**Resource allocation in *Eucalyptus***  
  
  
By

**Courtney Campany**  
  
  
**A thesis submitted in fulfilment of the requirements**  
**for the degree of Doctor of Philosophy**  
   
  
**2016**

# Acknowledgements

“I am the Lorax. I speak for the trees. I speak for the trees for the trees have no tongues.” --Dr. Seuss

I dedicate this thesis to my mother, for she has been my inspiration to become a scientist for as long as I can remember. Her passion for the natural world is infectious and her ability to pass her scientific knowledge to others is inspirational. It is because of you that I flip over rocks to see what is hiding underneath.

I would equally like to acknowledge my father for instilling in me the work ethic and drive that has carried me to this point. Without his undying support I might never have achieved the level of success I have been afforded.

À Caroline, rien de tout ça n’aurait été possible sans que tu sois à mes côtés. Tu as été un roc quand j’avais besoin d’ancrage et une lumière quand mon chemin semblait perdu.”

## Statement of Authentication

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

# Preface

# Table of Contents

# LIST OF TABLES

**Table 2.1**. Responses of plant and leaf characteristics of *Eucalyptus tereticornis* seedlings to soil volume treatments.

**Table 2.2**. Responses of root characteristics of *Eucalyptus tereticornis* seedlings to soil volume treatments.

**Table 2.3**. Responses of leaf level gas exchange parameters of *Eucalyptus tereticornis* seedlings to soil volume treatments.

**Table 2.S1**. Seedling growth model default parameters.

**Table 3.1**. *Eucalyptus tereticornis* leaf morphological and physiological traits between full sun and shade leaves under ambient and elevated temperature treatments.

**Table 3.2**. *Eucalyptus tereticornis* leaf gas exchange parameters for sun and shade leaves under ambient and elevated temperature treatments.

**Table 4.1**. Final harvest C mass of above and belowground tissues, cumulative aboveground tree C uptake () and specific leaf area (SLA).

# LIST OF FIGURES

**Figure 2.1**. Soil volume treatment means ± standard error of height growth (a), diameter growth (b), and seedling leaf area estimated from leaf counts (c) measured weekly of *Eucalyptus tereticornis* seedlings across the experiment duration in 2013.

**Figure 2.2**. Daily maximum and minimum temperature (a), total daily PPFD (b), and daily maximum vapour pressure deficit (c) across the experiment duration in 2013.

**Figure 2.3**. Soil volume treatment means of biomass partitioning to leaves, stems, and roots at harvest (a), bi-variate relationships between mass allocation to leaves and stems + roots (b) and leaf mass as a function of fine root biomass with ± standard error (c).

**Figure 2.4**. Soil volume treatment means ± standard error, across all measurement campaigns (n = 6), of light saturated rates of photosynthesis at 25°C.  
**Figure 2.5**. Photosynthetic capacity, on a leaf mass basis, as a function of accumulation of leaf starch (a) and leaf nitrogen content without TNC (b).

**Figure 2.6**. Total carbon mass for harvested and modeled seedlings versus predicted total carbon gain after 120 days (a) and reductions in final seedling carbon mass, both modeled and observed, as a function of the reduction in leaf photosynthesis across treatments (b).

**Figure 2.S1**. Sensitivity testing of seedling growth model to different carbon allocation strategies including; constraints of leaf mass fraction to treatment specific final harvest values (a) and increases in respiration of non-leaf tissue components by 50 % (b).

**Figure 3.1**. Bars represent the local light environment for sun and shade leaves during six gas exchange campaigns from October 2013 to April 2014.

**Figure 3.2**. (a) ACi curves for sun and shade leaves at elevated (ET) and ambient (AT) temperature treatments.

**Figure 3.3**. The response of *An* to gs (a) and gm (b) for sun leaves measured at high light and shade leaves measured at both low and high light under their respective elevated and ambient temperature treatments.

**Figure 3.4**. The mean ± 1 standard error of gs (a), gm (b) and *An* (c) of sun leaves and shade leaves at both low and high light pooled across six measurement dates.

**Figure 3.5**. (a) Response of instantaneous transpiration efficiency (ITE) to VPD for sun leaves and shade leaves at both low and high light with elevated and ambient temperature treatments. (b) The relationship between leaf 13C and leaf Na for sun leaves at high light and shade leaves at low light.

**Figure 3.6**. Relationship between the observed discrimination of 13CO2 measured during photosynthesis () and measured Ci/Ca for sun leaves measured at high light and shade leaves measured at both low and high light.

**Figure 3.7**. The mean ± 1 standard error of (a) intercellular CO2 concentration (Ci), (b) CO2 concentration in the chloroplasts (Cc) and (c) CO2 drawdown from substomatal cavities to sites of carboxylation of sun leaves and shade leaves at both low and high light (Ci-Cc).

**Figure 3.S1**. Daily maximum and minimum temperature (a), daily maximum VPD (b) and total daily PPFD (c) for each chamber across the experiment duration.

**Figure 3.S2**. Photosynthetic CO2 response (ACc) curves for sun and shade leaves at elevated and ambient temperature treatments.

**Figure 3.S3**. Response of *An* (a), gm (b) and Ci-Cc to leaf temperature for sun leaves and shade leaves at low and high light.

**Figure 3.S4**. Response of VPD (a), gs (b) and Ca-Ci to leaf temperature for sun leaves and shade leaves at low and high light.

**Figure 4.1**. Conceptual diagram depicting the major components of C flow among plant components including; uptake via photosynthesis, allocation to component tissues, tissue respiration and root exudation.

**Figure 4.2**. Whole tree C mass as a function of cumulative aboveground C flux for each WTC tree. Values of cumulative aboveground net C flux were measured over the final eleven months of the experiment.

**Figure 4.3**. Estimated canopy leaf area for each WTC tree over the final eleven months of the experiment (April 2008 to March 2009).

**Figure 4.4**. Treatment means of cumulative aboveground C flux as a function of mean daily canopy leaf area over the final eleven months of the experiment.

**Figure 4.5**. Treatment means of C mass fractions of leaves (a), stems (branches+boles) (c) and roots (e) as a function of tree size, via whole tree C mass.

**Figure 4.6**. Cumulative aboveground net C flux and additive C allocation to individual tree components from 15 April 2008 to 16 March 2009. Each panel represents mean values for each treatment combination (n=3).

**Figure 4.7**. Treatment means ± 1 standard error of cumulative aboveground net C flux, TBCA, and the residual belowground C flux ().

**Figure 4.8**. Total belowground C allocation as a function of cumulative aboveground net C flux across the final eleven months of the experiment.  
**Figure 4.S1**. Root mass as a function of shoot mass in *Eucalyptus saligna* for potted seedlings harvested before planting of WTC trees (n=17) and WTC trees harvested after 2 years (n=12).

**Figure 4.S2**. Cumulative aboveground net C flux and additive C allocation of individual tree components tree components from 15 April 2008 to 16 March 2009. Panels represent each individual WTC.

# LIST OF ABBREVIATIONS

*An* Net leaf photosynthesis rate  
aCa Ambient CO2 treatment  
ACi Photosynthetic CO2 response curves  
Amax Leaf net photosynthesis at saturating light and CO2 concentration  
Asat Leaf net photosynthesis at saturating light  
AT Ambient air temperature treatment  
C Carbon  
[CO2] CO2 concentration  
Ca Atmospheric CO2 concentration  
 Aboveground standing crop C mass  
Cday Predicted daily carbon assimilation  
Ci Intercellular CO2 concentration (or partial pressure)  
Cc Chloroplastic CO2 concentration (or partial pressure)  
 Total C mass of roots  
E Leaf transpiration  
eCa Elevated CO2 treatment  
ET Elevated air temperature treatment  
FACE Free-air CO2 enrichment experiments  
 Net aboveground carbon uptake  
 Residual belowground C flux  
free freely-rooted  
FRLD Fine root length density  
gs Stomatal conductance  
gm Mesophyll conductance  
ITE Leaf level instantaneous transpiration efficiency  
Jmax Maximum rate of photosynthetic electron transport  
Kl Leaf-specific hydraulic conductance  
LA Leaf area  
LMA Leaf mass per unit area  
LMF Leaf mass fraction  
N Nitrogen  
Na Leaf nitrogen on an area basis  
Nf TNC-free leaf nitrogen content  
PPFD Photosynthetic photon flux density  
Q10 Rate of change in respiration due to 10 °C increase in temperature  
*R* Leaf dark respiration rate  
RMF Root mass fraction  
SLA Specific leaf area  
SLAf TNC-free Specific leaf area  
SMF Stem mass fraction  
TBCA Total belowground C allocation  
TNC Total non-structural carbohydrate  
TDL Tunable diode laser  
Vcmax Maximum rate of rubisco carboxylation  
VPD Vapour pressure deficit  
VPDB Standard Vienna Pee Dee Belemnite  
WUE Water-use efficiency  
WTC Whole-tree chambers  
13C C isotope ratios of 13^C to 12^C expressed relative to standard Vienna Pee Dee Belemnite  
 C isotope discrimination during C3 photosynthesis  
l Midday leaf water potential  
pd Predawn leaf water potential  
s Self shading parameter

# Abstract

Plants must utilize external resources including light, CO2, water and mineral nutrients to support photosynthetic carbon (C) gain. This photoassimilate is then allocated within the plant as the essential C resource for growth, maintenance and storage. Theory and observations suggest that C allocation and leaf physiology are optimized to maintain functional balance for external resource capture and to maximize C gain. However, the impacts of a changing climate may disrupt the proposed balance of C allocation between above and belowground pools. Variation in resource distribution and leaf physiology within tree canopies is also not fully understood, thus all canopy leaves may not follow theories of leaf optimal behavior. This lack of understanding regarding C uptake and the fate of assimilated C inhibits our ability to precisely test the coordination between canopy photosynthesis and growth. To address these broad ecological questions, this PhD research utilized a diverse set of experiments which manipulated resource availability and climate factors on *Eucalyptus* tree species. My goal was to measure aspects of resource allocation and C uptake across different scales, from leaf to whole tree, to improve understanding of the physiological processes which determine tree growth and the sensitivity of these processes to changing environments.

First, I determined whether manipulations of soil volume would limit growth in *Eucalyptus tereticornis* seedlings by disrupting the balance between source and sink activity. Seedlings were grown in a large range of container sizes and planted flush to the soil alongside naturally planted freely-rooted seedlings (free). Aboveground growth of seedlings in containers was negatively affected compared to free seedlings soon after the experiment started. Despite large reductions in total growth across soil volume treatments, relative partitioning of mass to leaves, stems and roots was similar for all seedlings after 120 days. Leaf photosynthetic capacity decreased in containers compared to free seedlings, and was correlated to both leaf nitrogen (N) content and starch accumulation. Although belowground sink limitation resulted in a reduction of net leaf photosynthesis (*An*), a mass balance model concluded that these reductions were not large enough to explain observed growth responses. As *An* and growth were not tightly coordinated, the model predicted excess photosynthetic C not attributed to biomass in potted seedlings. Quantifying the fate of this excess C will be essential in evaluating feed-backs between sink strength and leaf C uptake in future studies.

Second, I investigated how light gradients within *Eucalyptus tereticornis* tree canopies affect the distribution of resources that define photosynthetic capacity of sun and shade leaves. Trees were grown in climate-controlled whole tree chambers under prevailing ambient and warmed (+3 °C) treatments and leaf gas exchange was coupled with online C isotope discrimination to measure *An*, stomatal conductance (gs) and mesophyll conductance (gm) of sun and shade leaves. Photosynthesis rates were reduced by ca. 40 % in shade leaves associated with a 75 % reduction in photosynthetically active radiation compared to sun leaves. Photosynthetic capacity (ca. 20 % lower Vcmax and Jmax) and leaf N were also lower in shade leaves than sun leaves however; gs was similar. Leaf Ci, estimated from both leaf 13C and gas exchange, was higher in shade leaves than sun leaves. Here, the optimization theory hypothesis that Ci should be optimized throughout the canopy was rejected because water use efficiency was lower in shade leaves, compared to sun leaves. When light intensity was increased from low light to high light for shade leaves, both gs and gm increased rapidly (within minutes), leading to increases in *An* greater than sun leaves at the same high light environment. This rapid response of gm with light likely enables shade leaves to respond quickly to sunflecks and possibly represents a new mechanism underpinning leaf gas exchange responses to light. This capacity of shade leaves to adjust their physiological behavior and increase C uptake when sunflecks occur likely plays significant role in whole tree C uptake for some tree species, albeit at the cost or reduced water-use efficiency. These findings reveal that plant resources within a canopy may be distributed to utilize sunflecks and the dynamic physiological responses of shade leaves to altered light environments must be accounted for when up-scaling leaf level measurements to predict whole canopy C gain.

Finally, I examined how net aboveground C uptake correlated to tree biomass growth and whether elevated [CO2] and drought treatments altered C allocation patterns above or belowground in *Eucalyptus saligna* trees. Trees were grown in climate-controlled whole tree chambers (WTCs) over a period of two years under treatments of two [CO2] (380 ppm and 620 ppm) and two watering regimes (well-watered and a four-month drought) in factorial combination. Additionally, we utilized a novel approach to calculate total belowground C allocation (TBCA) for each WTC as the residual between the measured aboveground net CO2 uptake and aboveground C mass. Measured cumulative aboveground net C uptake correlated positively to whole tree C mass production and leaf area over the final eleven months of the experiment. Contrary to previous studies, cumulative TBCA was unaffected by either elevated CO2 or drought treatments. As a fraction of total aboveground net C uptake, TBCA was also found to remain relatively stable across daily time steps for all trees. Increases in C allocation to leaves were detected in elevated CO2 treatments, while the effects of a 4 month drought were negligible on C allocation in aboveground tissues. These results reveal how climate change factors impact the investment of photosynthetic C in a *Eucalyptus* tree species and provide evidence that belowground processes may not be as sensitive to global change factors as previously thought.

In conclusion, this PhD research addressed interrelated questions regarding resource allocation in *Eucalyptus* tree species by linking leaf physiology to whole canopy C gain and allocation of photosynthetic C to whole tree growth. This study confirms that the distribution of photosynthetic resources constrain canopy C uptake, yet within canopy leaf physiology does not follow prevailing optimal theory regarding water use. Results from this work reveal how quantifying the fate of photosynthetic C among tissue pools, beyond biomass production, is imperative to accurately assess the impacts of environmental change on tree productivity. This research offers critical empirical data needed to refine process based models which predict canopy C gain from rates of *An* and forest growth models where C allocation is represented. Ultimately, this work contributes valuable information regarding the physiological and growth responses of *Eucalyptus* tree species essential for reconciling the impacts of resource availability and global climate change on Australian ecosystems and the productivity of *Eucalyptus* plantation forests.