Chapter 1  
General Introduction

# 1.1 Overview

## 1.1.1 Resource allocation in plants

Plants require resources including light, CO2, water and mineral nutrients to support growth and reproduction. Resource acquisition requires an energy supply, appropriate tissues for uptake and a transport system to deliver resources to their required destination (Grace 1997). The uptake of nutrients from roots is necessary for leaf growth. Leaves then fix the C, via net photosynthesis (*An*), required for growth of the entire plant. This assimilated C from source leaves, in the form of simple sugars, is in itself an essential C resource that must be allocated to the growth and maintenance of tissues or is diverted to a storage pool of carbohydrates. As a result, growth is driven by several simultaneous processes, including *An*, C investment among organs, resource acquisition and metabolic costs (Körner 2006, Fourcaud et al. 2008). Gaining an understanding of the sensitivity of these processes to environmental change is crucial for predicting future terrestrial C cycling (Friedlingstein et al. 1999), as there is currently little consensus on how C allocation should be modeled (Franklin et al. 2012, De Kauwe et al. 2014).

## 1.1.2 Resource allocation theory

Theoretically, growth under resource limitation will be maximized when investment into the acquisition of any single resource from the environment leads to an equivalent increase in growth (Bloom et al. 1985). The two critical assumptions of allocation theory are that the resource in question is in fixed supply and that allocation among competing functions is mutually exclusive (Bazzaz et al. 2000). Thus, trade-offs between different tissue C sinks will exist as resources are invested within the plant. Allocation of newly acquired resources to different tissues will then affect subsequent rates of capture of CO2 and soil resources (Shipley and Meziane 2002). In resource-saturated environments plants should maximize growth by allocating resources to support leaf growth to increase C acquisition (Monsi and Saeki 2005). Resource availability, however, is rarely saturated in natural ecosystems. For example, tree growth can be limited by the availability of carbon within the plant (carbon limitation) or by the tree’s ability to use available carbon via nutrient shortages (Wiley and Helliker 2012). As a result, shifts in allocation of external resources and assimilated C to different tissue or ecosystem components can occur. Debate still exists regarding which of these limiting resources most strongly limit plant growth or how they regulate carbon availability.

Shifts in resource allocation within plants have led to two main theories regarding allocation strategies. First, the balanced growth hypothesis suggests that individual plant tissues should provide a ‘balanced internal economy’ as each component supplies resources for the other (Davidson 1969). This functional equilibrium between tissues can then be adaptive if conditions limit *An* or soil nutrient uptake (Cannell et al. 1985), such that plants should allocate resources to the organ that is capturing the resource most limiting growth (Shipley and Meziane 2002). Changes in plant resource allocation are also theorized to be a function of allometric trajectories of plant development, independent of changes in nutrient supply (Müller et al. 2000). In this strategy, investment into leaf mass increases with both stems and root, but not proportionally, as a greater allocation of biomass to the stem exists as a simple function of plant size (Zens and Webb 2002). When constrained by ontogeny, plants are more likely to adjust tissue morphology, chemistry, metabolism or turnover to alter resource capture (Reich et al. 2002).

## 1.1.3 Tree canopy resource gradients

Incident PPFD declines exponentially with cumulative leaf area index from the top of the tree downward, creating steep light gradients within tree canopies (Monsi and Saeki 2005). Leaf photosynthesis responds strongly and non-linearly to irradiance (Evans 1995). As costs and limitations of light harvesting prevent plants from exposing all leaves to full sun (Niinemets 2010), it follows that a substantial portion of canopy C assimilation should occur in leaves with the highest exposure to light. Consequently, the distributions of resources required for *An* are partially defined by canopy light gradients. As the photosynthetic capacity of leaves is related to its N content (Field and Mooney 1986), a larger investment in N to the upper canopy should yield a larger return from whole canopy C assimilation (Ellsworth and Reich 1993). The supply of water also imposes limits photosynthetic C gain through direct limitations on leaf level physiology. The stomatal resistance to CO2 uptake is a function of the balance between transpiration losses and leaf water potentials (Farquhar and Sharkey 1982) and sun leaves frequently experience greater water limitations in the upper canopy (Sellin et al. 2008, Niinemets 2012). Thus, photosynthetic N investment in the upper canopy will be ineffective in enhancing *An* if water supply is insufficient (Niinemets 2012, Peltoniemi et al. 2012). Overall, the allocation of soil resources within the canopy constrains leaf physiology and photosynthetic capacity, thereby regulating the efficiency of CO2 uptake.

## 1.1.4 Fate of assimilated carbon

Carbon allocation represents the fraction of gross primary productivity distributed to different tissue components above and belowground. In trees, C allocation encompasses investment into tissue biomass production as well as fluxes including respiration, exudation and turnover rates (Litton et al. 2007). The fate of this assimilated C is regulated by the delicate balance between leaf C uptake (source) and the C sink strength of the different biomass pools. For example, the sensitivity of C source and sink activities to water and nutrient availability could lead to an imbalance between C supply and C used for tissue growth and respiration (Fatichi et al. 2014). Additionally, imbalances between source and sink activity can lead to investment into carbohydrate synthesis as a transient C storage sink (Paul and Foyer 2001).

As woody plants have competing tissue carbohydrate sinks, growth should principally depend on the allocation of leaf C assimilate among different sink organs (Kozlowski 1992, Lacointe 2000). In response to changing environmental conditions, however, trees may adaptively shift tissue C allocation to balance growth, storage and C loss. Due to conservation of mass, it is conceivably possible to track photosynthates from leaf C uptake to their eventual destination in above and belowground pools. Although mass balance approaches can be used to quantitatively assess tree C allocation, few studies so far have been able to provide direct empirical measurements of C allocation among component pools (Klein and Hoch 2015). Improving our understanding of tree C allocation will require novel experimental infrastructure capable of quantifying net canopy photosynthesis and the fate of C into growth, storage and C loss pools.

## 1.1.5 *Eucalyptus* tree species as model for research

Research on *Eucalyptus* trees is ecologically important for Australia as it is the most dominant tree genus (Boland et al. 2006). *Eucalyptus* forests are the continent’s most common forest type, covering about three-quarters of Australia’s native forests (92 million hectares) and occurring in all but the continent’s driest regions (SOFR 2013). *Eucalyptus* tree species are also economically important globally as they are commonly cultivated in plantations due to fast growth. Despite the fact that only a few *Eucalyptus* species have natural ranges outside continental Australia (Pryor and Johnson 1981), *Eucalyptus* trees are grown in plantations in over 90 countries (Booth 2013). This is because *Eucalyptus* species have been shown to exhibit both adaptive plasticity and genetic specialization to spatial variation in climate (Byrne et al. 2013). Currently, the global plantation area of eucalypts totals nearly 20 million hectares, accounting for around 15 % of the world’s total plantation forests (IUFRO 2015). Consequently, this iconic Australian tree species is an excellent model to investigate strategies of resource allocation in trees facing global climate change.

# 1.2 Current Knowledge Gaps

## 1.2.1 Resource allocation in trees

The distribution of assimilated C is a primary determinant of plant growth (Friedlingstein et al. 1999), yet our knowledge of the mechanisms by which allocation is regulated is poor (Poorter et al. 2012). A key issue with drawing generalized conclusions about the plasticity of C allocation in trees is with the inconsistency in terminology used to define C allocation to specific tissue or ecosystem components (Litton et al. 2007). Biomass partitioning, as the relative distribution of biomass between different tissue components, should not be confused with the allocation of newly fixed photosynthates to different organs. This is because the measured biomass at any time point represents the cumulative result of potentially dynamic C allocation over time (Poorter et al. 2015). This dynamic C allocation includes not only tree parts such as leaves, stems and roots but also respiration, exudation, turnover and transient C storage pools. As C allocation integrates all of these processes, it is extremely difficult using current methods to assess C allocation in whole trees. Disentangling the effects of resource supply on plant C allocation patterns is often assessed across “snapshots” in time, which should be done with caution (Reich et al. 2002). This is because of plants have developmental shifts in biomass partitioning, independent of resource supply, as they age (Müller et al. 2000, Poorter et al. 2015). Additionally, supplies of light and soil resources fluctuate continuously, making equilibrium with C allocation at any “snapshot” highly unlikely (Shipley and Meziane 2002).

As accurately measuring tree C allocation remains a difficult task, especially belowground, drawing conclusions that are applicable to whole plants or ecosystems remains a challenge. Currently, the representation of C allocation lags behind photosynthesis (*An*) in process-based forest models (Friedlingstein et al. 1999, Franklin et al. 2012, Iversen and Norby 2014) and our understanding of how global change impacts C allocation is incomplete (Litton et al. 2007, Warren et al. 2012). This knowledge gap of C allocation patterns in trees is of major concern due to the potential for forest ecosystems to sequester C in a changing climate. This deficiency requires more empirical data to derive basic principles that drive patterns of tree C allocation in changing environments. However, this will require novel experiments and approaches to better quantify shifts in C allocation above and belowground in future studies.

## 1.2.2 Coupling of photosynthesis and tree growth

On short timescales, *An* and total respiratory losses may not correlate with growth because of the dynamics of tissue C storage pools. On longer timescales, however, *An* and tissue respiration determine net plant C balance and must correlate to growth. This had led to the long standing debate over how strongly plant growth is controlled by either source or sink activity (Sweet and Wareing 1966, Körner 2013). To date studies manipulating either source activity (CO2 fumigation or defoliation) or sink activity (fruit removal, girdling or low growth temperatures) have not resulted in consensus when addressing this debate. This uncertainty arises from the difficulty in measuring the balance between C uptake and the fate of assimilated C among pools with long (biomass) or short (carbohydrate storage, respiration, exudation) retention times. When shifts in carbohydrate storage, tissue respiration or turnover rates occur, rates of C assimilation may not correlate with biomass production at a given time point (Rocha et al. 2006, Litton et al. 2007, Gough et al. 2008). To assess this balance will likely require integration of empirical and modelling approaches to assess leaf physiological and whole plant responses to manipulations of source-sink activity. To address this knowledge gap, new approaches are needed to test how interactions between source and sink activity affect the fate of assimilate C across different temporal scales.

## 1.2.3 Within canopy resource utilization

Due to the relationships between light, N and leaf photosynthetic capacity, it is commonly assumed that a limited availability of N should be distributed proportional to light availability within tree canopies. Observed canopy distribution of N is often less steep than optimal theory suggests, however, with shade leaves having more N than expected based on average light gradients (Peltoniemi et al. 2012). Additionally, constraints on water supply from the soil to the upper canopy may negatively impact the distribution of photosynthetic N to canopy light availability (Niinemets 2012, Peltoniemi et al. 2012). Whether insufficient hydraulic supply results in the observed sub-optimal canopy N gradients has yet to be empirically tested. Assessing leaf C gain as a function of light availability is also made difficult by frequent light fluctuations within a canopy, via sunflecks. Sunflecks cause temporal variation in PPFD that is not usually taken into account when considering what is optimal for a plant in terms of distributing resources along a gradient of light availability.

Leaves have been proposed to exhibit optimal physiological behavior in order to efficiently utilize and transport resources to maximize *An* (Thornley 1972). In trees, leaf physiology often focuses on full sun leaves and relationships between leaf physiological behavior and the availability of N, water and light between sun and shade leaves requires further attention. For example, gs has been hypothesized to be distributed within a canopy to utilize supplies of light, N and water to maximize *An* (Peltoniemi et al. 2012). In shade leaves, stomata might be expected to be more closed to efficiently use water with generally low *An*. To date, however, no clear picture has emerged on the relationship between gs and *An* within canopies (see Jifon and Syvertsen 2003, Tissue et al. 2006, Sellin and Lubenets 2010).

/ Additionally, mesophyll conductance (gm) also limits *An*, complex relationships may exist between canopy light gradients, leaf N and gm. Unfortunately, a scarcity of values for gm within tree canopies (see Lloyd et al. 1992, Piel et al. 2002, Warren et al. 2003, 2007) hinders our ability to relate individual leaf physiological behavior to optimal canopy C uptake. As the CO2 drawdown from the atmosphere to the site of carboxylation includes gs and gm, relationships between *An* with light availability, N and water within canopies will require the integration of both physiological parameters in future experiments. Incorporation of gm into process based tree growth models, similar to the progress made with gs, should be made a priority. Whether the limitations of gm on both leaf and canopy C gain can be parameterized accurately, however, has yet to be reported.

# 1.3 Thesis Objectives

The overall research goal is to evaluate how trees adjust their growth and physiology to maximize resource uptake and C gain. Specifically, this PhD research addresses knowledge gaps of how tissue C allocation, source and sink regulation and resource distribution affect the coordination between *An* and whole tree growth. In order to investigate key mechanisms that drive patterns in resource allocation in trees this research was carried out across multiples scales, from leaf isotope discrimination across the photosynthetic CO2 flux pathway to tissue specific biomass partitioning to total belowground C allocation. Understanding how resource allocation is correlated with individual leaf physiological behavior within tree canopies is crucial in accurately determining the capacity for whole canopy C assimilation, which is the essential resource for tree growth. Aspects of this research use manipulations of key global change factors, including elevated CO2, warming and drought to investigate the plasticity of observed physiological and growth responses to future climate scenarios. An improved understanding of how C is allocated within trees will supply much needed empirical data for process-based forest models where C allocation is currently poorly represented.

This research focuses on two Australian tree species, *Eucalyptus tereticornis* and *Eucalyptus saligna*, which have important roles in both native forests ecosystems and as commercial plantation timber. For example, *Eucalyptus tereticornis* is part of the critically endangered Cumberland Plain ecological community and *Eucalyptus saligna* is part of the critically endangered Blue Gum High Forest ecological community, with both communities having fragmented geographic distributions in the Sydney Basin bioregion (Hughes 2011). Both of these species are part of the “big nine” *Eucalyptus* species group which accounts for more than 90 % of planted *Eucalyptus* forests worldwide (Stanturf et al. 2013). As a result, the core findings of this PhD research have both conservation and commercial applications in addressing the productivity of these two important tree species in the face of global climate change. For example, considerable uncertainty remains as to the magnitude of CO2 fertilization on this continent as much of the vegetation is already under nutrient and/or water limitation (Hughes 2003).

This research was conducted using the state of the art Whole Tree Chamber experiment as well as a novel field-based seedlings container study at Western Sydney University. Using the two *Eucalyptus* tree species, fundamental principles of common optimization theories were tested at several tree growth stages. Leaf-level data were combined with tissue biomass production and canopy C fluxes to develop a better understanding of how resources are allocated to optimize whole tree growth. Empirical data were also integrated with a seedling growth model to test how resource limitation impacts the coordination between *An* and growth. Specifically, this thesis aimed to address current knowledge gaps by answering the following main questions:

1. **Where does the carbon go?**  
How will biomass partitioning and carbon allocation in *Eucalyptus* trees be affected by global climate change and belowground resource limitation?

2. **When do photosynthesis and growth not add up?**  
What do mass balance approaches reveal about the coordination of growth and photosynthesis at different temporal scales?

3. **Are whole canopies optimized for carbon gain?**  
How does resource availability within *Eucalyptus* tree canopies interact with dynamic physiology of sun and shade leaves to maximize canopy carbon gain?

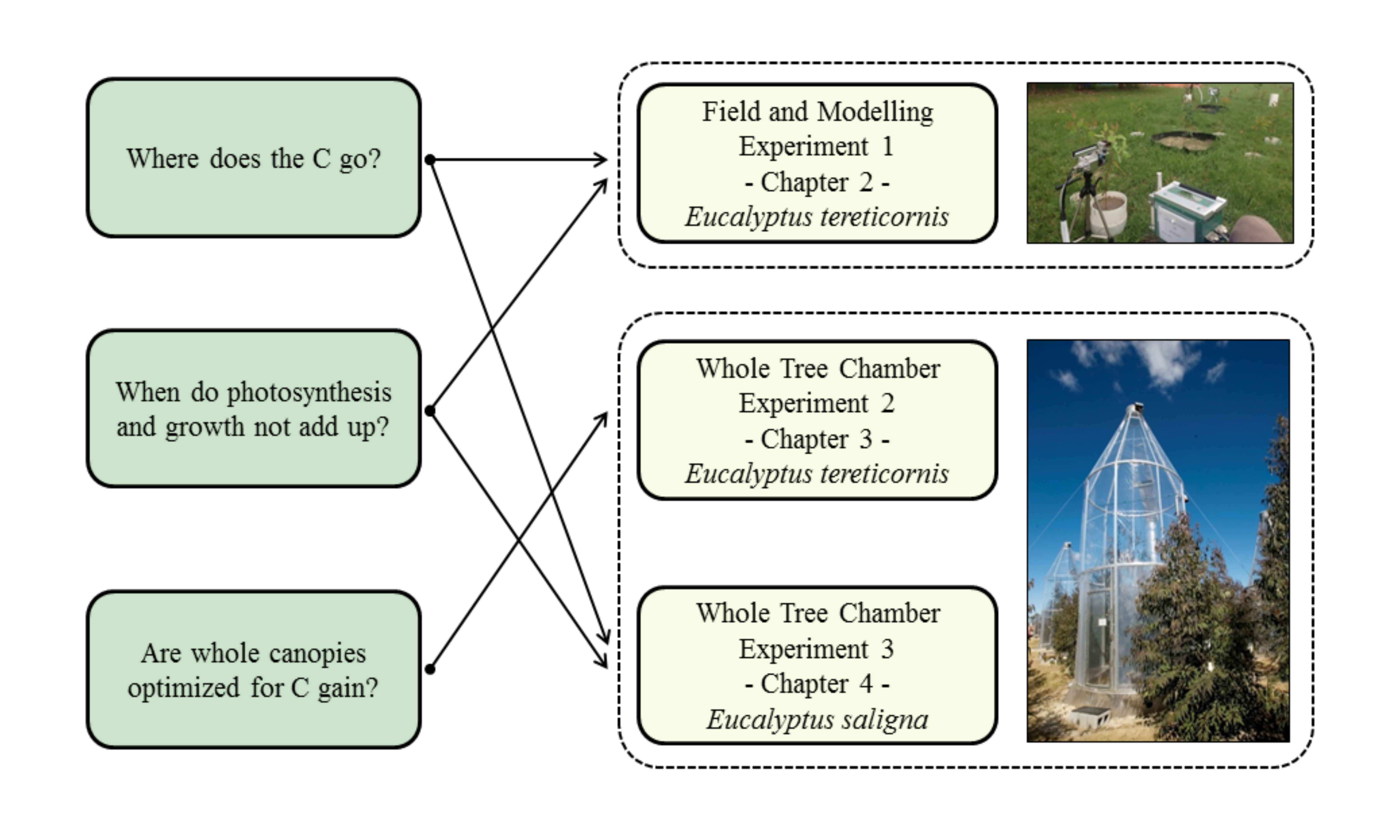
# 1.4 Thesis Outline

**Chapter 2** was designed to address thesis questions 1 & 2 by manipulating belowground sink strength in *Eucalyptus tereticornis* seedlings, via a range of container sizes, in a novel field-based experimental design. The effects of belowground resource limitation were then used to investigate patterns in biomass partitioning, leaf gas exchange and growth between container treatments and field grown seedlings. Empirically measured gas exchange parameters were then used to model daily C gain for each seedling to test the coordination between the reduction in *An* and biomass production of seedlings with soil volume restriction. The sensitivity of this model to different C allocation scenarios was used to speculate possible fates of photosynthetic C not accounted for in the default model. Results of this study are then used to address the ongoing debate over source or sink controls of *An* and growth. The flexibility of this mass balance modelling approach is used to highlight the importance of quantifying C allocation when evaluating the impacts of resource limitation on tree seedling growth.

**Chapter 3** addressed thesis question 3 by combining leaf gas exchange with online C isotope discrimination to measure the responses of sun and shade leaf physiology to light availability. The distribution of leaf N and leaf hydraulic conductance within *Eucalyptus tereticornis* canopies was examined to test if the resources required for *An* were preferentially invested into sun leaves, as predicted by standard optimal theory, to maximize whole canopy C gain. The physiological capacity of shade leaves to respond to increases in light availability was quantified to determine if shade leaves “lie in wait” for sunflecks. Trees were grown in climate controlled WTCs under ambient and elevated air (+3°C) temperature treatments to test the impacts of future climate warming on each of these processes. Rarely have relationships between *An* and both gs and gm been quantified within tree canopies, thus results from this experiment are used to reveal potential new mechanisms underpinning leaf gas exchange responses to light. Unexpected decreases in water-use efficiency in shade leaves were related to the capacity of inner canopy leaves to rapidly utilize sunflecks. Empirical data from this experiment improves our ability to predict whole canopy C gain by prioritizing both sun and shade leaf physiology, which may be optimized differently.

**Chapter 4** addresses thesis questions 1 & 2 by quantifying high resolution net canopy photosynthesis measurements and C allocation in *Eucalyptus saligna* trees grown under drought and elevated CO2 treatments in factorial combination. The unique WTC experimental facility measures cumulative net aboveground C fluxes which were compared to canopy leaf area and tree biomass production. A novel framework was also applied to calculate a more reliable estimate of the sensitivity of TBCA to global climate change. I then evaluated how potentially interacting climate change factors impacted C allocation to above and belowground pools through time. Results from this experiment emphasize the need to correctly define individual aspects of tree C allocation and separate impacts on measured biomass from other components of C allocation when evaluating tree growth responses. As empirical measurements of C allocation are difficult to obtain, especially with belowground processes, these results provide much needed empirical data to validate process-based model where C allocation is represented.

**Chapter 5** presents the synthesis and outlook of the major findings in my PhD research as they relate to each main thesis question. First, shifts in C allocation likely occurred as these two *Eucalyptus* species were impacted by changing environments, even though biomass partitioning of harvested trees remained relatively conserved. Combined results from Chapters 2 & 4 are used to discuss how observed responses of biomass partitioning and C allocation correspond to prevailing theory and how these mass balance approaches have improved our understanding of the investment of photosynthetic C in trees. Second, I show that coupling between total C gain and tree growth can be disrupted over shorter experimental time frames, while over longer time scales they are strongly correlated as a function of leaf area. Results from Chapter 2 use empirical data and modelling approaches to address the current debate over source and sink control over seedling growth, while Chapter 4 is used to discuss how unique measurements of net canopy photosynthesis correlate to tree productivity under future climate scenarios. Last, I show that sun and shade leaves exhibit different physiological behavior in order to utilize differential availability of external resources within *Eucalyptus tereticornis* canopies. Results from Chapter 3 are used to show that shade leaf physiology is likely optimized differently from sun leaves in order to respond to sunflecks, which has important consequence for current theories regarding how resources are allocated to optimize canopy C gain.

  
**Figure 1.1**. Each main thesis question linked to individual experiments designed to address current knowledge gaps. Experiment 1 was conducted with a novel field-based seedlings container study, while experiments 2 and 3 occured in the Whole Tree Chamber experimental system.

# 1.5 Reproducible Research

Science and hypothesis testing is driven by data, yet it is a challenge to ensure that reported experimental data are appropriately described, standardized, archived and openly available (Hanson et al. 2011). Reproducibility of analyses serves as a minimum standard for judging scientific claims when full independent replication of a study is not possible, which should include making available the data and the computer code used to analyze the data (Peng 2011). Not only does creating reproducible research increase the reliability and credibility of one's findings, but it encourages the engagement of the scientific community to advance new research ideas. Every aspect of this PhD research attempts to adhere to these key principles of reproducibility. Raw data and code for each experimental chapter are located in an easily accessible online repository. This entire thesis is also compiled as a reproducible document, including R code (R Development Core Team 2011) to analyze data, generate text and create tables/figures, which are all made available for open access. As a result, all necessary information required to reproduce this thesis, in its entirety, are located in repositories at <https://github.com/CourtneyCampany>.

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