegetation and typically non-linear sensor response to illumination. Both images show ring 6 (ambient) at EucFACE and are from 2021, November 11th for left image, January 16th for right image. Both images taken at 12pm facing south from 22m above ground level.

Selected images were then overlapped into a panorama image using PTgui 12.10 (New House Internet Services B.V.). This resulted in ~ 375 processed panorama images per ring, ~2250 total panoramas. The panorama process was batch processed without colour correction to maintain individual image colouration. Panorama images were processed to 2331x1580 resolution, 300dpi with 4.3x image crop following a roughly 7.4mm projection to maintain a hemispherical view of the lower canopy and stems of trees within the ring

(Fig.5.2). Original pixels are resized for the panorama, within PTGui a nearest neighbour interpolation is used to smooth the image without colour correction. While the panorama process was mostly automated, images where there are obvious signs of wind influence or lighting profiles that differed from the initial reference required manual alignment to create the panoramic image. Image series where camera alignment was altered or had drifted resulted in poor panorama stitching with large gaps or severe warping to the image. Camera drift on the automated mount lead to several image series not being included as there was insufficient overlap between images to register the panorama. Manual stitching required matching of control points between images. Overlap between images was mainly concentrated towards the centre of the panoramic image (Fig.5.2) as well as on the superstructures to the far sides of the panorama. The number of control points used varied between per panoramic image, with most aligned using 20-40 control points though some required ~50 control points.

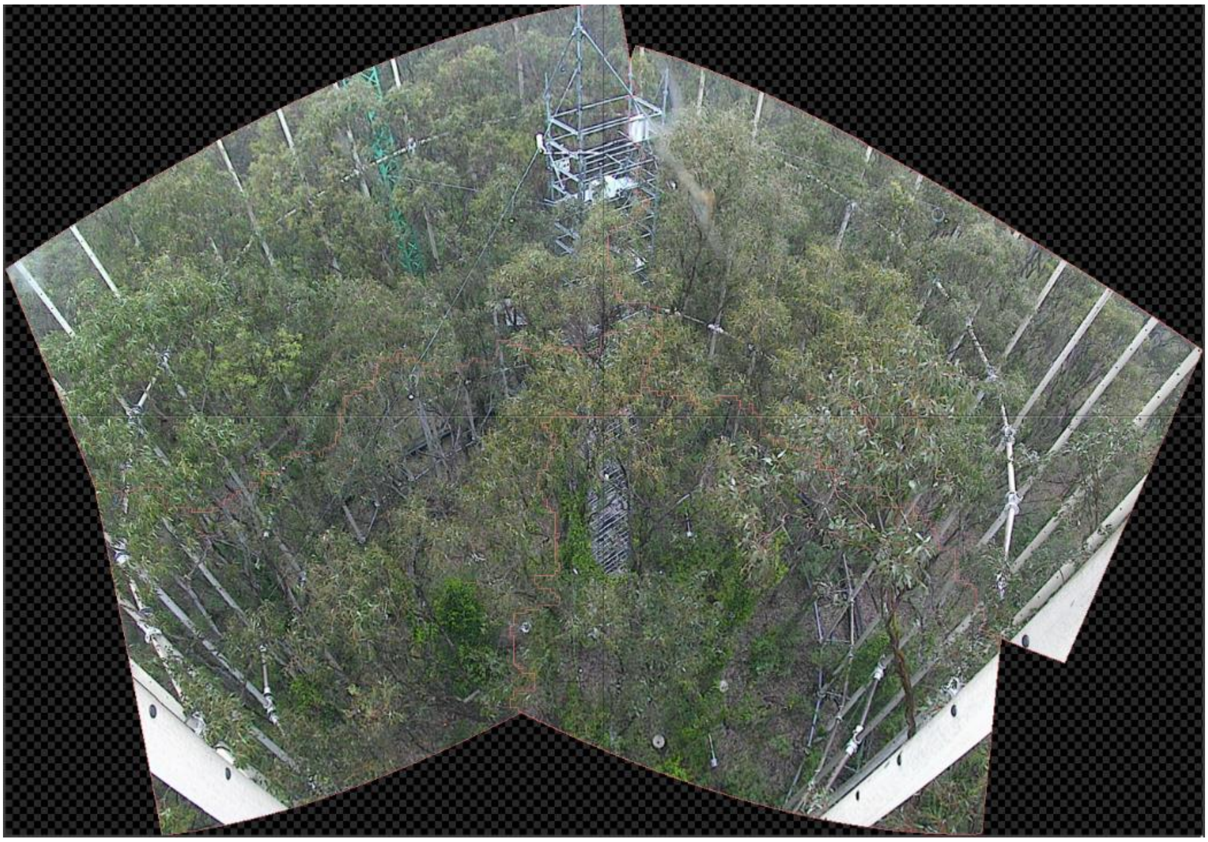

Figure 5. 2 Panorama image of ring 5 (eCO$_2$*) in PTGui. Panorama made from 4 images taken in October 2018 within 30 seconds on computer controlled gimbal at 22m. Red lines in image indicate individual images used to create the panorama. Lianas can be seen at the base of tree stems and encroaching on tower infrastructure in centre of image.*

5.3.3 Data extraction

As lianas and trees are visually distinctive in the panorama images, areas of interest (AOIs) were manually created around foliage that were either: (i) wholly liana foliage, (ii) wholly tree foliage, or (iii) a white reference – using the surrounding superstructure (fig. 5.3) and were focussed on sections of the image with the least interference from shadows and/or occlusion from windblown branches. AOIs were drawn in ERDAS Imagine using the polygon AOI tool, target foliage was checked against annotated site maps of tree locations, majority of liana AOIs were created where lianas had been previously reported via on-site censusing (chapter 4). AOIs were bespoke per ring, for each ring a minimum of 7 AOIs per lifeform were created, for rings with greater liana numbers (rings 5/6) it was possible to create 9 liana AOIs within the ring. The AOIs were used to mask the panorama image to derive an image from which pixel digital numbers could be extracted.

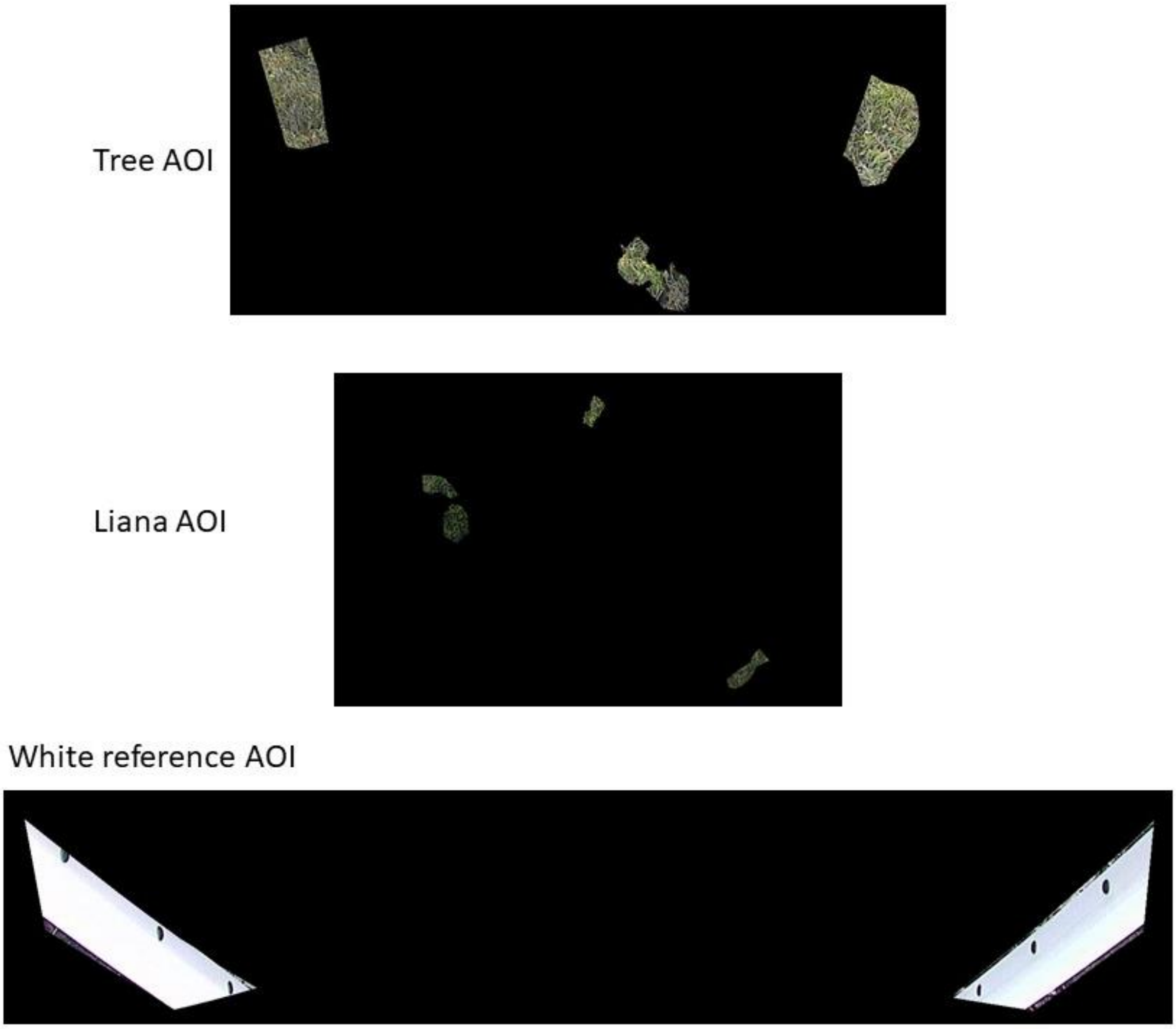

Figure 5. 3. Example AOI's for Ring 5. Top image tree only AOI. Middle image liana only AOI. Bottom image white reference AOI. White reference AOI taken on superstructure closest to elevated camera.

A greenness calculation can be used to determine whether there is a foliar response to external drivers. Due to variable sensor response to sunlight as well as to limit calibration issues an illumination agnostic ratio has been selected, specifically the calculation of the Green Chromatic Coordinate (GCC)(Morris et al., 2013) which is calculated as;

$$GCC = G/(R+G+B) \qquad \textit{Eq. 1}$$

Where G is the green channel in an RGB image, R is red channel and B is blue channel.

GCC was calculated per pixel for each masked AOI image. The influence of irradiance on GCC was examined using the mean irradiance of the date of image acquisition and explored using correlation plots. Effects of irradiance were not found after GCC transformation for either the lianas or the trees in both CO_2 regimes (Correlation plots $r^2 < 0.04$).

5.3.4 Environmental Data

Average daily soil volumetric water content at 30 cm depth was calculated using data collected at 15 min intervals from 48 soil moisture probes (CS650-L; Campbell Scientific, Logan, UT, USA) located within the six experimental rings (eight probes per ring). Daily precipitation was recorded on site but due to sensor drift, these data were not of sufficiently high quality to include within analysis.

5.3.5 Data Analysis

AOI images were amalgamated by date for both lianas and trees per treatment. For this amalgamated raster image, GCC was calculated per pixel.

To test for differences between lifeforms through time a bootstrapping approach was used. First, a composite observed mean per lifeform and treatment was created based on the GCC value for amalgamated AOIs per lifeform and treatment per image acquisition. Pooling GCC data removed influence of spatial variation with the forest (supplemental figure 5.1). To create confidence intervals around this composite mean, the GCC from a subsample of 25% of the amalgamated raster image (1000 pixels per image) was iteratively resampled with replacement 2000 times until bootstrapped mean GCC matched that of the observed mean. This was used to create a mean GCC per treatment and per lifeform alongside the 95% confidence interval (the 97.5 and 2.5th percentiles).

For each resample iteration, the difference between treatments for each life form and subsequently the difference between lifeforms was calculated. Bootstrapped differences were used to calculate a 95% confidence interval (the 97.5 and 2.5th percentiles). Bootstrapped difference confidence intervals allowed visual assessment of differences of liana or tree GCC over as differences between treatments and lifeforms were considered significant if confidence intervals did not intersect zero.

To determine how the observed GCC of lianas and trees varied and whether there was an effect of elevated CO_2, pooled mean GCC values from the original AOIs were tested with an ANCOVA fitted with mean soil moisture, image acquisition was lagged from soil moisture by 1 week to account for water transport uptake, treatment, either ambient or elevated, lifeform, either liana or tree, and season as factors. I fitted interaction effects between moisture and season, lifeform and season, mean soil moisture and lifeform. Prior studies have shown that leaf flush of *E. tereticornis* is closely related to change in soil moisture (Duursma et al., 2016), and that transpiration peaks within 5-10 days of peak soil moisture availability (Cramer et al., 1999; Wang et al., 2022), thus GCC is unlikely to be influenced by moisture content changes on that day, therefore lag between soil moisture and image acquisition was explored using correlation plots. Lags up to 28 days post soil moisture acquisition were tested against lifeform GCC, R^2 values peaked at the 7 day lag, although were generally low for both lifeforms (R^2 range 0.01-0.12).

5.4 Results

5.4.1 Liana responses to elevated CO_2

Lianas in elevated were typically higher in GCC than those in ambient for most of the experiment (Fig. 5.4). To explore how lianas respond to elevated CO_2 at the canopy I calculated the difference in GCC between ambient and elevated CO_2 lianas, shown in figure 5.5. The effect of elevated CO_2, i.e. the difference in GCC between lianas in eCO_2 and ambient, was greatest when moisture availability was at its highest $>0.2 m^3 m^{-3}$(Fig. 5.5). The effect of CO_2 on GCC was smallest during the drought between 2018 and 2020 where soil moisture was below $0.05 m^3 m^{-3}$ (Fig. 5.5). Thus there appears to be a similar response of these lianas to severe drought in elevated or ambient CO_2.

5.4.2 Tree responses to elevated CO_2

The effect of CO_2 on the GCC of trees was generally smaller than between lianas (Fig.5.5). The pattern shown in figure 5.5 indicates that peak difference in GCC is loosely seasonal for trees and the peak difference mirrors the start of the green up of trees also seen in figure 5.4. This indicates that the trees in elevated CO_2 are increasing in GCC both earlier and faster than the trees in ambient.

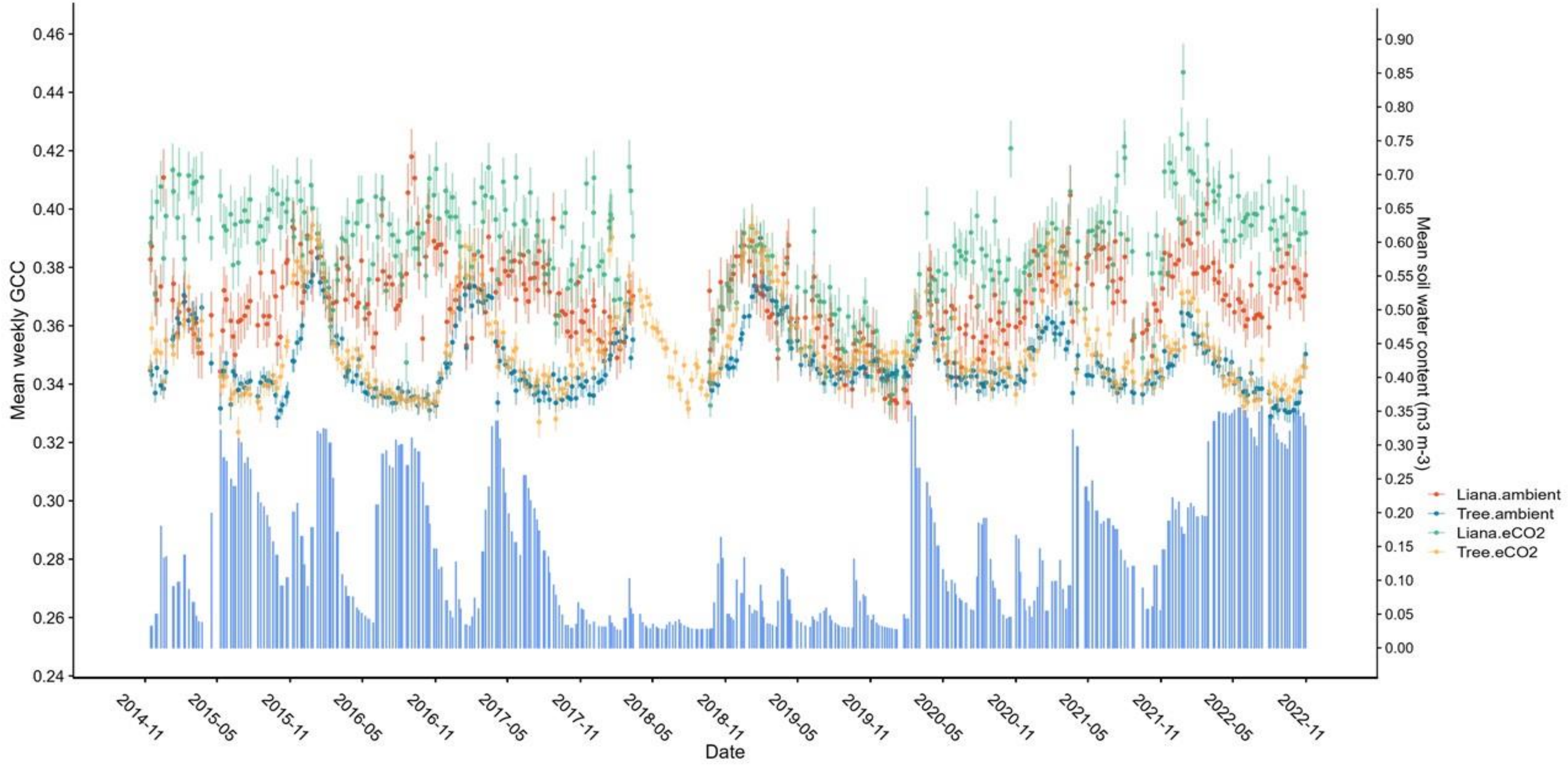

Figure 5. 4 Weekly mean GCC. Lianas in ambient shown in red, lianas in elevated CO_2 shown in green, trees in ambient shown as blue, and trees in elevated CO_2 shown in yellow. Lines indicate 95%CI's. Overlap of 95%CI's highlights similarity between treatments and lifeforms during seasonal peaks in tree GCC during height of summer in the early stages of the study and during the latter part of the recorded drought in 2018-2020. Data from 2018 was not recoverable for rings 2-6 due to a file compression error.

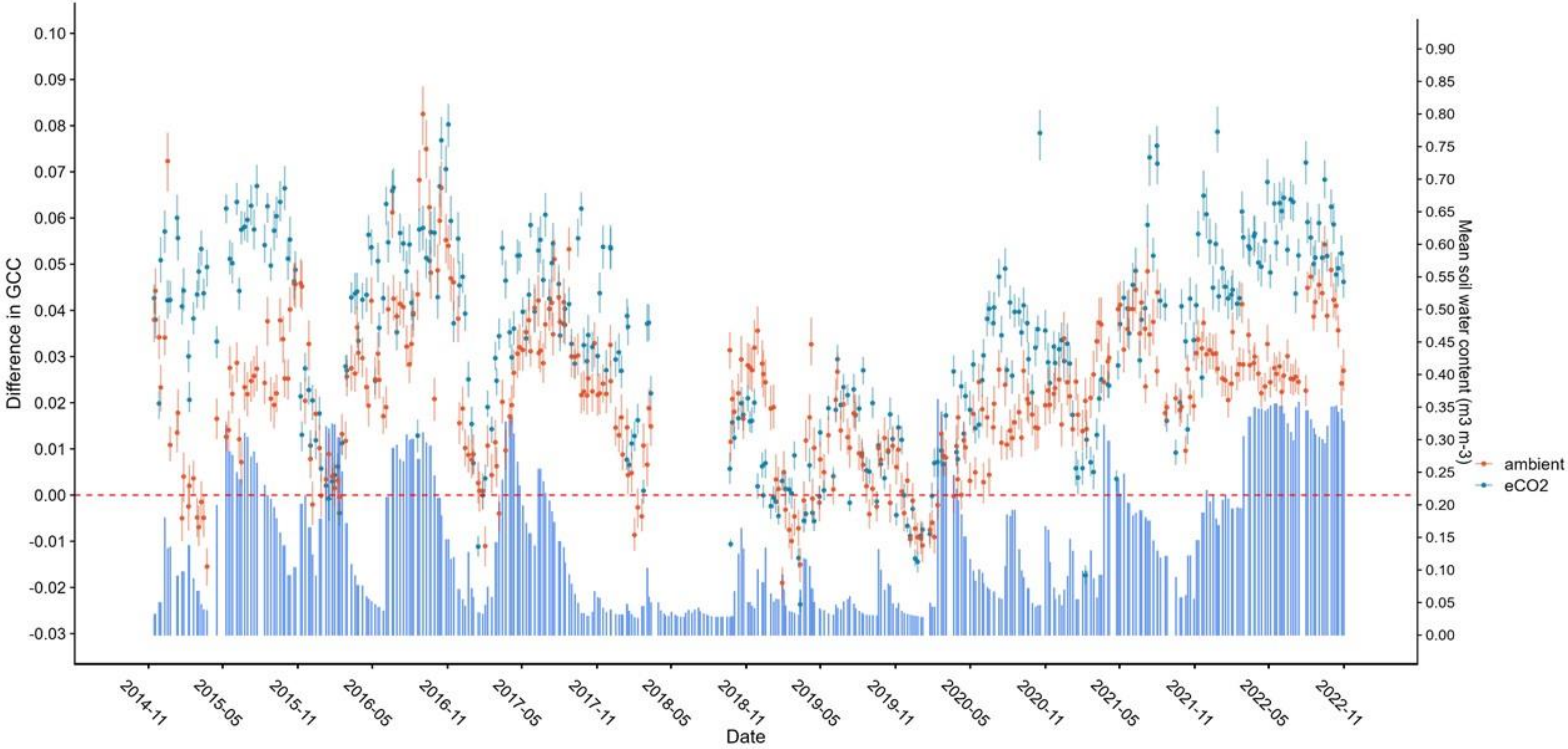

Figure 5. 5 Weekly GCC difference between trees and lianas. Elevated CO₂ shown in blue, ambient CO₂ in red both with 95% bootstrapped CI's. Monthly mean soil water content (mm). Positive values show greater GCC in lianas, negative values indicate higher GGC of trees.

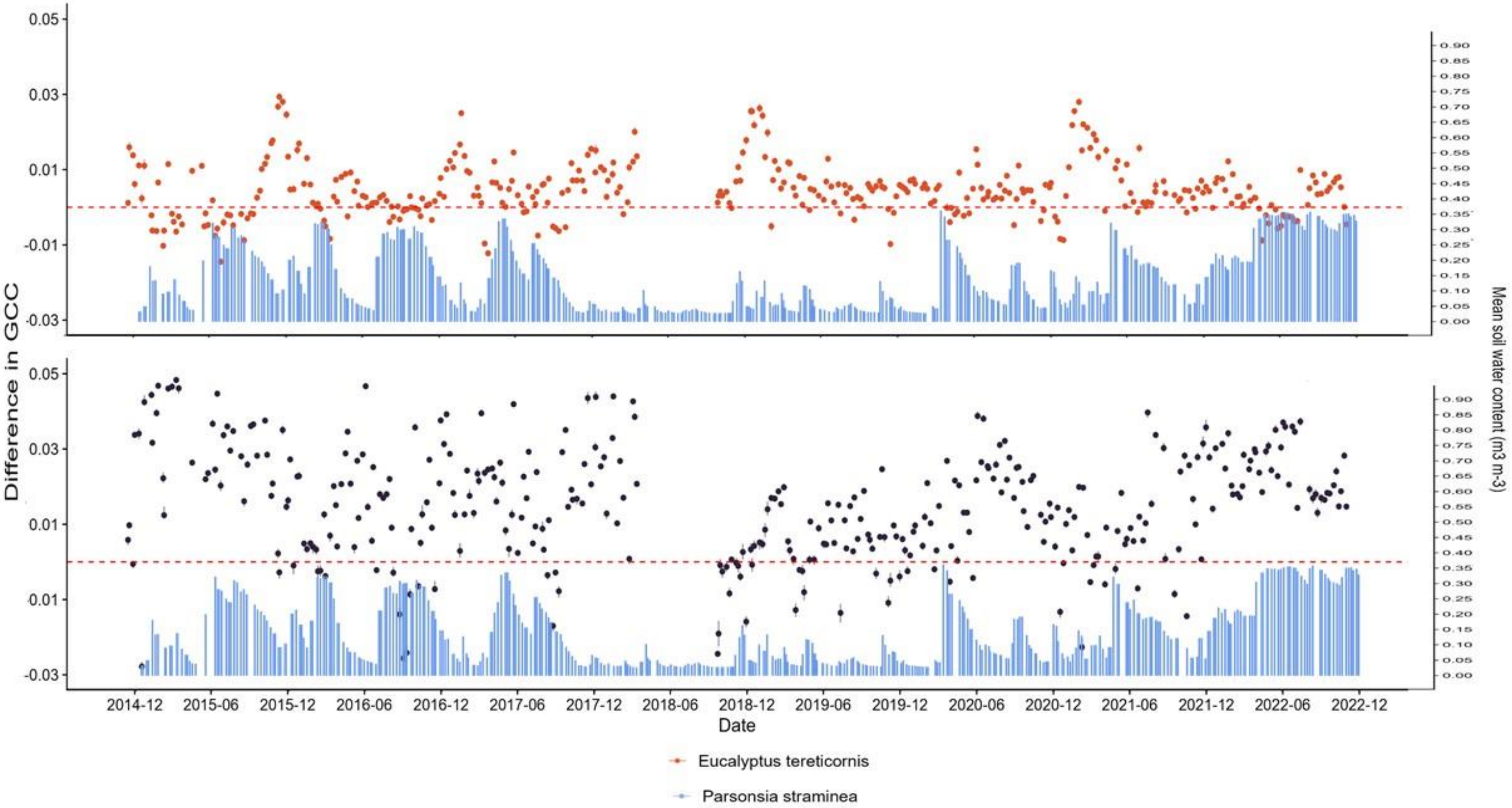

Figure 5. 6 Difference in GCC between Ambient and elevated CO_2 for E. tereticornis (red) and P. straminea (black) with bootstrapped 95CIs. Blue bars represent mean soil water content. Difference follows loosely seasonal pattern for trees, whereas P. straminea GCC difference does not show a clear pattern with season. Difference in GCC of P. straminea is typically higher than that of trees except during the severe drought between 2018 and 2020 where both life forms show similar difference patterns. Positive values show higher GCC in elevated CO_2. Red dashed line indicates no difference.

5.4.3 Differences in GCC patterns between lifeforms

GCC over the course of the EucFACE experiment differs by lifeform, i.e. whether *P. straminea* or *E. tereticornis* (ANCOVA DF= 1, F=2038.33, p<0.001), with the liana *P. straminea* generally showing higher GCC than trees of *E. tereticornis* (Fig. 5.4, Fig. 5.6). GCC of both lifeforms was influence by elevated CO_2 (ANCOVA DF=1, F=181.55, p<0.001), but less so than by plant type.

The difference in GCC between life forms in elevated CO_2 was typically higher than in ambient conditions, but this was not consistent throughout the whole experiment, as GCC of both trees and lianas were similarly affected by the drought in 2018 to 2020 (Fig.5.4). There was a significant interaction effect of mean soil moisture and lifeform on observed GCC (ANCOVA DF=1, F=150.84, p<0.001), indicating that lifeforms respond differently to soil moisture (Fig. 5.4), although the influence of soil moisture content alone was low (ANCOVA DF=1, F=28.83, p<0.001). I show this in figure 5.6 where the difference between trees and lianas increases after periods of high moisture availability. From these it appears that lianas retain higher GCC for longer than trees after the soil moisture starts to decrease.

A seasonal effect on GCC was shown (ANCOVA DF=3, F=44.968, p<0.001), with tree GCC higher in spring and summer than winter or autumn, however the additive effect of season and lifeform was low but significant (ANCOVA DF=3, F=15.05, p<0.001), indicating that there is variation to when lifeforms peak in GCC seasonally, i.e. trees were found to have highest GCC at the start of the Australian summer whereas peaks in liana GCC were more stochastic for both control and elevated CO_2 conditions. This effect is driven by the trees which appear to be following a more seasonal trend than the lianas, with highest GCC loosely aligning with the start of the Australian summer (Fig.5.4). The interaction effect between soil water content and season was low but significant (ANCOVA DF=3, F=16.69, p<0.001), indicating there is a response to when lianas and trees are able to access moisture, but this is not as deterministic as water availability alone.

5.5 Discussion

Here I show for the first time that lianas and tree canopies respond differently to elevated atmospheric CO_2 conditions using a temporally frequent data set of RGB images over a period of eight years. Lianas differed from trees in GCC values across the entire time period and the response of lianas to elevated CO_2 conditions was mediated by soil moisture availability, with GCC values of lianas exposed to elevated CO_2 conditions increasing in periods of increased soil water availability.

GCC seems to track seasonal soil moisture availability for trees, whereas lianas appear to be less seasonally responsive (Fig. 5.3). However, in periods of sustained drought (such as the 2018/2019 drought in Australia), when moisture availability was low ($<0.05m^3m^{-3}$), GCC values decreases for both lifeforms regardless of treatment. I show that the difference between lifeforms is highest, in both treatments, after periods of high moisture availability, suggesting that the GCC of lianas are less negatively affected by lower moisture availability than co-occurring trees (Fig. 5.4). This could be indicative of a water use advantage of lianas over co-occurring trees, which show decreased GCC when subject to the same soil moisture conditions regardless of CO_2 treatment. Prior work has shown that lianas have greater water use efficiency than trees (Chen et al., 2015; Werden et al., 2018), and that elevated CO_2 induces water savings in lianas (Venter et al., 2022).

Lianas at EucFACE, and their responses to elevated CO_2, respond to soil moisture differently to co-occurring trees. I present evidence in that greenness, which can be linked to chlorophyll content as well as plant health (Raymond Hunt et al., 2011; Reid et al., 2016; Richardson et al., 2018a), is higher for lianas in elevated CO_2 compared to those growing in ambient conditions. However, the difference in greenness between lianas growing in either elevated or ambient conditions was highest when soil moisture is not severely limited i.e. $>0.1m^3m^{-3}$ (Fig.5). Furthermore, when soil moisture is at its lowest during periods of protracted drought ($<0.05m^3m^{-3}$), between 2018 and 2020, lianas in both treatments are reduced in their greenness. This similarity in liana GCC between treatments is likely indicative of a similar response to protracted drought regardless of

CO_2 concentration. Furthermore this may show that for these lianas there is likely a moisture threshold beyond which any likely effects of eCO_2 is suppressed entirely (De Kauwe et al., 2021).

In contrast to the lianas, trees in elevated CO_2, show highest GCC in the Australian summer, which coincides with periods of water limitation (where soil moisture is between $0.1m^3m^{-3}$ and $0.15m^3m^{-3}$), but there is generally a lower difference in GCC between treatments than was found for lianas (Fig.5.5). Higher tree GCC in elevated CO_2 conditions corresponds to the findings of earlier studies that indicate there is an increase in the water use efficiency of trees in response to elevated CO_2 conditions (Kelly et al., 2016; De Kauwe et al., 2021; Jiang et al., 2021). However, other studies have yet to determine whether these water-use efficiencies differ between lifeform in drought under elevated CO_2. An earlier study at EucFACE found that water use efficiency was higher for the lianas at EucFACE than the trees in well-watered conditions although not responsive to elevated CO_2 (Laugier-Kitchener et al., 2022).

Mechanistically leaf water savings in elevated CO_2 are driven by enhanced stomatal closure, which leads to a reduction in water vapour loss due to transpiration (Boyer, 2015; Pathare et al., 2017; Buckley, 2019). Therefore sufficient leaf water retention prevents the cellular breakdown associated with less intense seasonal drought (Baccari et al., 2020). The higher GCC, indicating greater leaf greenness, in elevated CO_2 conditions suggests that lianas may be able to remain being photosynthetically active through periods where trees either limit or stop photosynthesis as a result of environmental stress (van der Sande et al., 2013; Baccari et al., 2020).

Lianas growing in elevated CO_2 conditions generally had greater leaf greenness values, during periods of reduced moisture availability. Lianas in elevated CO_2 conditions may therefore have a greater overall leaf condition, over those growing in ambient conditions, as greater GCC values can be indicative of better long term plant health (Nijland et al., 2014; Reid et al., 2016). Better overall leaf condition, i.e. less leaf damage, during droughts could be indicative of an ameliorating effect of CO_2 fertilisation, which may be indicative of lianas being able to facilitate greater productivity during seasonal droughts As lianas have been shown to perform better than trees during seasonal droughts in biomass accumulation in ambient conditions, (Bruy et al., 2017; Smith-Martin et al., 2019; van der Heijden et al., 2019), an ameliorating effect in elevated CO_2 conditions during the dry season could therefore facilitate a further increase liana biomass in seasonally dry forests. Liana proliferation increases competitive stress upon trees, through competition for nutrients, water resources and light (Wright et al., 2015a; Estrada-Villegas and Schnitzer, 2018) alongside increasing mechanical load on host trees, which can lead to mechanical damage and altered tree allometry (Rodríguez et al., 2021). This then impacts the ability of trees, and thus forests, to uptake and store atmospheric carbon (Schnitzer et al., 2014; van der Heijden et al., 2015), potentially tipping liana infested forests towards becoming a carbon source rather than a sink.

The use of the green chromatic coordinate (GCC) as a tool to monitor plant response to external stimuli has precedence in the literature (e.g. Collins et al., 2018), although prior studies have also included significant field monitoring of leaf and tree conditions (Brown et al., 2017). The majority of studies that propose the use of GCC have shown the robust links between GCC and plant phenology, specifically leaf deployment and senescence (Ide and Oguma, 2010; Klosterman et al., 2014; Liu et al., 2018). The leaf deployment of *E. tereticornis* follows increases in soil moisture, primarily driven by seasonal rainfall (Duursma et al., 2016), which matches our findings of changes in tree GCC driven by seasonal moisture availability for trees.

The seasonal timing of *P. straminea* leaf phenology, is currently unreported, from the imagery used in this study, there is no clear "leaf-off" period for the canopy of this liana. Constant leaf turn over, could therefore explain the higher GCC of lianas compared to trees, regardless of CO_2 regime, as new leaves typically have a higher GCC than older leaves (Sonnentag et al., 2012; Wu et al., 2018). Leaf flush in the liana *P. straminea* may therefore vary with CO_2 environment.

The security camera imagery from EucFACE, the data were subject to limitation from the camera operations. Depending on how poorly images overlapped, the projection (i.e. how spherical or warped an image is) would need to be manipulated, this changes how the pixels from the original data are interpolated to the new panorama image. As original pixels are resized for the panorama, these data were not sufficiently consistent to create an area-based analysis of foliage response to elevated CO_2, i.e. where there was canopy expansion or contraction. Despite this when the pixel values for colouration, the red, green, and blue channels, were checked against the original images and found to be stable enough for analysis using my index-based approach.

Using security type cameras can limit options for file output type (Brown et al., 2016), which can have further knock-on effects upon indices choice and use. The photographic data generated as part of the EucFACE project were limited to the JPEG file format, which importantly does not include records of pixel intensity. The lack of pixel intensity data precludes the use of certain indices such as HSI due to the images being 32bit versus the 64bit RAW standard, the data contained within the pixels is not substantial enough to calculate these indices (Sonnentag et al., 2012). Consumer grade cameras can present uncertainties as to what specific wavelengths are included within each of the red, green, and blue bands, white balance handling, and colour depth, however in examining an earlier camera from the same manufacturer as used in this study, Sonnentag et al. (2012) found these cameras "sufficient" for phenological or ecological research.

5.6 Conclusions.

In conclusion, lianas and trees differ in their optical response, as measured by GCC, to eCO_2 conditions. Lianas in elevated atmospheric CO_2 have particularly high comparative greenness in periods of low moisture availability, a result which correlates with the drought resilience of lianas found in other seasonal ecotypes. While further research into the leaf-level differences driving the difference in optical response is needed, we argue this is indicative of an ameliorating effect of CO_2 to short term moisture deficits. Amelioration of drought stress in an otherwise drought tolerant functional group of plants could lead to increasing liana prevalence in forests where seasonal moisture availability is limiting.

Chapter 6. Lianas and trees diverge in their spectral response to elevated CO_2 in a mature Australasian forest.

6.1 Abstract

Elevated CO_2 can affect the biochemical make up of plant leaves. As leaf chemistry is intrinsically linked to the spectral response of plants, hyperspectral analyses can be used to explore the response of leaves to changing environmental variables. Here, I use hyperspectral reflectance to assess the response of a liana and a tree species to elevated CO_2 in the Eucalyptus FACE (EucFACE) in Australia. My results indicate that liana and tree leaves differ in their response to elevated CO_2 concentrations. Both life forms showed the greatest response to elevated CO_2 in the visible spectrum and at the red edge (700-800 nm). However, the response to exposure to elevated CO_2 differed between the life forms. The reflectance of lianas increasing at green (500-600nm) wavelengths and decreases reflectance of blue (400-500nm) and red (600-700nm) wavelengths in elevated CO_2 conditions. Contrastingly, the reflectance of trees showed a decreased response at green wavelengths. Although liana and tree leaves were always spectrally different in their near infra-red (800-1200nm) reflectance, neither life form responded to elevated CO_2 in this area of the spectrum. Spectral indices also indicate contrasting responses between life forms with lianas showing increases in MCARI and NDVI scores, whereas NDVI for trees declined. These results suggest that the pigments responsible for colouration and photosynthesis differ between the two lifeforms. As such it appears that chlorophyll is increasing in lianas but not in trees, with increased atmospheric CO_2. As such it is likely that as lianas are already efficient in photosynthesising in ambient, and that to use elevated atmospheric CO_2 lianas are required to produce greater concentrations of chlorophyll. These metrics indicate a stress response to elevated CO_2 by trees, while the response of lianas indicates as an increase in vigour as CO_2 seems to have a fertilising effect. This evidence could therefore indicate that lianas will be more photosynthetically

active in a carbon rich atmosphere, in turn additional liana biomass is likely to increase competitive pressure on trees and negatively impact the forest carbon balance.

6.2 Introduction

The leaves of plants are the primary biological interface with atmosphere, as such many plant responses to elevated atmospheric CO_2, intrinsically link to leaf level responses to CO_2 (Norby et al., 1999). Responses of tree leaves to elevated CO_2 include photosynthetic enhancement (Eamus et al., 1995), decreased stomatal conductance (Medlyn et al., 2001; Gimeno et al., 2016), reduced foliar nitrogen (Kim et al., 2003; McGuire et al., 2003), decreased chlorophyll content and decreased photorespiration (Wujeska-Klause et al., 2019a, 2019b). Biochemical change at the leaf scale because of elevated atmospheric CO_2 concentrations could, therefore, impact on carbon uptake by terrestrial ecosystems (Norby et al., 1999; Wullschleger et al., 2015; Pan et al., 2022). As one of the largest terrestrial carbon sinks, forests and their associated responses to elevated atmospheric CO_2, have gained increasing interest in recent decades (Pan et al., 2013; Norby et al., 2016; Walker et al., 2021).

The chemical and physical properties of plants are associated with the spectral reflectance of their leaves, due to the interaction between light and the surface of leaves and their chemical compounds (Curran, 1989; Avalos et al., 1999; Carter and Knapp, 2001; Gamon et al., 2019). Key features of the spectral reflectance of plants are linked to the chemical and physiological make up of leaves, as shown in Table 6.1 (Curran, 1989; Barton, 2001; Ustin et al., 2009; Jiang et al., 2018). Studies have shown strong linkages between reflectance in the visible spectrum and photosynthetic tissues (Curran, 1989; Pacheco-Labrador et al., 2014; Wujeska-Klause et al., 2019a; Morley et al., 2020). The red edge and near-infra red (NIR) portions of the spectrum have been linked to leaf chemistry such as leaf moisture content and nitrogen content (Curran et al., 1991; Stone et al., 2001) as well as plant health (Dawson and Curran, 1998; Ustin et al., 2009). For example; stressed vegetation shows increased reflectance in the red wavelengths, with changes in both the position and intensity of reflectance at the red-edge, as foliar chemicals breakdown (Dawson and Curran; Curran et al., 1991; Ustin et al., 2009).

Table 6. 1. Chemical attributes and wavelengths. Bold wavelengths show highest correlation to foliar chemistry. Adapted from Curran 1989, Curran et al. 2001 and Boyd et al. 2006.

Chemical property	Associated wavelengths (nm)
Chlorophyll	418, 440, **460,** 478, **640,** 648, **660**
Lignin	1124, **1690**
Nitrogen	**1456**, 2172, 2352
Cellulose	**1780**, 1800, 1820
Water	1182, **1200**, 1216, 1920, 1926, **1940**
Protein	1008, **1510**, **2180**, 2352
Starch	978, 1208, **2100**

As foliar chemistry and leaf functions have been found to respond to elevated CO_2 (Smith et al., 2012; Drake et al., 2016; Wujeska-Klause et al., 2019b, 2019a), spectral reflectance provides an avenue into discovering how plants respond elevated CO_2 conditions. Early studies of the spectral response of plants to elevated CO_2 showed slight increases in reflectance in the visible spectra (400-700nm) of *Acer saccharum* in patterns associated with increasing chlorosis, i.e. increased red reflectance (Carter, 1993; Carter et al., 2000; Thomas, 2005). Similarly, Thomas (2005) found increased reflectance in three trees of the *Leguminosae* family of up to 23% in red wavelengths, between 600-650nm, which was accompanied by decreasing leaf chlorophyll concentrations, a symptom of chlorosis. Furthermore, work conducted in a temperate Australian forest found that leaf photosynthetic compounds of *Eucalyptus tereticornis* trees slightly decreased after exposure to elevated CO_2, corresponding to decrease in reflectance in the visible reflectance (Wujeska-Klause et al., 2019a). These decreases follow the same pattern of chlorosis, i.e. reduced chlorophyll and lowered green reflectance and increased red reflectance, hence why some studies have attributed spectral change to stress (Carter et al., 2000; Thomas, 2005; Oki et al., 2013). When photosynthesis is made more efficient by elevated CO_2, production and maintenance of photosynthetic compounds can be less

(Wujeska-Klause et al., 2019a), this could lower leaf nitrogen concentrations (Wujeska-Klause et al., 2019b) which could correspondingly increase reflectance in the infra-red (~1456nm).

Previous studies of how leaf reflectance is affected by elevated CO_2 conditions in forests have prioritised trees over other forest lifeforms (Carter et al., 2000; Thomas, 2005; Wujeska-Klause et al., 2019a). Lianas are a conspicuous component of forests worldwide. There is evidence that lianas are increasing in abundance and biomass in temperate and tropical forests (Phillips et al., 2005; Parthasarathy et al., 2014; Perring et al., 2020; Chandler et al., 2021b). Elevated atmospheric CO_2 concentrations may be one of the potential drivers of this liana proliferation (Schnitzer and Bongers, 2011). Little research has focussed on the leaf spectral or chemical response of lianas to elevated CO_2. Experimental evidence has shown that lianas positively respond to elevated CO_2 with studies showing stimulated growth, increased leaf biomass and increasing water use efficacy (Körner and Arnone, 1992; Granados and Körner, 2002; Hättenschwiler and Körner, 2003; Belote et al., 2004; Mohan et al., 2006; Marvin et al., 2015). Comparative evidence has shown that both liana and tree growth are stimulated, but there was no evidence of an enhanced effect of CO_2 on lianas when compared to trees (Marvin et al., 2015). The only study that assessed changes in the spectral response of trees and lianas found that trees and lianas were similar in their response to elevated CO_2 (400 pm compared to ambient) in visible parts of the spectrum (Oki et al., 2013). They found that reflectance response varied by intensity, between tree and liana species (Oki et al., 2013). This same study showed that when chlorophyll reflectance ratios were examined, all lianas and trees showed similar decreases in chlorophyll, concluding that this was aligned to a response to stress rather than a CO_2 fertilising effect (Oki et al., 2013).

Using solely the raw reflectance of plants to detect changes in physiology and biochemical composition can be complicated by reflectance crossover, i.e. where two, or more, properties of leaves contribute to reflectance. For example chlorophyll a and anthocyanin share similar reflectance properties around 600nm but not towards the red-edge and infra-red (Matson et al., 1994; Curran et al., 2001). Therefore vegetation indices have been developed to retrieve foliar information from hyperspectral data while reducing the influence of conflicting properties, through an indexing approach (Stone et al., 2001; Ustin et al., 2009; Cheng et al., 2012; Cherif et al., 2023). Vegetation indices are based on the contrast between wavelengths that are linked, or sensitive to a particular biochemical, and generally one or more insensitive wavelengths, thus decreasing the influence of other biochemicals (Main et al., 2011; Mielke et al., 2012). The derivation of chlorophyll content from hyperspectral returns has been extensively studied, with a multitude of indexes derived from reflectance e.g. Chlorophyll Near Infra-Red Ratio (Gitelson and Merzlyak, 1996), Modified Chlorophyll Absorption in the Reflectance Index (MCARI; Daughtry et al., 2000), Normalised Difference Vegetation Index (NDVI; Kriegler et al., 1969), Structure Insensitive Pigment Index (SIPI; Peñuelas and Filella, 1995). The MCARI index, when applied at the leaf scale, can be used as a method of estimating chlorophyll content from reflectance spectra and is more sensitive to leaf chlorophyll content than other intrinsic indices, i.e. indices with no external correction for soil or water (Daughtry et al., 2000; Xue and Su, 2017). The MCARI calculation only makes used of the visible and red-edge spectra, and consequently can be more widely utilised on a range of instruments including Near Infra-Red (NIR) sensitive cameras. Similarly, the NDVI has been closely related to chlorophyll and plant health at a canopy scale, and has been using in research focussing on the response of vegetation to elevated CO_2 conditions. The NDVI is routinely used as part of data analysis from satellite, unoccupied aerial system, and proximal sensor deployments (e.g. Carlson and Ripley, 1997; Hunt et al., 2010; Hmimina et al., 2013; LaRue et al., 2018). As we are interested in how lianas and trees differ in their response to elevated CO_2 conditions, and whether the biochemical properties of these lifeforms are affected, the MCARI and NDVI approaches allows for a comparable metric between this and other studies investigating biochemical change of leaves in elevated CO_2 conditions.

There are few experiments that that allow for testing of the effects of elevated CO_2 *in-situ*. The EucFACE facility in Australia is situated in a mature Eucalypt woodland with lianas reaching the forest canopy (Chapter 4), therefore offers a unique opportunity to study the effects of elevated CO_2 concentrations on lianas (*Parsonsia straminea*). Prior work at EucFACE has shown that over a 10-year period the proportion of trees that support lianas has increased, but that this increase was not driven by elevated CO_2 (Chapter 4). When examined with in-situ photographic analysis, it was found that, lianas responded to elevated CO_2 with increased greenness while trees were less responsive (Chapter 5). As Chapter 5 only considered the spectral response in the visible spectrum, using finer spectral resolution data that encompasses spectra into the infra-red may provide more detailed information to determine whether and how the species of liana and tree in this ecosystem 1) differ spectrally and 2) how lianas and trees differ in their spectral response to elevated CO_2 conditions. This chapter will also use two commonly used vegetation indices to examine whether physiological change has occurred in either trees or lianas as a response to elevated atmospheric CO_2. Furthermore we will examine leaf moisture and how changes in leaf moisture may relate to changes in spectra for both lifeforms in response to elevated CO_2 conditions.

6.3 Methods

6.3.1 Environmental conditions

Leaf sampling took place at EucFACE in May 2022. In the month prior to sampling there had been ~100mm of rainfall (Station 067105, BOM 2022) at EucFACE, soil moisture was high with much of the site waterlogged and abundant standing water within the rings. Daily temperatures during field sampling ranged from 16 to 27°C (Station 067105, BOM 2022).

6.3.2 Hyperspectral Sampling

Leaf sampling took place at EucFACE in February 2022. Leaves from all individual trees (species: *E. tereticornis*) and lianas within the six rings (species: *P. straminea*) were sampled opportunistically from various positions within the canopy using cranes to reach the canopy. During sample collection every effort was made to collect both young and mature leaves to test whether leaf age influences response to elevated CO_2. However, young liana leaves were scarce (eCO_2 n= 9, aCO_2 n =5) at the time of sampling. Due to this I opted to exclude them I show spectral curves of juvenile vs. mature leaves in supporting figure 6.1. Leaf samples were removed from branches using clippers and placed in a sample bag inside a chilled storage container. Leaf spectra were recorded using an Analytical Spectral Devices (ASD) Fieldspec Pro spectrometer using a leaf clip with integrated light source within 1-2 hours after collection. The ASD records spectral reflectance between 400-2400nm spectral range, at a spectral resolution of 3 nm at 700 nm and 10 nm at 1400/2100 nm. These spectra were then smoothed using a weighted mean moving average over a 5 nm sample. Wavelengths within 5nm of a sensor cross point over (1000nm, 1800nm) were excluded from analysis. In total, the spectral reflectance of 627 tree (386 in eCO2 and 241 in ambient) and 397 liana (98 in eCO2 and 299 in ambient) mature leaves were measured.

First derivative spectra were calculated per lifeform for each treatment. These allowed discrimination of where reflectance has shifted to longer or shorter wavelengths (Dawson and Curran; Kumar et al., 2010)(Supplementary figure 6.2). Since the first derivative of a curve gives its slope, the difference can illuminate where reflectance peaks have shifted in wavelength rather than solely intensity (Kumar et al., 2010). Second derivative spectra were also calculated and are shown in supplementary figure 6.3.

To determine whether these spectra show CO_2 effects on the leaf physiology of both trees and lianas, I test whether there is a difference in leaf moisture content (LMC) and assess whether the spectra have predicted the response of these data. Differences in LMC between trees and lianas are well reported in other forested ecotypes (Asner and Martin, 2014; Ewers et al., 2015; van der Sande et al., 2019). The liana and tree leaves used for spectral reflectance measurements were therefore weighed (wet weight) before leaves were oven dried at 75 °C for at least 48 hours after leaf weight reached a constant weight. The leaf moisture content for each leaf was determined by dividing the difference between wet and dry weight by the wet weight.

Leaf chemistry via a laboratory analysis was not possible at the time of leaf sampling. However, it should be possible (in theory) to estimate the effect of elevated CO_2 upon chlorophyll content of leaves and leaf health using the reflectance spectra. To do this, two intrinsic vegetation indices, the Normalised Difference Vegetation Index (NDVI; Kriegler et al., 1969) (Equation 1) and the Modified Chlorophyll Absorption in the Reflectance Index (MCARI; Daughtry et al., 2000) (Equation 2) can be used. Both of these indices have been shown to be predictors of change in chlorophyll content and plant health respectively (Daughtry et al., 2000; Kimura et al., 2004). These allow estimation of whether chlorophyll content or plant health in lianas and trees has changed due to exposure to elevated CO_2. Spectral indices were calculated for each recorded spectra and averaged across lifeform and treatment.

$$NDVI = (R_{800} + R_{680})/ (R_{800} - R_{680}) \qquad \textit{(Equation 1)}$$

Here, R_{800}, and R_{680} are the reflectance values at 800 and 680 nm.

$$MCARI= (R_{700} - R_{670})-0.2(R_{700} -R_{550})(R_{700} / R_{670}) \qquad \textit{(Equation 2)}$$

Here, R_{700}, R_{670}, and R_{550} are the reflectance values for 700, 670 and 550 nm.

6.3.3 Data analysis

To test whether the spectral response of lianas and trees differed between ambient and elevated CO_2 treatments, mean reflectance curves were calculated from the observed reflectance for both lifeforms per treatment. Difference in the mean spectral returns were calculated per lifeform and subsequently per treatment in the observed and first derivative spectra.

A bootstrapping methodology was followed to generate confidence intervals around these composite means, and assess whether there was a significant difference in the mean spectral response of the different life forms to elevated CO_2. For each lifeform and CO_2 treatment, the full spectral returns, i.e. the entire spectral curve, were iteratively resampled 5000 times at which point the bootstrapped and composite means were near indistinguishable. For each iteration, spectral differences between lifeforms and treatment were calculated to generate confidence intervals at the 97.5 and 2.5 percentiles. Differences between treatments and lifeforms were considered significant when confidence intervals did not intersect zero.

NDVI and MCARI spectral indices were created from the composite mean spectral returns. A two way ANOVA with post-hoc Tukey’s HSD tests were used to test whether the spectral indices, related to chlorophyll, and leaf moisture content differed between life forms and treatments. Interactions between lifeform and CO_2 treatment were included in the analyses. All data analysis were performed in the R programming environment (R Core Team 2023).

6.4 Results

6.4.1 Raw reflectance

6.4.1.1 Differences between lianas and trees

In ambient CO_2, trees were more reflective than lianas in the visible spectrum, especially in the blue (400-500nm) and red wavelengths (600-700nm) (Fig. 6.1a). Similarly, when exposed to elevated CO_2, trees were more reflective than lianas, although the difference between lianas and trees at the green peak (~550nm) was reduced (Fig.6.1b. Supplemental Fig. 6.1).

Liana leaves from the ambient treatment showed higher reflectance than trees across the red-edge (750nm) and the infra-red spectra (Fig. 6.1. Supplemental Fig. 6.1). Lianas exposed to elevated CO_2 were also more reflective than trees in the same regions as in ambient CO_2. (Fig. 6.1 and 6.2).

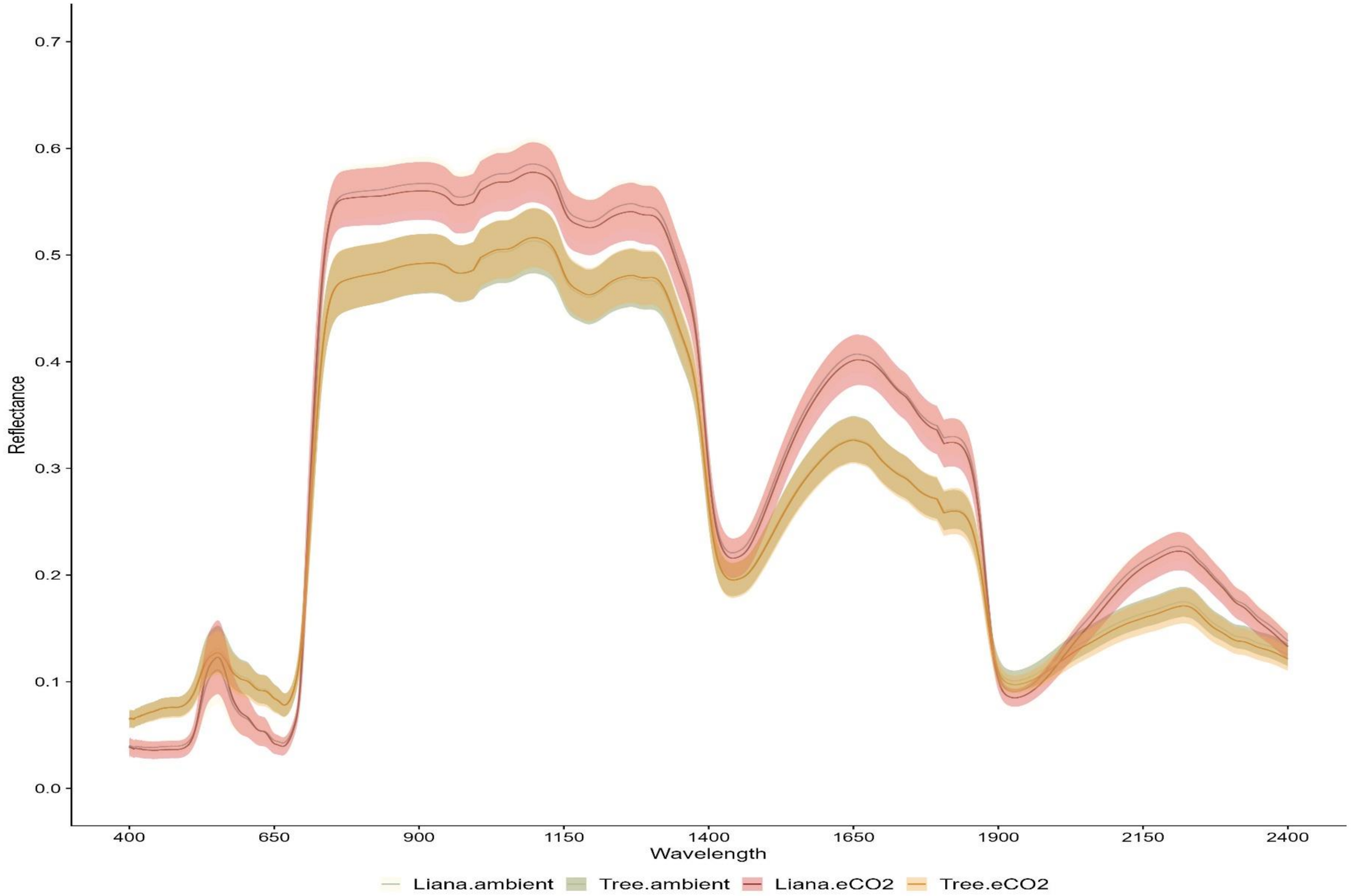

Figure 6. 1 Mean observed reflectance. Ribbons show 95CIs. Coloured by lifeforms, Lianas in ambient green line with yellow ribbon, Tree in ambient in grey green line and ribbon, lianas in eCO$_2$ redline with pink ribbon, Tree in eCO$_2$ orange line and ribbon.

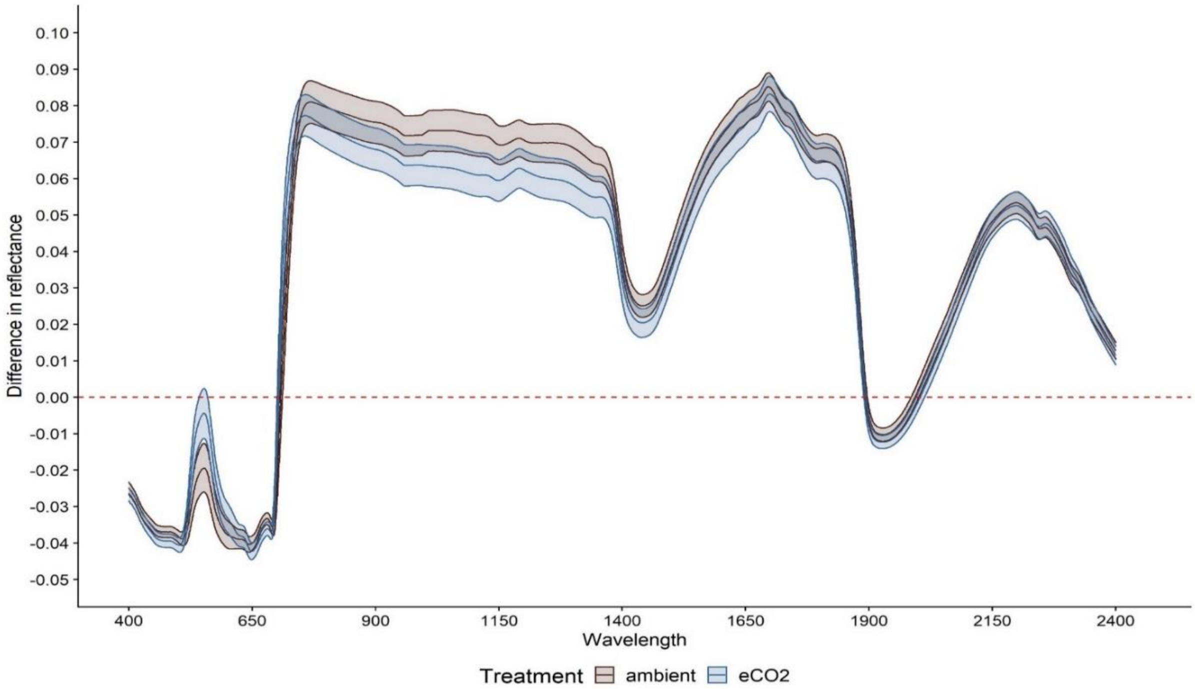

Figure 6. 2 Difference of raw reflectance between lianas and trees. Grey is difference in ambient, blue is eCO₂ with bootstrapped 95%CIs.

6.4.1.2 Liana responses to elevated CO₂

The reflectance of lianas increased around 550nm and 700nm in elevated CO₂ (Fig. 6.3a). Between 640-690nm, the red region, lianas in elevated CO₂ were less reflective than in ambient (Fig. 6.3a). Liana reflectance in elevated CO2 was lower than in ambient between 400-500nm, the blue spectral bands and in the infrared region between 900–1150nm, 1250-1350 nm, 1450-1500 nm, 1800-2200nm and 2350-2400nm (Bootstrap 95CIs) (Fig. 6.3a).

6.4.1.3 Tree responses to elevated CO₂

Trees showed less difference in raw reflectance than lianas between treatments and contrasted lianas in the pattern of spectral response to elevated CO₂ (Fig. 6.1). Trees in elevated CO₂ were less reflective in wavebands in 540-600nm, the green peak, and around 700nm, the red edge, than those growing in ambient conditions (Fig. 6.3a). Reflectance was higher in the 1370-90nm range for trees growing in elevated CO₂. I also show that in the 1900-2400nm range trees are more reflective in ambient than in elevated CO_2 (Fig. 6.3a).

6.4.1.4 Change to the difference between lianas and trees.

The difference between lianas and trees is altered by CO_2 treatment between 465-500, 520-585, 660-735, 950-1410 and 1880-1895nm inclusively (Fig. 6.3b highlighted in orange), which indicate differences in blue reflectance, green reflectance, red reflectance, red edge and near infra-red respectively. The greatest change in the difference between trees and lianas was found at the green peak and at the red edge areas of the spectrum (Fig. 6.3b), where lianas in CO_2 had an increase in reflectance.

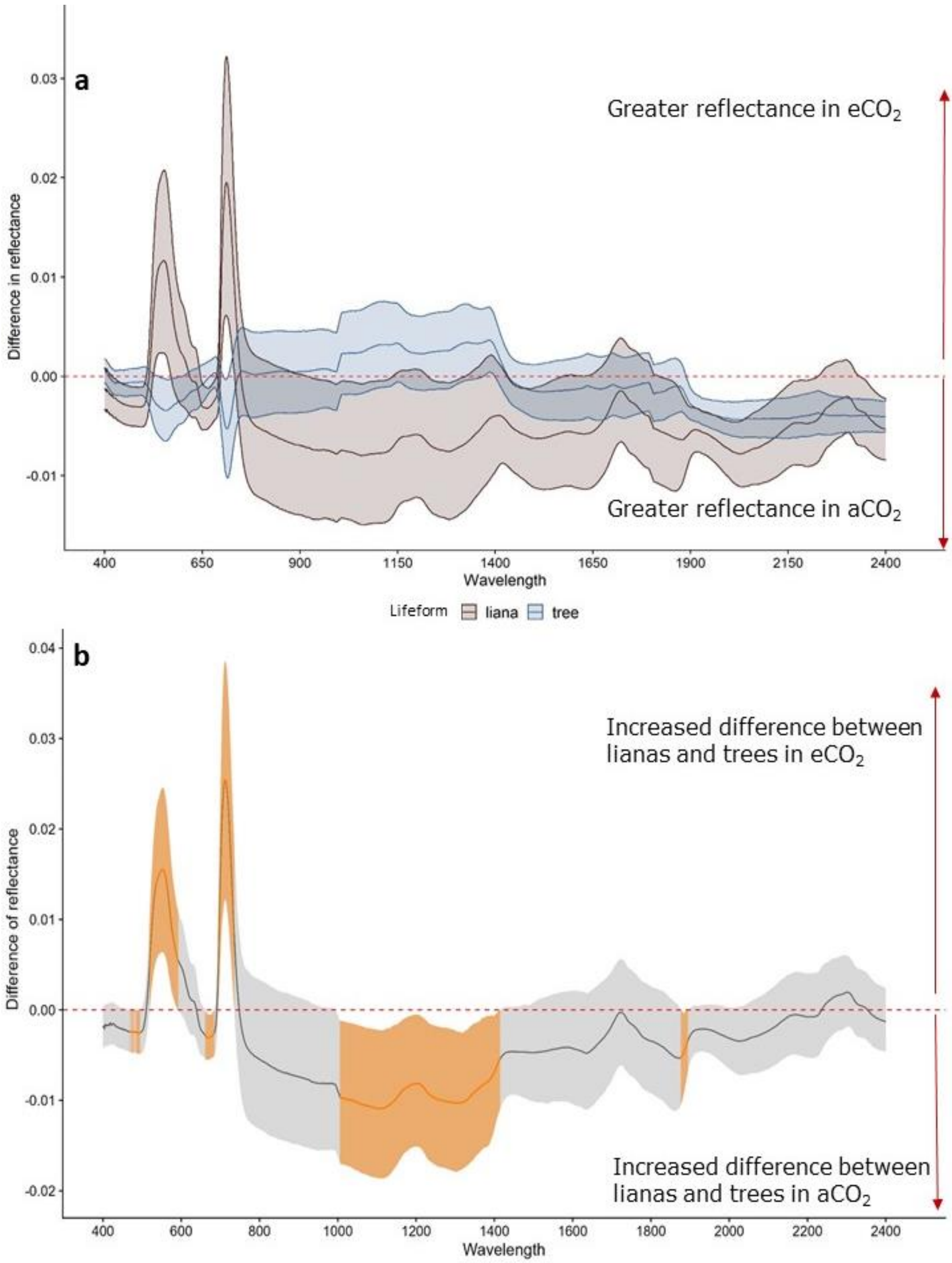

Figure 6. 3 Panel a. Difference of reflectance between treatments. Coloured by lifeform, lianas in grey, trees blue. Panel b. Difference of differences between lifeforms. Calculated as difference between lifeforms in eCO_2 *– between lifeforms in ambient* CO_2*. Dashed red line indicates zero difference. Differences are only considered significant where 95%CIs do not intersect zero highlighted in orange. Differences between trees and lianas follow similar patterns in both treatments except for the green peak, red edge and between 1000 and 1400nm.*

6.4.2 Spectral Derivatives

The difference between lianas and trees at the first derivative was greatest between 500 and 700nm, the green peak and red edge in both treatments (Fig 6.4), with some slight variations across the near and shortwave infra-red (Fig. 6.5b. Significant differences highlighted in orange).

Liana first derivative response to elevated CO_2 was primarily at the green peak of the spectrum and the red edge this was consistent with change found in the raw spectra (Fig. 6.5a). Between treatments, the slope of the red-edge shifts to shorter wavelengths, "blue shift," the maximal point of the red-edge shifts by ~4nm indicating that the red edge of lianas has shifted to a shorter wavelength (Fig. 6.5a). In trees, the difference in first derivative showed that the red edge reflectance of trees had shifted to longer wavelengths by ~4nm (Fig. 6.5a).

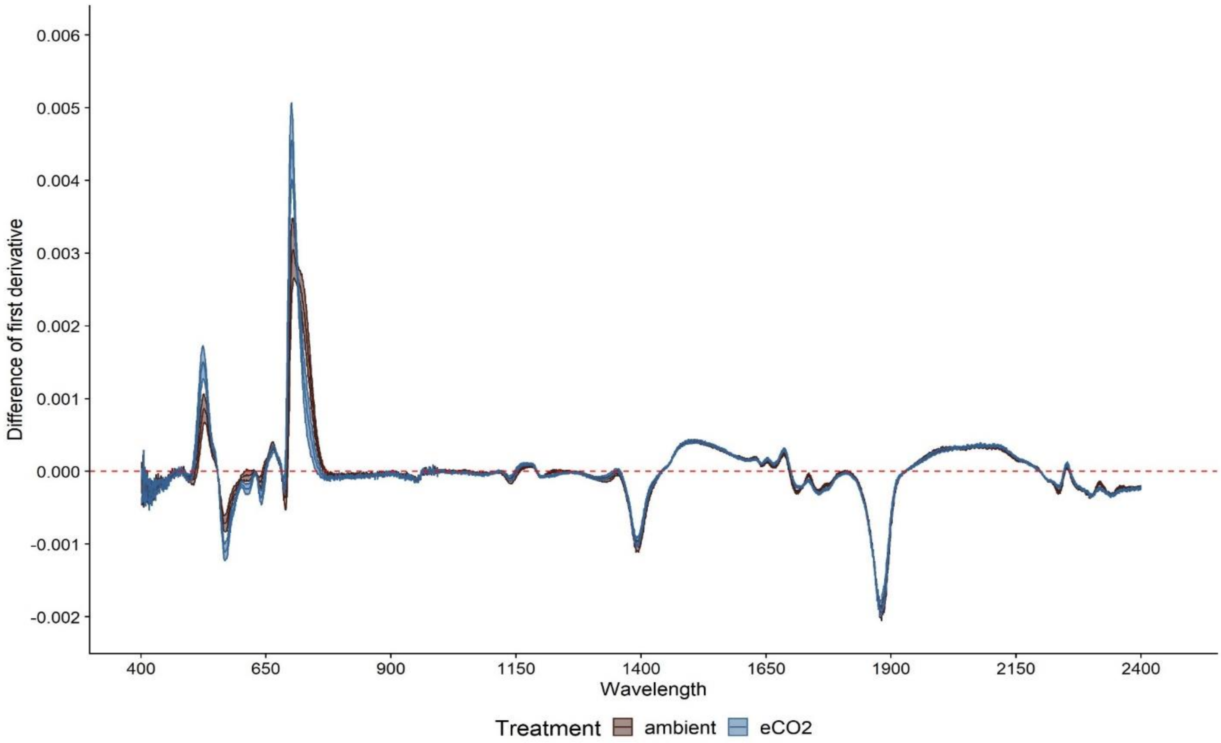

Figure 6. 4 Difference of first derivative spectra between lianas and trees. Grey is difference in ambient, blue is eCO_2 with bootstrapped 95%CIs.

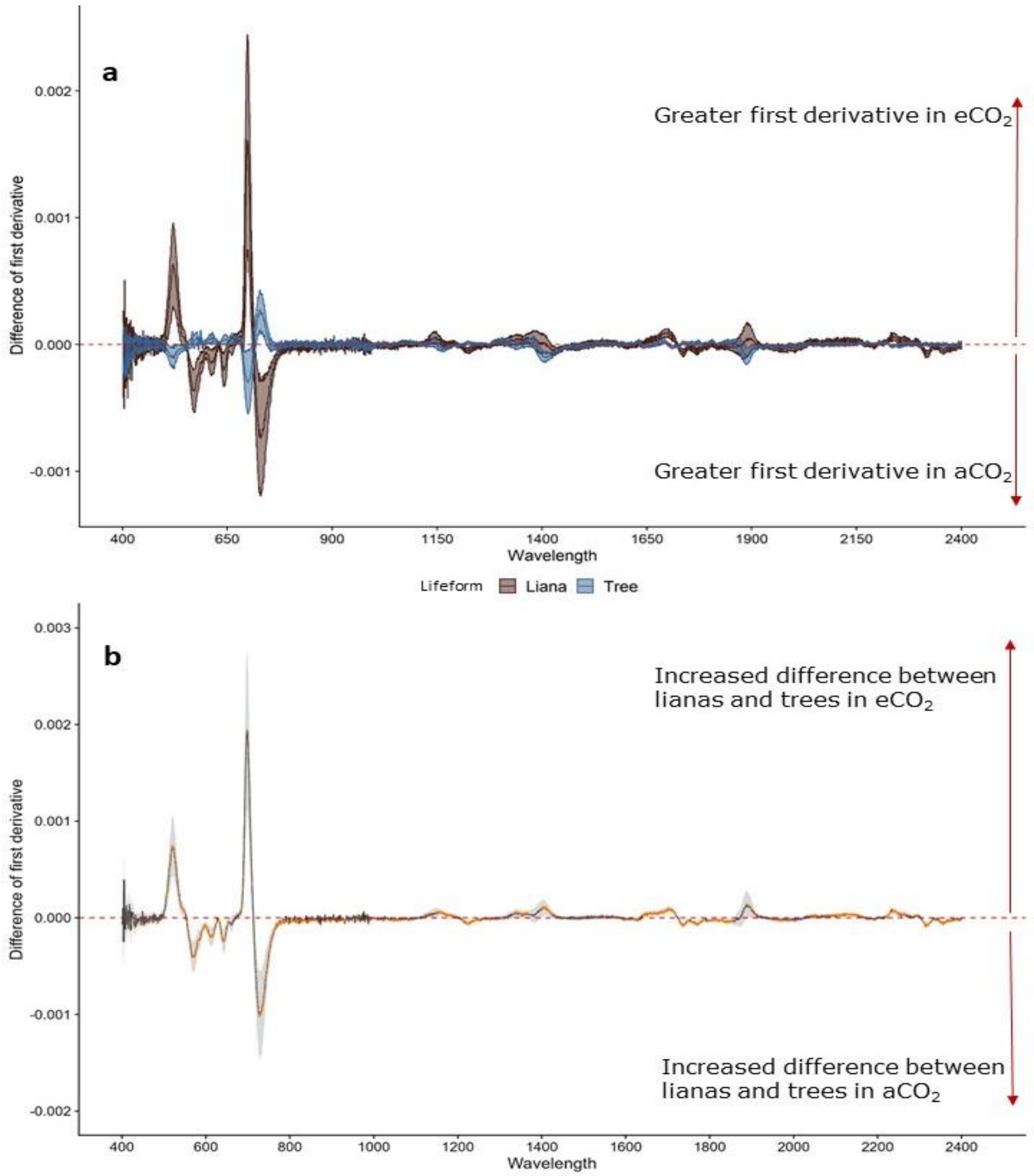

Figure 6. 5 Panel a. Difference of First derivative spectra between treatments. Separated by lifeform, lianas in blue, trees grey. Positive values represent greater derivative values in elevated CO_2, negative represent derivative values in ambient conditions. Panel b. Difference of differences between lifeforms. Calculated as difference between lifeforms in eCO_2 – ambient difference. Dashed red line indicates zero difference. Differences are only considered significant where 95%CIs do not intersect zero, highlighted in orange.

6.4.3 Leaf Moisture

Lianas and trees differed in moisture content regardless of treatment, with lianas having greater leaf moisture content overall which correlates with the deeper absorbance features for water in the infra-red (~1200nm and ~1800nm) (Fig. 6.6). The influence of elevated

CO_2 on leaf moisture content is more pronounced for lianas, for whom leaf moisture increases, than for trees, which are slightly negatively affected but not significantly so (Fig. 6.6).

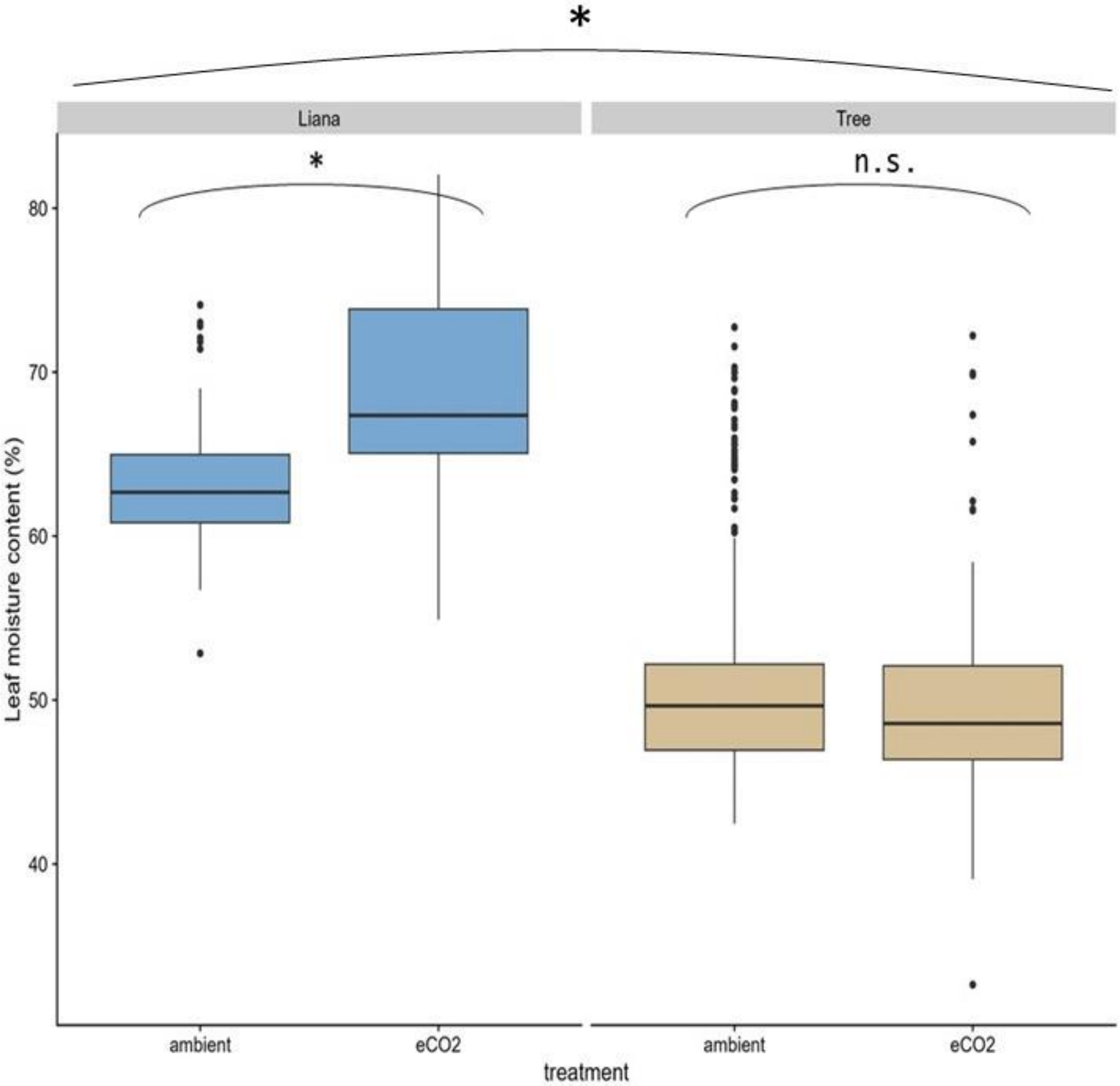

*Figure 6. 6 Leaf moisture content of trees and lianas separated by CO_2 treatment. Leaf moisture content significantly different between trees (yellow) and lianas (blue) in both treatments (ANOVA F= 675.66, p < .001, 95% CI = 0.50, DF = 1.00). Significant difference in treatment means from Tukey's HSD test (p<0.05) shown by *, n.s. = no significant difference between treatment means.*

6.4.4 Spectral Indices

MCARI values, which provide a unit-less estimation of chlorophyll, show that chlorophyll concentration is greater in lianas than trees in both treatments (Fig. 6.7). MCARI values in the elevated CO_2 treatment increased in lianas, whereas the MCARI value of trees in elevated CO_2 was unresponsive, the ANOVA interaction effect between treatment and lifeform, was significant (ANOVA F= 54.3547, DF=1 p < .05).

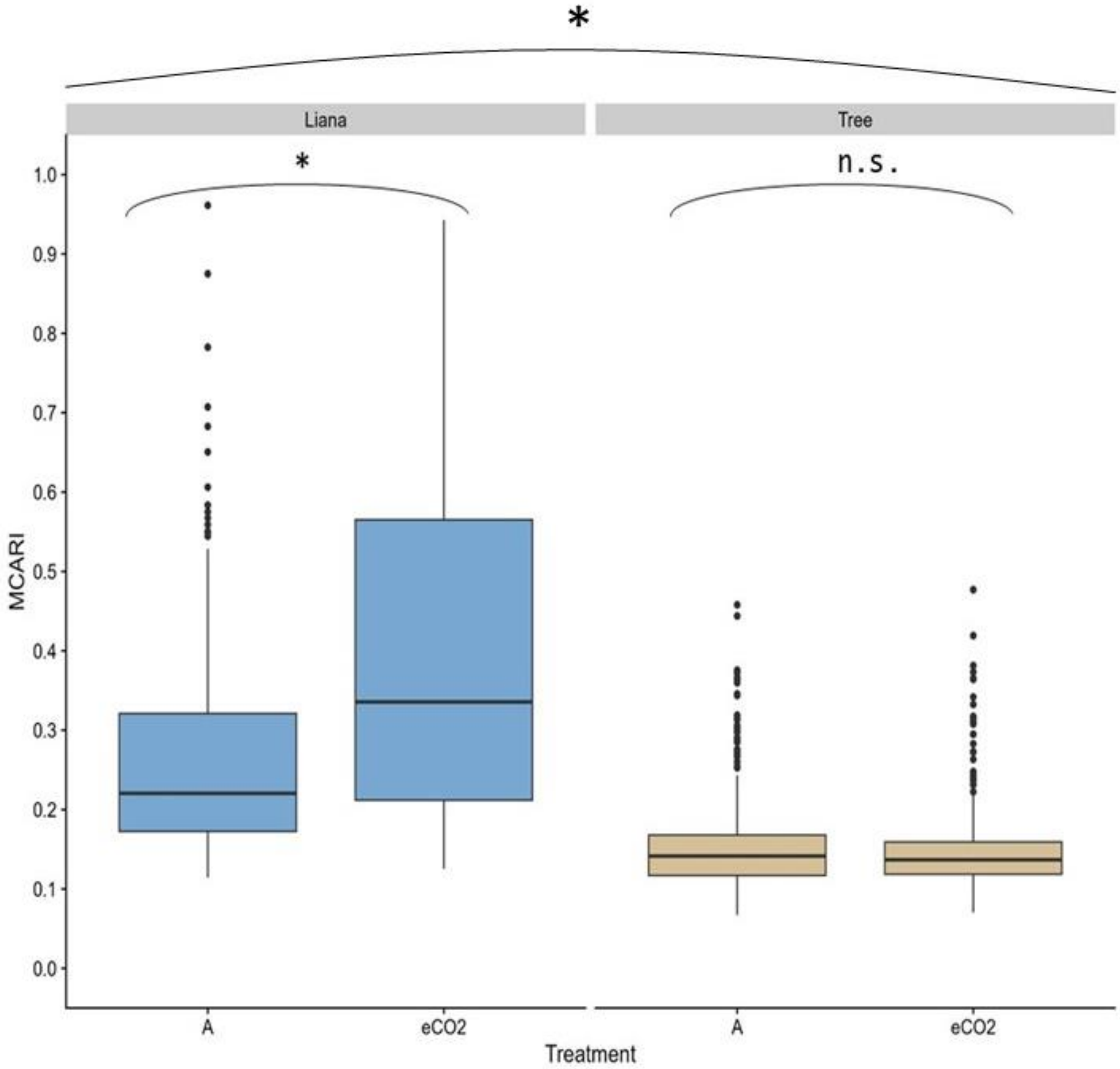

*Figure 6. 7 MCARI of trees and lianas. Lianas in blue have significantly higher MCARI than trees, shown in yellow, in both treatments (ANOVA F= 534.2944, DF=1 p < .05). Significant difference in treatment means from Tukey's HSD test shown by *, n.s. = no significant difference between treatment means.*

The NDVI of liana and tree leaves differed, with liana leaves having higher NDVI values then trees regardless of treatment (Fig. 6.8). Elevated CO_2 has a positive effect on liana NDVI, whereas the NDVI for trees was lower although neither showed a significant change in NDVI.

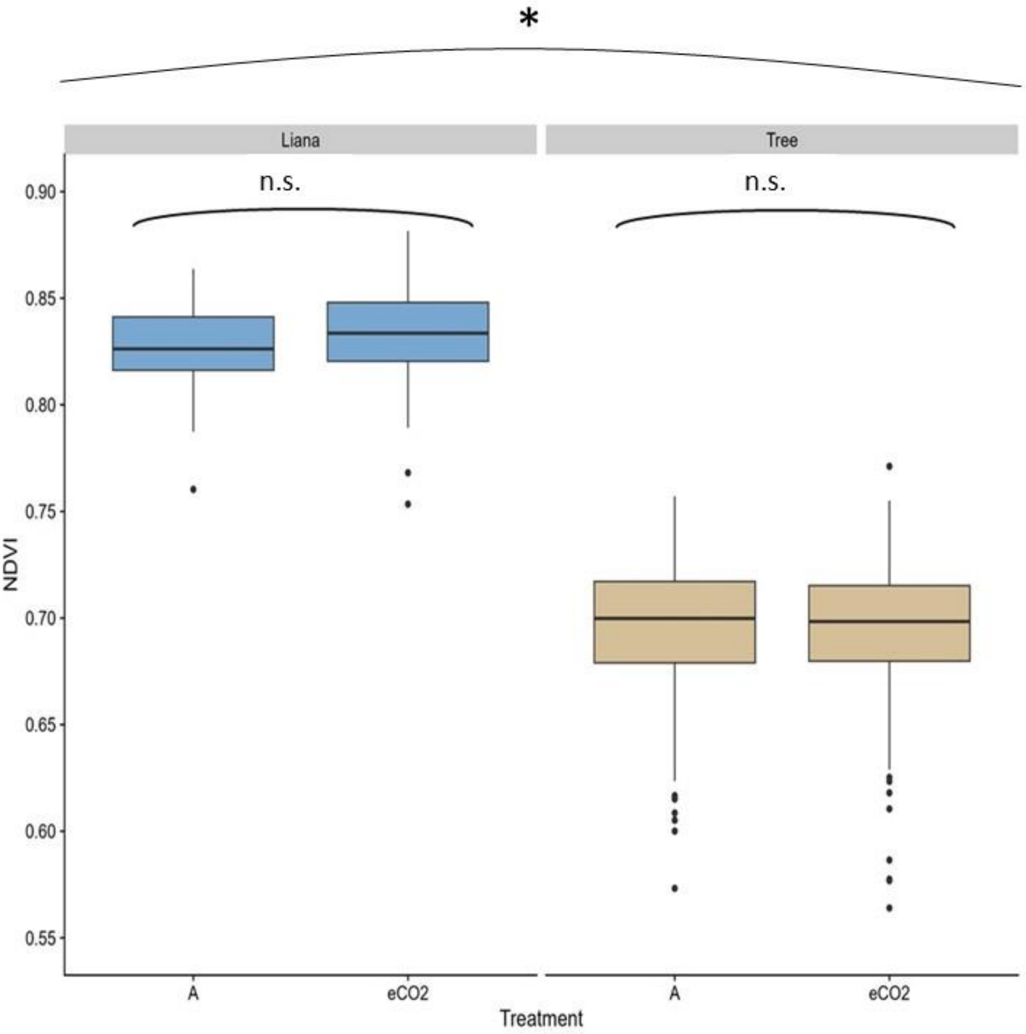

*Figure 6. 8 NDVI of trees and lianas. Lianas in blue significantly different to trees in yellow (ANOVA F= 4043.188, DF = 1, p<0.05). Significant difference in treatment means from Tukey's HSD test shown by *, n.s. = no significant difference between treatment means.*

6.5 Discussion

Here, I present evidence that co-occurring lianas and trees differ in the spectral response to elevated CO_2 conditions, particularly in the visible spectrum (500-700nm) and the red edge (700-800nm) (Fig. 6.1 and 6.2). However, the spectral reflectance of both lianas and trees appears unresponsive to elevated CO_2 at in the NIR and SWIR region of the spectral response (Fig. 6.1). Exposure to elevated CO_2 increased leaf moisture content and values for the MCARI vegetation index in liana leaves, but not for trees. As MCARI is an indicator of chlorophyll content, these results suggest that increasing atmospheric CO_2 concentrations leads to increases in chlorophyll content, and therefore potentially productivity (ref), for lianas. There were differences in NDVI between life forms, but the NDVI for neither life form changes as a response to elevated CO_2 conditions.

Within lifeform spectral differences

The differences in spectral response to elevated CO_2 conditions both for lianas and trees were limited primarily to the visible (500-700nm) and red edge (700-800nm) regions of the spectrum (Fig. 6.3a), although the difference was not consistently unidirectional, i.e., either higher or lower reflectance across the spectrum. *P. straminea* showed greater response to elevated CO_2, with a decrease in reflectance in blue (400-500nm) and red (600-700) wavelengths, while simultaneously increasing in reflectance in green (500-600nm) (Fig. 6.3a). While reflectance at longer wavelengths (>900nm) was relatively unaffected by elevated CO_2 there were differences in the reflectance around 1250nm, 1400nm and 1800nm with lianas in elevated CO_2 being less reflective around these wavelengths (Fig. 6.3a). The differences found between lianas in elevated and ambient CO_2 are found at or within 10nm of wavelengths found to be related to; chlorophyll (460nm, 660nm), starch (1208nm), water (1200nm), and water/cellulose (1800nm) (Curran, 1989; Boyd et al., 2006). Thus, it is likely that there are biochemical changes occurring but it is not possible to say by how much from these spectral curves alone. Conversely, there was little difference of in the spectral response of *E. tereticornis* to eCO_2, with changes to the spectral reflectance and derivatives being both lower and often in a different direction as that of lianas (Fig. 6.3a/5a). In elevated CO_2, lianas and trees were most noticeably different in their response at the red edge (Fig. 6.3b). The lianas show signs of a "blue shift," i.e., a shift to shorter wavelengths, while the trees showed an opposing shift to longer wavelengths.

An earlier study at EucFACE found a decrease in the spectral reflectance of tree foliage in wavelengths between 400-700nm when exposed to elevated CO_2 concentrations, while my study only shows a decrease of reflectance at the green peak (650nm) (Wujeska-Klause et al., 2019a). The earlier study related the observed decrease in reflectance to relate to lower chlorophyll *a* concentrations for tree leaves exposed to elevated CO_2 (Wujeska-Klause et al., 2019a). My study however did not detect a decrease in chlorophyll in trees in elevated CO_2 using the MCARI index, although the MCARI index does not distinguish between chlorophyll *a* or *b.* A key constraint of using the MCARI index is also that it is unit less, therefore my results are indicative of directional change rather than a direct biochemical measure.

Leaf moisture contents

Leaf moisture content differed significantly between trees and lianas regardless of CO_2 treatment (Fig. 6.6). There was no difference in leaf moisture content of trees between the CO_2 treatments. Liana leaf moisture content was greater in the elevated CO_2 treatment, and correspondingly there was a greater different in reflectance at the water features (1200 and 1800nm) (Fig. 6.3a), with less reflectance in these wavelengths for liana leaves growing in eCO_2 conditions.

Greater moisture content of liana leaves has been suggested to be a product of the relative efficiency of liana vascular systems (Schnitzer et al., 2005; Sánchez-Azofeifa et al., 2009; Gallagher and Leishman, 2012). Furthermore, elevated CO_2 has been shown to facilitate tighter stomatal control, thus losing less water via stomatal openings (Clark et al., 1999; Wullschleger et al., 2002; Pathare et al., 2017), which could explain the increased leaf water content of lianas in elevated CO_2 conditions.

Contrasts with prior spectral studies in eCO_2

For trees, my findings broadly concur with those found in an earlier comparative study in the dry tropics. Oki et al. (2013) also found the spectral reflectance of trees decreased between 500-700nm when exposed to ~800ppm CO_2. However, the findings of Oki et al. (2013) with respect to lianas contrast with the findings of this chapter. They found that the spectral response of lianas to eCO_2 was not as pronounced as that for trees, with reflectance in wavelengths between 500-700nm remaining broadly unchanged (Oki et al 2013). In contrast, my results show that liana reflectance intensity changes across the visible spectra. Furthermore, Oki et al (2013) showed that the spectral response of lianas increased in the infra-red at 800 nm and that the NDVI of lianas leaves decreased in eCO_2.

However, the results of Oki et al. (2013) contradict some of the evidence at EucFACE, where the spectral response of liana leaves at 800nm decreased in eCO_2 and their NDVI increased slightly. Similarly our results contrast the recognised body of evidence of how other woody plants respond to elevated CO_2. It has been shown in multiple studies that woody plants reduced chlorophyll concentrations in response to elevated CO_2 (Carter et al., 2000; Galvíncio et al., 2011; Ellsworth et al., 2017b; Wujeska-Klause et al., 2019a). Simultaneously it has been shown that photosynthesis is stimulated (Gimeno et al., 2016; Pathare et al., 2017; Wujeska-Klause et al., 2019a), thus it is concluded that photosynthesis is more efficient in elevated CO_2 (Norby et al., 1999; Wujeska-Klause et al., 2019a; Pan et al., 2022).

Therefore, it is surprising then that these lianas appear to be increasing in chlorophyll concentration. Although, lianas in elevated CO_2 have been shown to photosynthesize at higher rates than those in ambient treatments, (Laugier-Kitchener et al., 2022). It may be though that lianas were already photosynthesising efficiently in ambient conditions, as it has been shown that lianas are more efficient in water use, exert higher stomatal control and greater CO_2 assimilation per unit mass than co-occurring trees (Cai et al., 2009; Laugier-Kitchener et al., 2022), which are all key controls of efficient photosynthesis

(Smith and Keenan, 2020). If lianas are already at a peak photosynthetic efficiency in an ambient CO_2 environment, then increasing chlorophyll concentrations would, at least in theory, be a likely explanation as to how lianas continued to increase photosynthesis in elevated CO_2 conditions, although further work is needed to test this.

Implications for lianas in elevated atmospheric CO_2

Increased photosynthesis due to elevated atmospheric CO_2 could lead to increases in liana growth through enhanced carbohydrate production (Rowe and Speck, 2005; Wu et al., 2019). As lianas compete strongly with their host trees (Ingwell et al., 2010; Tobin et al., 2012; Wright et al., 2015a), the potential for increased growth of lianas may come at the expense of trees. Lianas negatively influence their host trees, increasing host mortality and negatively impacting tree allometry (Phillips et al., 2005; Kainer et al., 2006; García León et al., 2018; Peters et al., 2023; Rodríguez et al., 2021). Lianas are thus disproportionately able to decrease carbon uptake and storage in forests (Schnitzer et al., 2014; Brienen et al., 2015; van der Heijden et al., 2015), and the uptake of carbon by lianas lags far behind that of trees and does not replace that which is displaced by the competitive effects of lianas (van der Heijden et al., 2013, 2015). Thus, if elevated atmospheric CO_2 drives increased liana growth this may spell an increase in the severity of liana occupations. This in turn would have potentially severe consequences for trees hosting lianas and thus the carbon capture potential of our already embattled forests.

Despite clear spectral responses to elevated CO_2 conditions, the lianas at EucFACE have so far shown no eCO_2 driven increases in growth nor are their photosynthetic rates higher than those of trees under elevated CO_2 conditions (Laugier-Kitchener et al., 2022). A lack of a clear growth response of *Parsonsia straminea* is consistent with the tree focused research stemming from the EucFACE site. There are limited effects of elevated atmospheric CO_2 on the productivity or growth of the *Eucalyptus tereticornis* trees, which was attributed primarily to the phosphorous limitation of the site (Ellsworth et al., 2015, 2017a; Duursma et al., 2016). It is therefore possible that liana growth at EucFACE is similarly constrained.

This does not however mean that all lianas respond to elevated CO_2 in the same way. As discussed earlier, our results for the single liana species *Parsonsia straminea* differs from the responses of the three lianas tested by Oki et al. (2013). Liana species are concurrently present with trees in many different plant families. The response to elevated CO_2 conditions may vary more strongly with genera or family rather than by growth form, i.e. liana or tree. As the atmospheric CO_2 concentrations continue to rise, discerning the diverging responses of forest lifeforms becomes more valuable to both ecology and to forest management practitioners to predict future forest productivity. Knowledge of how the response of lianas and trees differ allows us to broaden our knowledge of how our forest resources will respond into future years and would be especially valuable in those areas where lianas have been reportedly increasing, such as the Neotropics. Key amongst this would be understanding how chemical changes, such as the indicated change in chlorophyll shown here, could drive changes in forest community. As this study focuses on a single liana and tree species it may not be fully indicative of each lifeform, as prior studies have shown contrasting spectral response of lianas to elevated CO_2 conditions (Oki et al., 2013).

Other potential influences on the spectral response of lianas and trees

The change to spectral response shown in this chapter may not only be related to chlorophyll. Spectral reflectance in the visible light portion of the spectrum, where the majority of the spectral differences reported here occurred, is influenced by several key biophysical properties (Curran, 1989; Curran et al., 2001; Pacheco-Labrador et al., 2014). Pigments such as xanthophyll and anthocyanin play a role in the attenuation and reflectance of light from plant foliage (Stone et al., 2001; Sims and Gamon, 2002; Wujeska-Klause et al., 2019a). Production of anthocyanin is linked to photo-inhibition in trees, protecting sun saturated trees from damage, but is also released in leaves that are suffering from other stressors (Chalker-Scott, 1999; Stone et al., 2001; Hughes et al., 2007). In *Eucalyptus* sp. trees, anthocyanin, which has an attenuating effect on visible light, is increased in elevated CO_2 (Wujeska-Klause et al., 2019a) thus affecting the reflectance as anthocyanin and chlorophyll both absorb and reflect light in very similar wavelengths. Increases in anthocyanin, or rather the spectral signatures associated with the increase, could therefore be responsible for why the spectral response of trees, both in this study and in others (e.g. Galvíncio et al., 2011b; Oki et al., 2013; Wujeska-Klause et al., 2019a) is similar to that of stressed vegetation (Carter, 1993; Stone et al., 2001; Smith et al., 2005).

Soil water inundation may have also played a role in the reflectance of both the lianas and trees in this study across both control and elevated CO_2 conditions. Site conditions were described as flooded during field sampling, which while both lifeforms are capable of tolerating moderate inundation (Marcar, 1993; Tozer et al., 2010; Grieger et al., 2019), soil water salinity can stress trees, supressing growth and canopy health (Marcar, 1993; Nasim et al., 2009; Grieger et al., 2019). Soil inundation, can negatively influence transpiration, especially in anoxic conditions i.e. where soil water oxygen content is depleted (Akeroyd et al., 1998), and could therefore have a knock on effect upon the water balance of foliage and thus the reflectance. As both treatments were similarly inundated, further work would be needed in contrasting soil moisture conditions for both treatments, to elucidate whether the reflectance curves of both lifeforms showed an influence of soil inundation.

Limitations

Spectral reflectance was only sampled once during a period when moisture availability was particularly high and soils were waterlogged. During this period liana greenness was particularly high in both treatments (Chapter 5). Further sampling, especially in periods where liana and tree greenness are more similar, e.g. during periods of seasonal or prolonged drought, could further elucidate differences in liana and tree reflectance and how responses to elevated CO_2 conditions may change in relation to moisture and seasonal change.

The patterns in spectral reflectance and any changes in chemical properties within the leaves were not corroborated using leaf chemical analyses (*sensu* Boyd et al., 2006). As some NIR and SWIR regions of the spectral response have been specifically tied to chemical composition of the leaves, such as leaf nitrogen concentrations, which differ between trees and lianas (Asner et al., 2009, 2015; Asner and Martin, 2012). In this study, liana and trees differ in their reflectance in nitrogen and protein related features in both treatment. It could be then that leaf nitrogen content changes equally for both lifeforms in elevated CO_2 conditions, however without suitable lab analysis it is unclear whether this is an increase or decrease in nitrogen.

6.6 Chapter conclusions

I have presented the spectral response of an Australasian liana and tree species, *Parsonsia straminea* and *Eucalyptus tereticornis* respectively, to elevated CO_2 conditions. I have found that change in spectral response is primarily limited to the visible and red-edge spectra, while differences between trees and lianas are most consistent between treatments in the near to shortwave infra-red spectra. Lianas had a higher spectral response in the green wave lengths and decreased reflectance in the blue and red wavelengths when exposed to elevated CO_2. By contrasts, the spectral reflectance of trees was lower in the green and increased in both the blue and red wavebands. These responses may be related to an increase in photosynthetic compounds in the liana, but also potentially a decrease in chlorophyll content in tree leaves because of elevated CO_2 conditions. I conclude then that these results indicate *Parsonsia straminea* may benefit from rising atmospheric CO_2, however further research is needed to elucidate the magnitude of these indicated changes in biochemistry.

Chapter 7. Synthesis of experimental chapters

Rising atmospheric CO_2 can cause increase in growth of woody plants (Körner and Arnone, 1992; Mohan et al., 2006); increase in water use efficiency (Avila et al., 2020; Venter et al., 2022), and decrease in photorespiration (Wujeska-Klause et al., 2019b; Avila et al., 2020). It has been hypothesised that elevated CO_2 is a key driver in the proliferation of lianas (Schnitzer and Bongers, 2011). As atmospheric CO_2 is predicted to rise further in the next century (Friedlingstein et al., 2022), could lead to increased liana proliferation and biomass across the globes forests. As lianas place intense competitive pressure on their hosts (Paul and Yavitt, 2011; Wright et al., 2015a; Tymen et al., 2016; Reis et al., 2020), increased liana pressures would further negatively influence the productivity of forests in high CO_2 scenarios (van der Heijden et al., 2013, 2015). Increased liana pressure could then have the potential to drive forests from carbon sink to carbon source further exacerbating the current and future climate crisis. Thus understanding the drivers of liana proliferation is imperative for forecasting how forests will develop in higher CO_2 environments. However there remains limited opportunity to explore this in the field. My thesis therefore used the only currently operational Free Air Carbon Enrichment (FACE) experiment (EucFACE) that has a resident population of tree canopy reaching lianas. As the EucFACE site had been in operation for almost a decade at the outset of my study, I leveraged novel remote sensing techniques to retrospectively explore how this liana had developed and responds to elevated CO_2.

My thesis aimed: a) to determine the effects of elevated CO_2 on the locally abundant liana *Parsonsia straminea*, and b) assess whether the response of these lianas contrast with *Eucalyptus tereticornis* trees in an Australian temperate sub-tropical forest. Within this thesis I have used a remote sensing-based methodology to further our understanding of how rising levels of atmospheric CO_2 affects the colonisation and growth (chapter 3); canopy spectral response (chapter 4) and leaf spectral response (chapter 5) of an Australian liana, *Parsonsia straminea* and *Eucalyptus tereticornis.*

7.1 Chapter summaries

7.1.1 Chapter 4

It has been hypothesised that there will be an increase in trees infested by lianas and increased growth of lianas in elevated CO_2 (Schnitzer and Bongers, 2011); however this is still untested in the field. My first chapter focuses on quantifying the proliferation of lianas within the forest community present at EucFACE and whether any changes in liana abundance on trees was driven by elevated CO_2 levels. At the start of the experiment, presence of lianas on trees was relatively low and lianas were not present in the canopy. Liana surveys, such as liana stem counts, diameter and liana load carried by the trees, were therefore not included in the standard measurement protocols that were implemented from the start of the experiment. However, anecdotal observations suggested that liana abundance was increasing across the experimental set up.

As field-based data were not available, an alternative method was needed to assess whether liana abundance was changing over time and whether this change was driven by elevated CO_2 concentrations. Terrestrial laser scanning (TLS) data was collected consistently in 2–3 year intervals throughout the experiment. TLS scanning has previously been used to monitor large diameter lianas in forests, calculating volumetric estimates and liana impacts on forest vertical strata (Krishna Moorthy et al., 2018, 2020). TLS is primarily used to create non-destructive volumetric measurements of woodlands (Calders et al., 2015; Newnham et al., 2015). As TLS produces a 3-D representation of the forest structure, it is possible to virtually census liana load on the trunk of the trees through time. TLS data has therefore been used to assess whether changes in liana load are driven by elevated CO_2 conditions. This chapter focusses on two main questions: whether CO_2 fertilization i) changes the proportion of trees that supported lianas, and ii) alters the vertical progression of the lianas on tree stems over time.

I show that liana infestation of trees at EucFACE has significantly increased from 2012 to 2022 across both ambient and elevated CO_2 treatments. However, there was no difference in increases the proportion of trees that carried lianas between treatments. Instead, the increase the proportion of trees carrying lianas in both treatments seems to correlate with periods where EucFACE was subjected to disturbance from a) site establishment (2012), b) defoliator attack on trees (2014/2015), and c) severe water logging post drought (2020-2022).

Despite not being able to use this data to measure liana stem diameter or biomass, it was possible to identify vegetative features, most commonly leaf and stem tangles, of lianas on the tree trunk. This allowed calculation of liana attained height, which is the distance from the ground to the last place on the tree trunk where lianas were recognisable in the TLS data. I show that lianas in both treatments are increasing in height upon the stems of trees and that the change in height is not related to the CO_2 regime. The vertical progression of lianas is an important part of how lianas interact with their hosts, as competition for light between trees and lianas is at its highest intensity when lianas are prevalent within the tree/forest canopy. An acceleration of lianas reaching the canopy could reduce the time between liana understory establishment and liana canopy dominance, thus decreasing the time in which trees might respond to increased liana load. However, I show here that the vertical progression of lianas does not appear to be increasing in elevated CO_2 conditions. My results indicate that liana vertical progression, and likely growth, may not constrained by atmospheric CO_2, but is likely constrained by other variables, e.g. nutrient limitation as the EucFACE site is Phosphorus limited.

While these lianas were increasing in numbers in the EucFACE woodland, the increase has not been as a response to elevated CO_2. If this trend is indicative of a global scale response of lianas to increasing CO_2, we may be observing a scenario where the response of lianas to elevated CO_2 is disconnected with liana load or prevalence.

7.1.2 Chapter 5

In this chapter, I use distance proxy data, captured by security cameras initially installed to monitor the permanent structures within the experimental site. These cameras afford a broad field of view, albeit with low resolution, of the top of the canopy of the woodland. These cameras captured the woodland within the rings daily, which allows for observations of yearly and seasonal trends in the foliage of both trees and lianas. With this I seek to answer whether there are canopy level responses to elevated CO_2 and whether are linked to environmental factors such as moisture availability. To do so, I opted to take a simplistic greenness ratio approach, as simplistic greenness ratios have been applied to lianas before and have been shown to be suitable for identifying liana presence in the tree canopy after a single survey (Chandler et al., 2021b), with canopy greenness increasing with severity of liana load.

Throughout the EucFACE experiment, the site has been subject to a semi-seasonal pattern of moisture availability. Typically, periods of highest moisture availability have been at the start and end of the Australian summer, although between 2018 and 2020 there was a severe drought as well as periods of severe waterlogging between 2020 and 2022. It is likely therefore that there is an interaction between the environmental effects of water availability and the effects of elevated CO_2 (Pathare et al., 2017; De Kauwe et al., 2021; Venter et al., 2022).

Methodologically this chapter explores whether a simple ratio such as the green chromatic coordinate (GCC) can separate lianas and trees both generally and across seasons. This chapter's main aims are to test: i) whether and how tree and liana canopies respond to elevated atmospheric CO_2 conditions, ii) whether those responses to CO_2 differ between life forms, and iii) whether changes canopy response to CO_2 are related to seasonal or severe drought.

I show here that lianas and trees are distinct throughout most of the experiment in GCC, regardless of CO_2 treatment. However, the longer (+2 years) drought exposure between 2018 and 2020 decreased this difference until the optical response of lianas and trees were indistinguishable using the GCC ratio. Thus, it is likely that if this methodology were to be repeated in seasonal forests, that lianas and trees would be adequately distinguishable, allowing for identification. This is with the caveat that extreme droughts may confound the usage of a GCC based identification process.

I also present that the difference in GCC between lianas growing in ambient and elevated CO_2 is responsive to soil moisture. During short term periods of soil limitation, i.e. where soil moisture is between $0.1m^3m^{-3}$ and $0.15m^3m^{-3}$, lianas in elevated CO_2 retain higher GCC values. Higher GCC during periods of seasonal water limitation can indicate that more leaves are photosynthetically active within the area of the pixel (Brown et al., 2017). More photosynthetically active leaves in seasonal droughts would indicate that lianas are able to maintain hydraulic safety, i.e. leaves are receiving sufficient water for photosynthesis, when exposed to elevated CO_2 (Baccari et al., 2020; Medina-Vega et al., 2022b). Thus, elevated CO_2 levels could ameliorate the effect of seasonal moisture limitation on these lianas in this ecosystem (Laugier-Kitchener et al., 2022). This is in direct contrast to trees, for which GCC did not differ between ambient and elevated CO_2 conditions. Peaks in tree GCC across both treatments is driven by patterns of water availability which is consistent with research that showed these *Eucalypts* flush new leaves following rain events (Duursma et al., 2016). It is likely therefore that lianas show different strategies of drought security than trees especially during high CO_2 conditions, by retaining hydraulic connectivity (Gimeno et al., 2016; van der Sande et al., 2019). Local increases in CO_2 will likely benefit lianas more so than mature trees during when soil moisture is limited, thus this may reinforce the observed dry season advantage of lianas (Cai et al., 2009; Tobin et al., 2012). In turn this is likely to advantage the growth of lianas in the dry season(Schnitzer et al., 2014), thus placing a greater competitive pressure on trees, which may negatively affect forest carbon balance in the dry season (van der Heijden et al., 2013, 2015; Peters et al., 2023).

7.1.3 Chapter 6

My final chapter expands upon the response of leaves to elevated CO_2. While my previous chapter used data that is limited in spectral range to red, green, and blue channels, this chapter expands the spectral range to include the near and shortwave infra-red. Hyperspectral data, i.e. data that captures a greater range across the electromagnetic spectrum from 400 to 2400 nm, allows observation of responses to CO_2 that occur in the near or shortwave infra-red as well as the visible. The spectral response of plants can be linked to their leaf biochemistry (Curran, 1989; Curran et al., 2001). For example, reflectance in the visible range links to pigments responsible for photosynthesis, and near and shortwave infra-red reflectance can be linked to chemicals such as; water, starch and leaf nitrogen (Curran, 1989; Pacheco-Labrador et al., 2014; Wujeska-Klause et al., 2019a; Morley et al., 2020). Using the spectral response from across the full range of wave lengths, it is therefore possible to estimate if plants respond to elevated CO_2, by observing how reflectance increases or decreases at specific wavelengths. Furthermore, it is possible to use leaf spectral reflectance to calculate robust spectral indices to estimate the effects of elevated CO_2 on chlorophyll pigments and plant health. Thus, I used hyperspectral spectroscopy to investigate whether there is a spectral response of *P. straminea* and *E. tereticornis* to elevated CO_2 and whether these responses differed with lifeform.

My results show that the response of these lianas to elevated CO_2 differs to that of the co-occurring trees, primarily in the visible spectra and the red edge. While the lifeforms differ in spectral reflectance in the near and shortwave infra-red, the relative changes between the lifeforms are much smaller than those found in the visible spectra. I found that reflectance of lianas in green wavelengths increased (500-600nm), while simultaneously that in the blue (400-500nm) and red wavebands (640-690nm) decreased. The decrease in leaf reflectance of light at blue and red wavelengths is often used as an indicator for increased photosynthetic pigments, thus a likely increase in chlorophyll content in the leaves of lianas as a response to elevated CO_2 conditions. The spectral reflectance of lianas when exposed to CO_2 also decreased around the absorption features associated with water and starch (~1200nm), protein (~1550nm, ~2180nm), cellulose (~1800nm), and water and cellulose (~1900nm), indicating an increase of these leaf components (Curran, 1989; Boyd et al., 2006).

In comparison, trees were found to increase in reflectance in the blue and red wavelengths and decreased reflectance in the green wavelengths, which could indicate either decreased chlorophyll content or an increased carotenoid content. Trees were also found to increase in reflectance around the water and cellulose absorption features (~1900nm), which could indicate that there is decreased water/cellulose content in tree leaves (Curran, 1989; Curran et al., 2001; Boyd et al., 2006). To corroborate whether leaf reflectance can predict field measurable data, I present leaf moisture for both treatments. I found that the liana leaves had higher moisture content in elevated CO_2 conditions, which corresponds with the higher absorption in the water related wavebands in their leaf spectrum. Conversely, there was no change in leaf moisture content between ambient and elevated CO_2 conditions for trees, which was similar to a more muted spectral response in the water absorption bands. In both treatments, tree leaves had a lower moisture content than the lianas, indicating that water use strategies likely differ between lifeforms.

To further explore these spectral results, I applied two robust spectral indices, the Modified Chlorophyll Absorbance in Reflectance Index (MCARI) (Daughtry et al., 2000) and the Normalised Difference Vegetation Index (NDVI) (Kriegler et al., 1969) to examine photosynthetic pigments and plant health respectively. Comparing the response of trees to elevated CO_2, I found that the MCARI index of *E. tereticornis,* closely mirrors those of a previous study at EucFACE. Wujeska-Klause et al. (2019a) found *E. tereticornis* leaves were lower in chlorophyll in the elevated CO_2 treatment with similar patterns of spectral response to my study i.e. increased reflectance at blue and red wavelengths. Similarly studies of European temperate, and neo-tropical trees have also shown that leaf chlorophyll decreases with exposure to elevated CO_2 (Oki et al., 2013; Walker et al., 2019). This decrease of as a result of increased atmospheric CO_2 concentrations, shows that the response of trees to CO_2 is not only similar between species, but also across ecosystems (Aranda et al., 2006; Oki et al., 2013; Wujeska-Klause et al., 2019a).

The MCARI score of the liana *P. straminia* increases in leaves exposed to elevated CO_2, indicating an increased leaf chlorophyll content, which might be expected to give a proportionately large increase in photosynthesis compared to trees. However, Laugier-Kitchener et al. (2022) explored the photosynthetic response of both lianas and trees at EucFACE to elevated CO_2, finding that both lifeforms increased photosynthetic rates in elevated CO_2 conditions, but there was no evidence of a larger response to CO_2 by lianas. It may be then that lianas are already highly photosynthetically efficient, and that to use elevated CO_2 lianas would be required to increase production of chlorophyll. There is however a caveat to this hypothesis, firstly is the use of the MCARI index, as this index is unit less, it does not provide a measure but simply an indicator that there is an increase of chlorophyll.

My application of NDVI, also shows some consistency with prior studies on trees in the literature. For trees at EucFACE, NDVI decreased but not significantly so under elevated CO_2 conditions, similarly to a study by Oki et al. (2013). A decline in NDVI is consistent with other literature that posit that plant leaves show symptoms of stress when exposed to elevated CO2 (Lakkaraju et al., 2010; Jiang et al., 2015; Xu et al., 2015). The NDVI response of *Parsonsia straminea*, however, is contrary to responses shown in the literature. I found NDVI increased, although not significantly so, for this liana species under the elevated CO_2 treatment, whereas the NDVI for the neo-tropical lianas tested by Oki et al. (2013) decreased similarly as the co-occurring trees from that study. An explanation for the discrepancy in results may be that lianas are benefiting from the elevated CO_2 (~150ppm above ambient) up until a certain level, and after which further increases in CO_2 increase plant stress and reduce productivity. Alternatively, the response of lianas to elevated CO_2 is species dependant, i.e. there is no one universal liana response to elevated CO_2 and the responses are as diverse as the differing levels of leaf traits and biochemistry present within lianescent plants (Sánchez-Azofeifa et al., 2009).

7.2 Synthesis of results

Through this thesis I have focussed on whether the liana *Parsonsia straminea* responds differently to elevated atmospheric CO_2 than its co-occurring host tree *Eucalyptus tereticornis* in a mature Australian woodland. While there has been a large research effort into assessing the effects of elevated atmospheric CO_2 as part of the EucFACE project, most of the research output in terms of the vegetation has focused on trees and the understory vegetation, but not the lianas. This thesis constitutes the largest body of work that focusses on the understudied but widely distributed liana *P. straminea,* offering critical insight into an otherwise overlooked life form in this woodland system. This study also encompasses the longest period of exposure of lianas and trees to elevated CO_2. The time period of exposure in other studies ranges from a few months (Oki et al., 2013) to ~six years (Mohan et al., 2006). Thus, this thesis has one of the longest inter-seasonal records of CO_2 enriched forest flora and is likely to have captured seasonal and yearly trends in plant responses to a 150 ppm rise in atmospheric CO_2 concentrations.

Through this thesis I have explored the effects of elevated CO_2 on several scales, at a community scale in chapter 3, at a canopy scale in chapter 4, and finally at the leaf scale in chapter 5. My work has highlighted that *P. straminea* is responsive to elevated CO_2 at the canopy/leaf scale but did not explain changes in proportion of trees hosting lianas or liana attained height. Chapter 4 shows that while the liana presence at EucFACE has increased over time, these increases were similar across treatments. In both chapters 5 and 6, I show that there is a clear difference in the greenness index (GCC), and the full spectral reflectance of leaves, of liana leaves when exposed to elevated CO_2, which suggests a difference in chemical composition. Trees on the other hand appeared to be less influenced by elevated CO_2 than the lianas, i.e. GCC values differed less between treatments than those of lianas, although there were spectral responses which indicate stress.

It appears that the liana *Parsonsia straminea* is responsive to elevated CO_2 and that this is mediated by soil moisture. Considering the increases in liana load found at EucFACE (chapter 4), the period with both the lowest change in liana load and liana attained height, 2018 - 2020, correlates with the lowest greenness of lianas in both treatments (chapter 5). Indicating that the effects of a prolonged drought are detectable in changes to how a liana infestation develops and when intense enough can remove the spectral signature of elevated CO_2 from the canopy. Broadly speaking the results of these chapters show a prolonged effect on the development, and likely health of lianas, of a protracted drought are greater than the potential ameliorating effects of elevated CO_2, e.g. increased water use efficiency (Venter et al., 2022). However, the results that these lianas were not prevented from colonisation, in either treatment, during this prolonged drought shows that liana proliferation is limited but not prevented by lengthy droughts. As droughts are predicted to lengthen and intensify with climate change (Dai, 2013), this result is of particular importance. Extended droughts typically drive increased tree mortality (Allen et al., 2015; Reis et al., 2022), thus increasing forests gap and conditions that are more favourable for increasing (Gerwing, 2004; Foster et al., 2008), which combined with my finding that liana proliferation continues during prolonged drought could result in severe forest degradation due to the feedback between liana driven and drought driven tree mortality.

The spectral response of lianas to elevated CO_2 (chapter 6), alongside the increased MCARI, imply that the leaves of *P. straminea* have increased chlorophyll concentrations in elevated CO_2. These results suggest an increase in photosynthetic capacity of these lianas under elevated CO_2 conditions (Nishio, 2000; Croft et al., 2017). Although this is counter to the expected result in elevated CO_2. Conventionally, woody species have been found to both decrease chlorophyll concentration and increase photosynthetic rate and thus leaf productivity (Pathare et al., 2017; Wujeska-Klause et al., 2019a). In fact the earlier EucFACE study found a similar increase of liana photosynthesis as was found in trees, in elevated CO_2 (Laugier-Kitchener et al., 2022). Thus, it would be logical to assume that the lianas might follow the same pattern of decreasing chlorophyll as trees. In fact, I have found the opposite, however from the application of MCARI alone, this cannot be quantified. It is likely, as discussed earlier, that the increase in chlorophyll may be due to lianas already being highly efficient in photosynthesis (Zhu and Cao, 2009; Smith and Keenan, 2020), and requiring greater concentrations of chlorophyll to use elevated CO_2.

The differences in spectral response of lianas, between my study and Oki et al. (2013) could be explained by our CO_2 enrichment concentrations. The study of Oki et al. (2013) used a much higher concentration of CO_2, 800ppm (400ppm above ambient, than is tested at EucFACE, ~550ppm (150ppm above ambient). This difference of +250ppm CO_2 may be the difference between CO_2 having a fertilizing effect and it inducing a stress response, whereby increases in CO_2 stimulate plant growth up to a threshold and it potentially limiting a growth response beyond that threshold. There is some evidence that this may be happening as in a study by Granados and Körner (2002), which tested 5 different CO_2 concentrations between 280ppm – 700ppm, liana biomass increased non-linearly up to 560 ppm after which the liana biomass increase levelled off (Granados and Körner, 2002).

However, co-limiting factors, such as the phosphorus limitation of EucFACE, could also drive these non-linear relationships in the liana response to elevated atmospheric CO_2. In elevated CO_2 conditions, trees increase the recycling of phosphorus, which mitigates phosphorus limitation (Ellsworth et al., 2015). If lianas growing in elevated CO_2 conditions recycle phosphorous is a similar way, it could trigger a growth response in lianas, which may result in a higher abundance of lianas and trees supporting lianas over time in sites where soil phosphorous may otherwise be a limiting factor (Pasquini et al., 2015).

The leaf level response, i.e. increased chlorophyll and higher rates of photosynthetic rates (Laugier-Kitchener et al., 2022), to elevated CO_2 conditions does not appear to be mirrored by a CO_2-driven vegetative growth response (Chapter 4) of lianas. There is no evidence of a CO_2-driven response of liana attained height or the proportion of trees supporting lianas at EucFACE. Clearly then the relationship between photosynthesis, growth and colonisation of new host trees is complex. Growth of lianas can be influenced by many external factors including nutrient limitation (Pasquini et al., 2015) and soil water availability (Medina-Vega et al., 2022b) as discussed earlier, but can also relate to life history traits (van der Sande et al., 2019). Liana growth mechanisms link with relative shade tolerance, Cai et al. (2007) found that shade intolerant lianas prioritised stem elongation while shade tolerant lianas prioritised fine root growth. As *P. straminea* is relatively shade tolerant (Benson and McDougall, 1993; Fairley and Moore, 2000), these lianas could therefore be prioritising root growth rather than stem, which would not have been detectable by the methods used in this thesis, regardless of any CO_2-driven increased growth. A CO_2-driven increase in root mass, would likely be a competitive advantage for lianas over trees, increased fine roots specifically could increase a lianas ability to acquire nutrients and moisture more efficiently compared to trees (Avila et al., 2020; Smith-Martin et al., 2020), although very little is currently known about liana roots. A similarly functional trait, response of lianas that was unable to be tested but may be influenced by increased photosynthesis, is CO_2-driven wood density change. Wood density can increase in response to elevated atmospheric CO_2 for other woody lifeforms (Yazaki et al., 2005; Kostiainen et al., 2009), although this appears to be heavily species specific (Kim et al., 2020). Increased wood density can infer water savings mechanisms and be indicative of increased drought tolerance (Markesteijn et al., 2011) promoting liana competition with trees in water limited forests as atmospheric CO_2 continues to rise. There is however, considerable work needed to elucidate how liana functional traits, such as wood density or root biomass, are affected by elevated CO_2 conditions as while above ground traits are well studied (Gallagher and Leishman, 2012; Letcher and Chazdon, 2012; Gallagher, 2014), the below ground interactions of lianas are still poorly understood.

7.3 Study limitations

Studying lianas at EucFACE was not part of the original experimental design, as such very few of the original monitoring protocols were set up in a way that would facilitate study into lianas. This has led to some limitations within this study, which I will discuss here.

The first key limitation arising in this thesis is the problem of lianas versus data spatial resolution, and the influence of this on measurement of the effects of elevated CO_2 on liana development. My TLS data were collected and rendered at a 20mm resolution, which for structural and volumetric modelling of trees is a typically appropriate resolution (Calders et al., 2014; Newnham et al., 2015). However, most of the lianas at EucFACE are <20mm diameter, thus limiting geometric accuracy when rendering liana stems with TLS scans. This prevent volumetric calculation of these lianas, which prevented me from being able to report on whether liana biomass is responsive to elevated CO_2. Furthermore, due to occlusion, from other woody material, and the narrow diameter of these lianas, detecting the stems of lianas within the canopy of trees proved difficult. This limits both the utility and accuracy of measurements of liana length, thus I reported on the distance between the ground and greatest height at which liana vegetative structures, such as leaves or stem tangles, could still be identified. This liana attained height is an inherently conservative measure of liana progression as this was limited to advances on the tree stem only and not of height advances within the canopy. As such there may be within canopy response of lianas to elevated CO_2 that have not been observed, for example it is unknown whether liana leaf deployment is influenced by elevated CO_2.

When using the security camera imagery from EucFACE, the data were subject to limitation from the camera operations that required a high degree of data filtering and removal. For example, some of the imagery was out of alignment or poorly overlapped with the other imagery. While the cameras were operated by computerised pan, zoom, and tilt mountings, there were periods where these mounts would lose alignment. This misalignment resulted in imagery that either did not overlap sufficiently for the panorama processing, or, as found for the imagery from ring 4, images that only captured data outside of the rings. Depending on how poorly overlapped these images were, the panorama processing could be manipulated by hand to register the panorama, although this often created images with blank spaces. When images needed manual intervention in the panorama, the projection (i.e. how spherical or warped an image is) would need to be manipulated, this changes how the pixels from the original data are interpolated to the new image. As the original pixels are resized for the panorama, within PTGui a nearest neighbour interpolation is used to smooth the image. Although when combined with a manipulated projection, this could result in imagery where there were substantial differences between patch sizes of liana or tree foliage, occasionally warping the image to where tree stems no longer appeared to match with their known shape. As such these data were not sufficiently consistent to create an area-based analysis, of foliage response to elevated CO_2, i.e. whether there was canopy expansion or contraction. Despite this the pixel values for colouration, the red, green, and blue channels, were checked against the original images and found to be stable enough for analysis using my index-based approach.

It would have been desirable to have sampled the lianas and trees through multiple seasons using spectroscopy. As noted from the RGB imagery analysis, lianas differ between treatments when soil moisture is seasonally limited but prolonged drought showed similar responses of greenness. My hyperspectral data was collected in a period of high moisture availability, where liana greenness was particularly high, compared to the trees, in both treatments. Further sampling, especially in periods where liana and tree greenness is similar such as during a prolonged drought, could elucidate the differences in liana and tree water saving mechanisms, as well as how the lack of available moisture appears to diminish the effects of CO_2. Furthermore lab chemical analysis would have allowed for further corroboration of the hyperspectral data (*sensu* Boyd et al., 2006) and may have elucidated why the response of both lianas and trees to elevated CO_2 does not influence the spectral response of longer wavelengths (>900nm). These wave lengths have been tied to leaf chemistry, such as leaf nitrogen content, which has been shown to differ between trees and lianas (Asner et al., 2009, 2015; Asner and Martin, 2012) and has been predicted to change with CO_2 increase (Will and Ceulemans, 1997; Wujeska-Klause et al., 2019b).

More broadly this study is limited by the lack of diversity in the woody species present at EucFACE. This site only hosts one liana species *Parsonsia straminea* and one dominant tree species *Eucalyptus tereticornis*. As lianas are a highly diverse poly-phyletic group, rather than a clade of related plants, there is a high degree of variability between species (Sánchez-Azofeifa et al., 2009; Gallagher and Leishman, 2012). As discussed below as a future research direction, there is likely a role of species specific traits, e.g. climbing mechanism, leaf structure, nutrient usage, that may influence the response of plants to elevated CO_2 conditions (Oki et al., 2013; Wullschleger et al., 2015; Ainsworth and Long, 2021). Oki et al. (2013) showed that, of the three co-occurring lianas that were studied, two showed similar responses to elevated atmospheric CO_2 whereas the third species, from a different genera, showed a different spectral response. Therefore it is difficult to attribute the results from this experiments to the lianescent life form as a whole.

The EucFACE site and FACE sites more generally are subject to local environmental conditions. In the case of EucFACE specifically this includes a protracted drought which culminated in what was described by the Australian media as the “Black Summer” where drought conditions led to large scale bushfires (Davey and Sarre, 2020). This drought had negative effects on the survival of the vegetation present (Peters et al., 2021). Results from both chapters 4 and 5 show that in drought conditions liana attained height increases were lower and GCC of both lianas and trees was negatively influenced regardless of CO_2 treatment. Therefore, the drought may also have impacted the growth, survival and physiology of the lianas, if these are similarly affected by long-term droughts, regardless of atmospheric CO_2, it would be likely that there is no advantage offered by elevated atmospheric CO_2 under drought conditions. However direct measurement of liana growth, mortality and physiology in response to the drought, were not available due to technical limitations discussed above as well as the impact of the COVID-19 pandemic.

FACE experiments are resource and financially intensive, consequently FACE experiments are still relatively rare in forested environments (Norby et al., 1999, 2016). As such there are inherent limitations which all FACE sites are subjected to, that of low reproducibility and replicates (Calfapietra et al., 2010). The current generation FACE experiments are designed maximise statistical power, through higher replicates than the previous generation and being designed to be integrated into global carbon modelling approaches (Calfapietra et al., 2010; Norby et al., 2016). EucFACE contains 3 replicates of the elevated CO_2 treatment and 3 of the ambient (control) conditions, located randomly throughout the larger forested site (Crous et al., 2015; Duursma et al., 2016). The Birmingham Institute of Forest Research (BIFoR) FACE experiment follows a similar replicate design with the addition of three plots with no superstructure as additional control conditions to derive greater statistical power (Hart et al., 2020).

7.4 Future directions

My research provides a substantive body of evidence that liana leaves are responding to elevated atmospheric CO_2. However, there are still questions left unresolved about what effects these leaf-level responses may have on liana growth and allometry, and consequently on forest assemblages more generally. I did not find any evidence of augmented liana growth as a response to elevated atmospheric CO_2, but there are clear and present differences in the spectral response of lianas, which indicates that the chemical composition of those lianas exposed to elevated atmospheric CO_2 differs from those growing in ambient conditions. The relationship between these indicated changes and the growth of lianas is complex, and more research is needed to explore their interconnectedness. This leads to the first of the future questions arising from my research:

How does elevated atmospheric CO_2 affect the allometry of lianas?

Elevated atmospheric CO_2 has been shown to affect vessel structure and cambial tissues (Yazaki et al., 2005; Watanabe et al., 2010), wood density and ring structure (Kilpeläinen et al., 2007; Kostiainen et al., 2009; Watanabe et al., 2010; Drew et al., 2017; Arsić et al., 2021) of trees. These effects of elevated atmospheric CO_2 have been shown to be species specific within trees (Watanabe et al., 2010; Drew et al., 2017), with evidence of both increases and decreases of wood density (Kostiainen et al., 2009; Watanabe et al., 2010; Drew et al., 2017; Arsić et al., 2021). We are yet to explore effects of elevated CO_2 conditions on liana wood traits. However, this could be a key area of research as liana stem development is atypical of other woody lifeforms, with less investment in supportive tissues, wider transport vessels, and an increased sapwood to hardwood ratio (Rowe and Speck, 1996; Hoffmann et al., 2003; Rowe et al., 2004). As the wood of lianas is typically less dense than that of co-occurring trees, it is likely that increased productivity driven by elevated atmospheric CO_2 (Laugier-Kitchener et al., 2022; Venter et al., 2022), could lead to denser more tree like wood. Potentially were lianas to follow trends of increasing wood density, this could further increase the mechanical load placed on trees thus placing them at greater risk of injury (Rodríguez et al., 2021).

Secondly, there is no information available on the root systems of the lianas. As such it is currently unknown how they may respond to elevated CO_2 conditions. Until recently it was presumed that lianas had deeper root systems than those of trees (Andrade et al., 2005; Chen et al., 2015), however recent evidence has shown that lianas have wide spreading horizontal root systems (De Deurwaerder et al., 2018; Smith-Martin et al., 2020). Due to the difficulty associated with studying root development, the response of liana root system growth and formation to elevated CO_2 concentrations could not be explored in this thesis. Elevated CO_2 conditions could provide lianas with an opportunity to increase root growth, further increasing the potential for efficient water transport and allocation of resources (De Deurwaerder et al., 2018; Smith-Martin et al., 2020). As lianas show traits that align with resource acquisition, e.g. high hydraulic efficiency, low leaf development cost (Gallagher et al., 2011), it would be logical for lianas to increase fine roots, resource gathering, rather than larger structural roots (Smith-Martin et al., 2020). An increase in root development would provide a significant advantage over trees in the competition for essential nutrients. An advantage that may be key to the development and proliferation of lianas in nutrient limited soils, such as those found at EucFACE and the neo-tropics.

Exploring the effects of elevated atmospheric CO_2 on below ground structures, would prove challenging, yet none of the forest FACE sites have expanded into the belowground component of plants. Utilising root traps, cylindrical cages inserted into the soil to allow removal of portions of roots, could help to accelerate our understanding of whether belowground plant structures respond to elevated atmospheric CO_2, although this process could facilitate the introduction of pathogens to the target rootstock. Utilising a rhizotron root viewing system could be one solution to this when a FACE site is established, but these systems are limited to where roots grow alongside the rhizotron window and are identifiable (Huck and Taylor, 1982). It would be likely then that the most efficient method of sampling to determine the effects of atmospheric CO_2 on liana root development would be to destructively harvest as/when FACE experiments are wound down.

The answering of how CO_2 influences allometry is undoubtedly easier for the above ground structures of lianas, although would still present its own challenges. Through this thesis I have explored some of the data that would be needed for answering how liana allometry is affected by elevated atmospheric CO_2 in the use of terrestrial laser scanning. As discussed above and in the work of Krishna Moorthy et al. (2019, 2020, but also Gonzalez de Tanago et al., 2018) it is possible, at least in theory, to use volumetric modelling to explore the allometry of lianas. The limitations of using TLS for volumetric calculations can be somewhat mitigated for with i) development of lower beam divergence scanning, and ii) greater number of scans and scanning location. Lower beam, divergence would allow for rendering of finer scale points (sub 2mm) in the point cloud derived from TLS data, i.e. the 3-D representation of these data (Krishna Moorthy et al., 2018, 2019). While this would increase the point density of TLS point clouds, these data would allow for more precision when attempting geometric or volumetric measurement of small diameter lianas. As the EucFACE experiment has developed an increased number of scanning locations have been identified, including using the scanners at tree crown level, using the ring superstructure. These data were gathered in the most recent scanning period (2022) and will be included in future analysis of forest structural dynamics at EucFACE.

My results show that *P. straminea* responds to elevated atmospheric CO_2 differently to the neo-tropical lianas presented by Oki et al. (2013), suggesting that there may not be an overarching response of all lianas to elevated CO_2. As lianas are included in over 130 plant families (Putz, 1984a; Gentry, 1991; Schnitzer and Bongers, 2002), there is great variation between the functional and mechanistic traits of lianas which would ultimately lead to species specific responses to CO_2. This leads to a potential future research question:

How do liana species differ in their responses to elevated atmospheric CO_2*?*

To test whether there are liana species specific responses to CO_2 would require a broad sampling of lianas from across the globe. Establishing forest FACE sites is a costly endeavour (Norby et al., 1999; Körner et al., 2007) leading to under representation of tropical and sub-tropical forests as these forest typically reside in nations that cannot afford to sustain such resource intensive studies. Thus, smaller scale experiments involving targeted gas injection of foliage, (*sensu* Oki et al. 2013) or manipulative experiments using growth chambers (*sensu* Granados and Korner 2002) have provided some avenues to study response to elevated CO_2 conditions with comparatively less financial outlay. Despite there being sporadic studies into the effects of CO_2 on lianas there have been underlying inconsistencies including CO_2 concentration, light regimes, moisture regimes, and measurement protocols, which a more unified effort may come to solve. As forests are spread across multiple elevations, latitudes, and climates a multi-biome, multi-species study consisting of multiple field scale experiments would also be able to test whether there is an effect of location of how lianas, and forests more generally respond to elevated atmospheric CO_2. The majority of FACE sites are located in the geographic north, with much of the evidence for plant response to elevated atmospheric CO_2 coming from species limited studies with low numbers of experimental replicates (Norby et al., 2016). As such we are still limited in our understanding of how forests of the geographical south may respond to elevated atmospheric CO_2. There is however work commencing to rectify this, at the time of this thesis going to press, the AmazonFACE is undergoing testing (home - AmazonFACE). This represents the first FACE experiment to be located within a tropical forest and may shed further light on how the liana dense forests of the tropics will respond to elevated atmospheric CO_2.

7.5 Conclusions

It has been hypothesised that elevated atmospheric CO_2 is a key driver in the proliferation of lianas (Schnitzer and Bongers, 2011), however until this study, the opportunity to test how lianas respond at a forest scale has been non-existent. My thesis is the first to explore how elevated atmospheric CO_2 impacts lianas in a large-scale field experiment using novel remote sensing techniques, aiming to a) determine the effects of elevated CO_2 on the locally abundant liana *Parsonsia straminea*, b) assess whether the response of these lianas contrast with *Eucalyptus tereticornis* trees in an Australian temperate sub-tropical forest.

This thesis shows, for the first time, that the liana *Parsonsia straminea* does respond to elevated CO_2 at canopy and leaf scale, and that the response of lianas is greatest during seasonal water limitations. Furthermore, this thesis is the first to show that these leaf and canopy responses can be detected using consumer grade, low spectral resolution, sensors. The apparent ameliorating effect of elevated atmospheric CO_2 on liana leaves in periodic water limitations, is likely to infer an increasing dry season advantage over trees. Thus, it is likely that further changes to the severity of seasonal droughts will likely continue to advantage the growth of lianas over their host trees. Consequently, this may show that seasonal forests may be at risk of liana driven community shifts in an elevated CO_2 world, thus decreasing the potential for carbon storage and sequestration in seasonal forests.

Furthermore, my results show that while liana proliferation is slowed during periods of long term drought, it is not stopped. This indicates that these lianas are capable of proliferating in conditions which would negatively affect their host trees. Consequently, this is likely to negatively influence the survivability of droughts for forest trees, potentially causing a feedback loop between increasing liana pressure and drought stress. Changing climatic conditions, and the associated increases in length and severity of droughts may, therefore, alter liana load and increase liana impacts on tree canopies.

As one facet of the research into the response of plants to elevated atmospheric CO_2 and climate change, this thesis provides the first look into how an Australian liana species, *Parsonsia straminea,* has been influenced by elevated CO_2 in field conditions. With this I have shown that these lianas respond in a way that is uncharacteristic of others explored in the literature.

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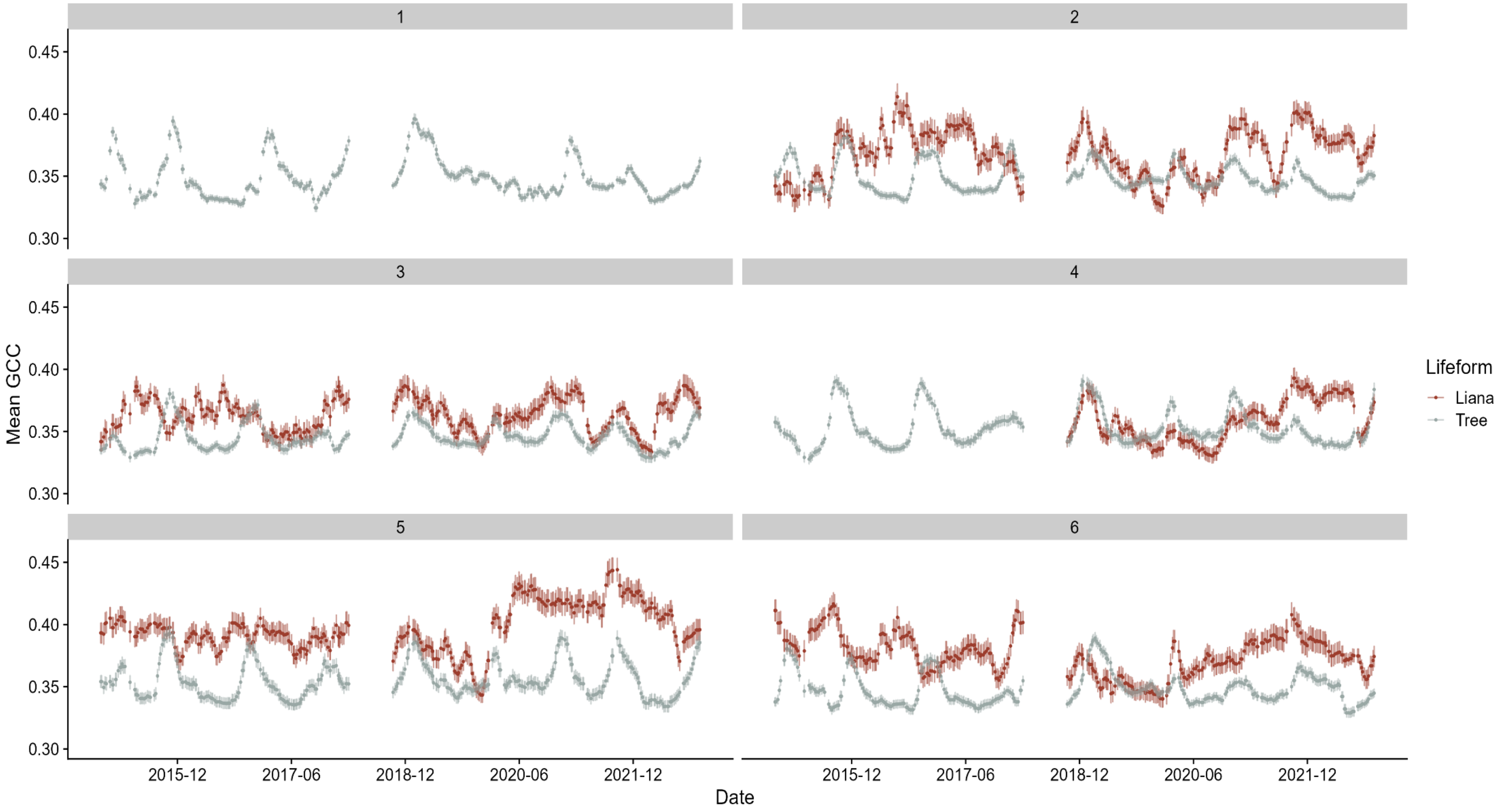
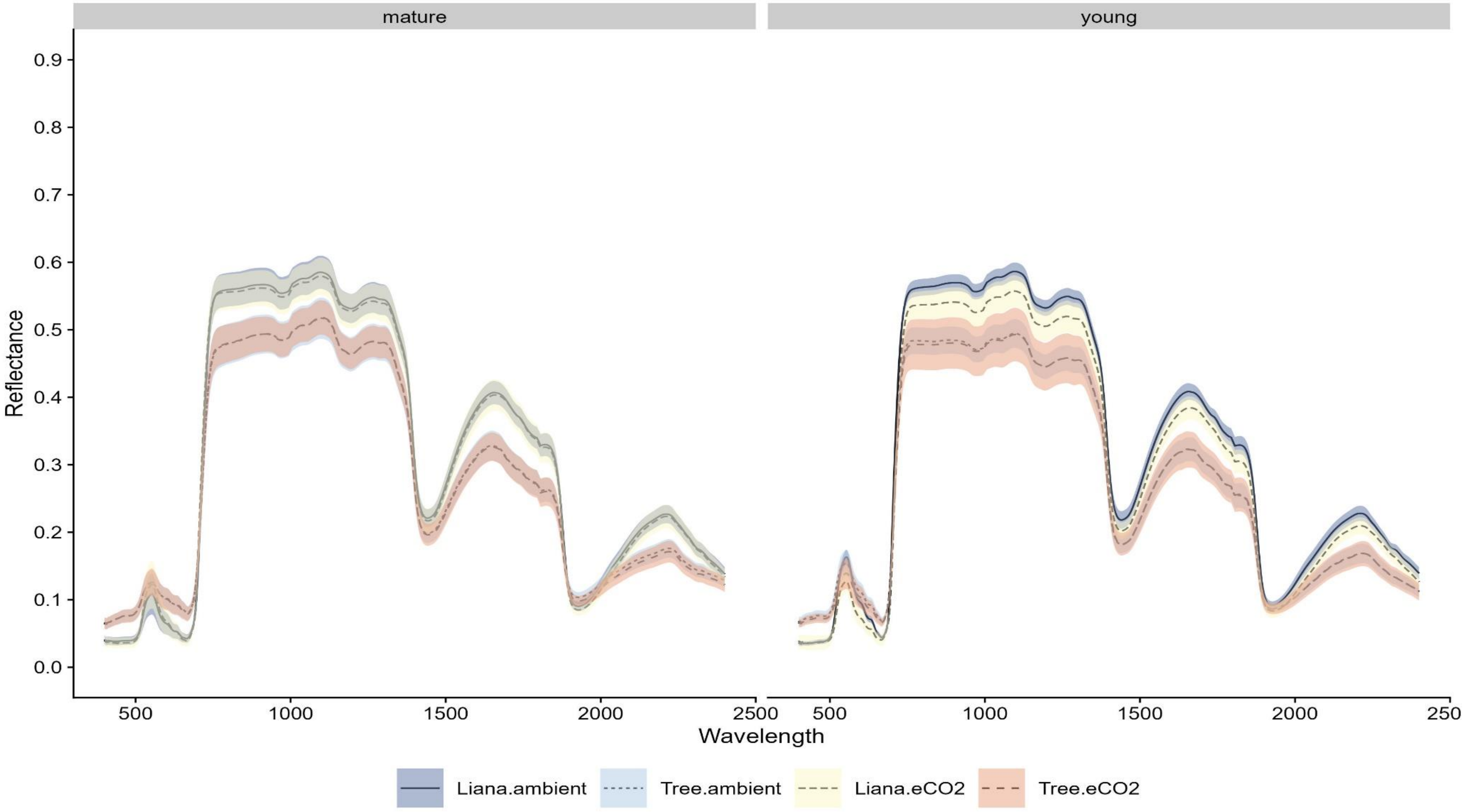
Supplemental material

Supplemental table 4. 1 Percentage of living trees hosting lianas at EucFACE. Lianas found on dead trees were surveyed as part of the manual census but are excluded from analysis.

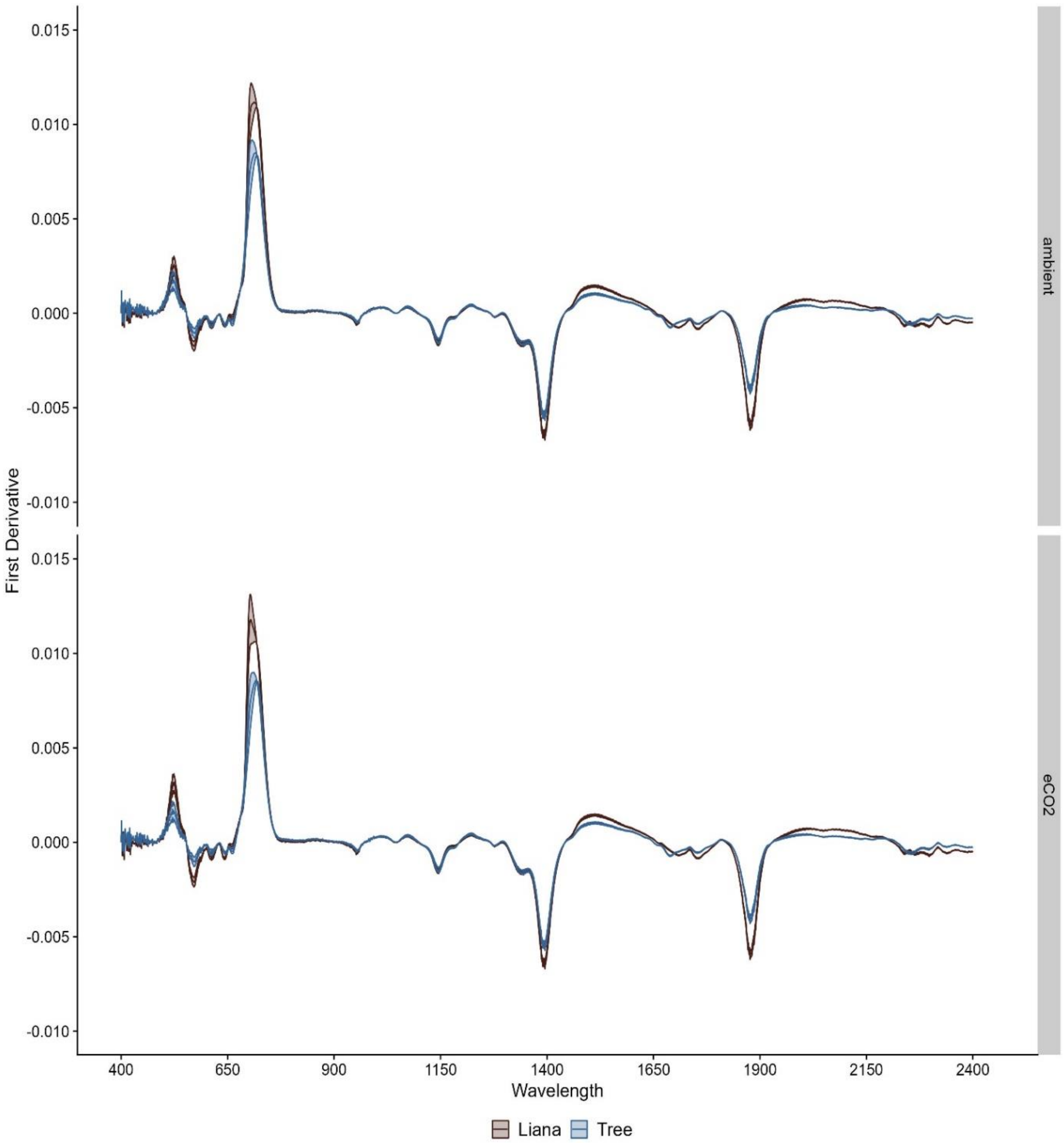
% of live trees hosting lianas		
Census	Ambient	Elevated CO2
Manual	65	38
TLS	66	41



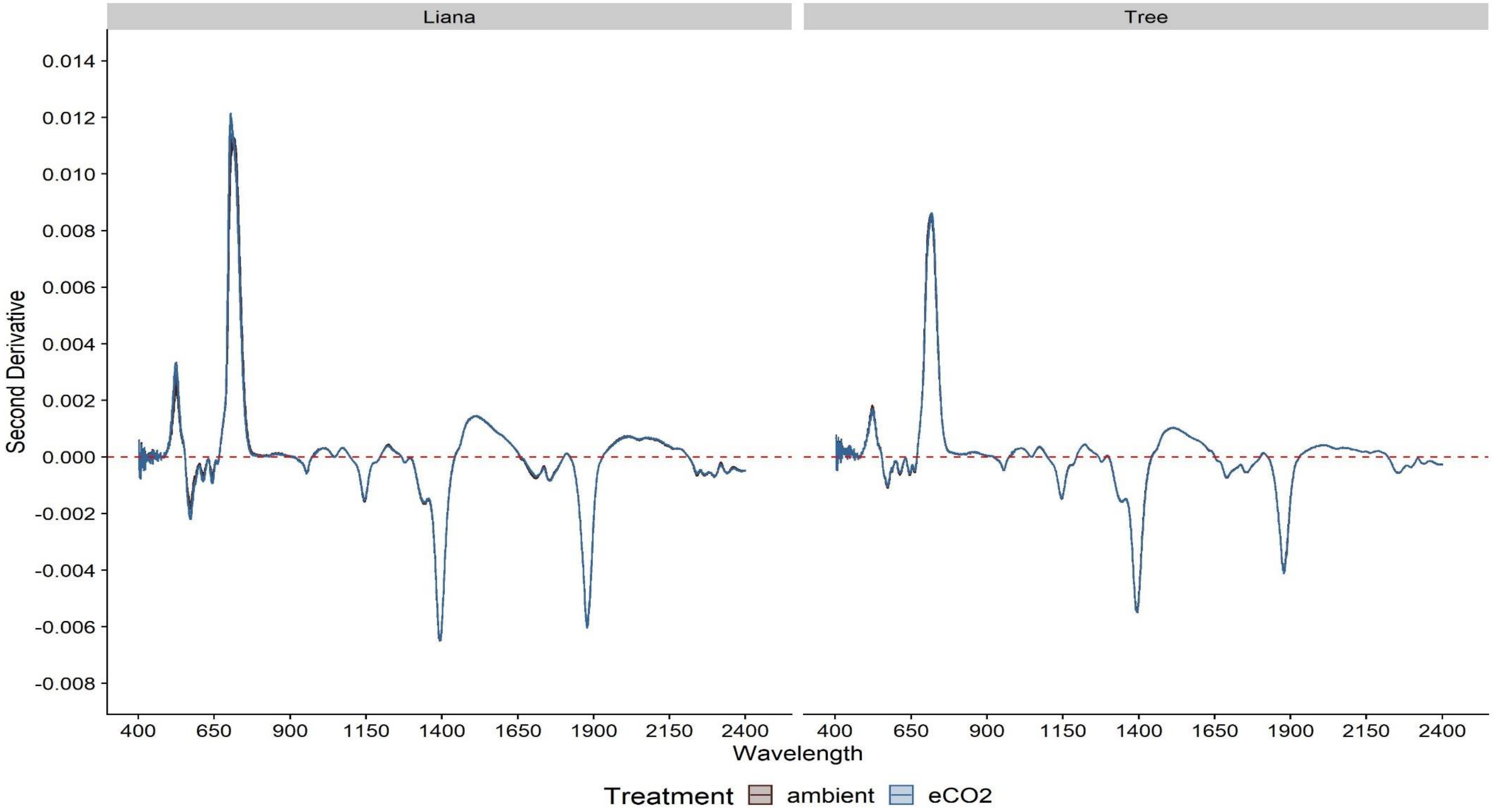
Supplemental figure 5. 1 Liana and Tree GCC per experimental ring. Grey points show trees, red points indicate lianas, both with bootstrapped 95CIs. Ring 4 (eCO$_2$) only had visually detectable lianas post 2018. Ring 4 camera alignment was facing ~10% of ring from 2018 to start of 2020.



Supplemental figure 6. 1 Reflectance of trees and lianas. Left panel mature leaves. Right panel young leaves. Ribbons show ±1 standard deviation.



Supplemental figure 6. 2 First derivative spectra of lianas (left panel) and trees (right panel) with standard deviations. Coloured by experimental treatment, ambient in grey, eCO$_2$ in blue. Ribbons show ±1 standard deviation. Positive values indicate a shift towards shorter wavelengths, negative values indicate a shift towards longer wavelengths.



Supplemental figure 6. 3 Second derivative spectra. Second derivative spectra showed same patterns in peak slope maxima as first derivative spectra.

Appendix 1

Impacts of COVID

This thesis was affected by the impacts of the COVID pandemic. The Author struggled throughout the lockdown periods with their mental health, and this has negatively impacted the timeliness of the completion of this thesis. The long-term impacts of the decline in the Authors mental health continued long after the lockdowns finished, and thus further impacted the completion of this thesis.

As the study site, EucFACE, is in Australia, this thesis was impacted due to the border closures enforced by the Australian government. Consequently, the availability and timings of fieldwork was severely limited.