Edaphic and ecophysiological responses to early establishment weed control and fertilisation in F₁ hybrid pine plantations of southeast Queensland

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Abstract

Post-planting silviculture in the exotic pine plantations of Southeast Queensland focuses on fertilisation and weed control at early plantation establishment. Early establishment silviculture in pine plantations aims to reduce the competition for light, nutrients and water in the short term, while maximising resource conversion for growth in the long term. However, silviculture can be applied in a systematic way without necessarily considering the limitations to maximum tree growth at each site. Accordingly, silvicultural treatments could be applied in a site specific manner to better reflect the limitations to tree growth at each site (e.g. nutrition and/or water), or for maximum effectiveness based on seasonal limitations (e.g. weed competition, water availability).

This research aimed to investigate the effects of early establishment weed control and fertilisation practices on soil carbon (C) and nitrogen (N) cycling (as an indicator of soil fertility), tree nutrition (particularly N nutrition), growth and eco-physiological responses, in the F₁ hybrid exotic pine plantations (Pinus elliottii Engelm var. elliottii x Pinus caribaea Morelet var. hondurensis (Sènècl.) W.H.G. Barett & Golfari.) in the subtropics of Southeast Queensland. Chapter 1 introduces each data chapter and summarises the major findings of this thesis. Chapter 2 reviews the literature previously reported on other silvicultural investigations as well as outlining the effects of weed control and fertilisation on soil fertility, tree growth and physiological variables. Chapters 3 and 4 report the effects of routine and luxury fertilisation, and routine and luxury weed control in an 8 year old F₁ hybrid plantation at Toolara State Forest (26° 1.556′S, 152° 48.805′E). Chapters 5 and 6 report on 2 year-old trees at adjacent sites with different soil types, in Beerburrum State Forest (27°2.55′S, 153°1.18′E), under five weed control and two fertiliser treatments. The soil types at each site in Chapters 5 and 6, yellow earth and Grey Podzolic, are typical
of those at two landscape positions, mid-slope and lower-slope, within the management area.

Weed biomass (t ha$^{-1}$) was positively correlated to soil total N, potentially mineralisable N (PMN), soil moisture content (MC), hot water extractable organic carbon (HWEOC) and hot water extractable total nitrogen (HWETN) at the Toolara site at 8-years-old, indicating that routine weed control treatments increased C and N cycling in the labile pools by 8-years-old. Soil C isotope composition ($\delta^{13}$C) was also positively correlated to weed biomass, which indicates increased organic matter inputs under these treatments after 8 years. Conversely, in the most intensive weed control treatment (referred to hereafter as luxury weed control), weed biomass was significantly less and resulted in significantly higher soil N isotope composition ($\delta^{15}$N), and non-significant, elevated nitrate N (NO$_3^-$-N) in the soils in the inter-planting rows. Soil $\delta^{15}$N at this site was also negatively correlated to soil total C, total N, labile C (HWEOC) and N (HWETN) pools, indicating that reduced C cycling to the soil and lack of weeds to immobilise mineral N may be a possible mechanism reducing N transformations in the soil.

At the 2 year-old site, foliar N concentrations and $\delta^{15}$N were negatively correlated to relative weed cover at 0.8 and 1.1 years on the Yellow Earth soil type. However, due to the recent cultivation, uniform soil N mineralisation across all treatments reduced the effectiveness of using foliar $\delta^{15}$N techniques to quantify the changes in soil N cycling processes resulting from weed control treatments at the 2 year-old plantation site. In addition, chemical fertilisation with urea had a dilution effect on foliar $\delta^{15}$N and hence fertilisation with N fertiliser may limit the use of the foliar $\delta^{15}$N technique to identify the changes in soil N cycling as a result of management such as weed control.
At the 8-year-old site, soil $\delta^{13}$C was negatively correlated to foliar $\delta^{15}$N at 13 of the 15 tree canopy sampling positions, indicating a potential link between increased organic matter inputs in the soils (as indicated by soil $\delta^{13}$C) and N sources available for tree growth. This relationship suggests that although there was lower N transformations due to slower N cycling under the routine weed control treatment, the N source available for growth may have been more-so available through symbiotic relationships with N fixing fungi, which resulted in decreased foliar $\delta^{15}$N under these treatments. Further research in this area has been recommended to confirm this although this principle has been supported by other research (Silva and Anand 2011).

At both Toolara (Chapters 3 and 4) and Beerburrum (Chapters 5 and 6), tree water use efficiency (WUE) was positively correlated to both tree growth variables and foliar $\delta^{15}$N. However, only the physiological surveys (Chapters 5 and 6) were able to link the effects of silviculture on the C gain (growth) to tree water use efficiency (WUE), xylem pressure potential ($\Psi_{XPP}$) and N nutrition (foliar N concentration, foliar $\delta^{15}$N and photosynthetic N use efficiency (PNUE)).

In Chapters 5 and 6 a survey of physiological variables indicated that tree WUE was triggered in trees with greater N and was dependent on whether the limitation to physiological processes came from stomatal (increased water loss by transpiration) or non-stomatal limitations (by physiological variables such as xylem pressure potential ($\Psi_{XPP}$) or N nutrition). On the Yellow Earth soil type, photosynthesis was explained by the relationship between stomatal conductance and leaf internal CO$_2$ concentration ($C_i$). Silvicultural treatments also influenced the relationship between photosynthesis and stomatal conductance which were significantly greater in the luxury weed control and luxury fertilisation compared with the nil, mechanical and routine weed control treatments. In addition, height and height periodic annual increment (PAI) at 1.7 years were negatively related to the capacity for stomatal conductance and transpiration in the
morning measurements. While, in the afternoons, $C_i$ was positively related to diameter growth, and diameter growth was negatively related to $\Psi_{XPP}$ and WUE$_i$ and height was negatively related to WUE$_i$.

On the other hand, on the Grey Podzolic soil, photosynthetic nitrogen use efficiency (PNUE), photosynthesis and transpiration were each explained by the relationship between stomatal conductance and $C_i$. In addition, photosynthesis was negatively related to $\Psi_{XPP}$, where the luxury weed control had significantly greater photosynthesis for any level of $\Psi_{XPP}$. Stomatal conductance was also related to foliar N concentrations where luxury weed control and luxury fertilisation had higher stomatal conductance for any level of foliar N concentration. Luxury weed control also had the highest intercept and slope in the relationship between foliar $\delta^{13}C$ and transpiration in the mornings where trees with lower transpiration had increased foliar $\delta^{13}C$, while trees with higher PNUE had greater transpiration and lower foliar $\delta^{13}C$.

The $C_i$ in the mornings was also negatively related to diameter growth on the Grey Podzolic soil type but by the afternoon there was a positive relationship between diameter at ground level (DGL) PAI at 1.7 years and $C_i$ or transpiration. There were significant positive relationships between intrinsic WUE and diameter (DGL and DBH) or height at 1.7 years growth in the mornings. Finally, in the Grey Podzolic soils there were negative relationships between foliar N concentration and $\Psi_{XPP}$, between $\Psi_{XPP}$ and foliar $\delta^{13}C$, and significant positive relationships between photosynthesis and foliar $\delta^{13}C$ or foliar N concentration although the afternoon measurements did not vary significantly between the treatments, suggesting non-stomatal limitations to photosynthesis resulting from variations in $\Psi_{XPP}$ and foliar N concentrations on these soils.

In summary, this research has concluded that the use of soil $\delta^{13}C$ and $\delta^{15}N$ techniques was sensitive to the soil C and N dynamics influenced by the silvicultural
practices at 8 years after establishment, but their effectiveness was reduced at earlier establishment (<2 years) due to cultivation effects on soil N mineralisation. Increased N transformations (faster N cycling) resulted from the luxury weed control and fertilisation treatments, and led to increased tree growth and WUE. Increased tree stem size was also related to increased WUE and lower basic density, which links stem anatomy to drought tolerance. Hence, weed control and fertilisation treatments can have significant implications for plantation water and nutrient resource availability, and can therefore be applied to maximise growth in consideration of individual site conditions i.e. low site water and N availability (soil on upper slopes) or increased weed competition (soils on lower slopes or moister soils) at early establishment. Furthermore, weed control and fertilisation treatments can have significant implications for longer term soil fertility due to C and N cycling processes and can provide an important factor for managing soil C and N into the future.
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Declaration of Originality

I certify that this thesis is my original work and has not been previously submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

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Preface

This research was designed in collaboration with my supervisors Professor Zhihong Xu, Dr Tim Blumfield and Dr Ken Bubb. I undertook the establishment of Experiment NC 677 and 678 with the assistance of my supervisors and the collection of data and samples through either assistance from DPI Forestry staff or university colleagues for the field experiments (see acknowledgements). I have been advised in statistical theory and procedures initially by Professor Janet Chaseling from Griffith University and thereafter by Dr Carole Wright from Agri-Science Queensland in the Department of Agriculture, Fisheries and Forestry. Chapters 3, 4, 5 and 6 were prepared in the form of manuscripts for publication in peer-reviewed journals. These chapters have been modified for inclusion within this thesis. I was also responsible for all research conducted in these papers unless otherwise stated and the co-authors were my doctoral program supervisors or mentors (tree physiology and statistics).
Papers published from this thesis


Papers submitted and under consideration for publication from this thesis

Ibell, Paula T., Blake, T., Xu, Zhihong, Blumfield Timothy. J. Effects of weed control and fertilisation on tree physiological processes, foliar δ^{13}C and δ^{15}N and growth at early establishment in an exotic F_{1} hybrid pine plantation of subtropical Australia. Submitted to Journal of Soils and Sediments. November 2013

Published abstracts as a result of this thesis

Acknowledgement of published papers included in this thesis

Section 9.1 of the Griffith University Code for the Responsible Conduct of Research ("Criteria for Authorship"), in accordance with Section 5 of the Australian Code for the Responsible Conduct of Research, states:

To be named as an author, a researcher must have made a substantial scholarly contribution to the creative or scholarly work that constitutes the research output, and be able to take public responsibility for at least that part of the work they contributed. Attribution of authorship depends to some extent on the discipline and publisher policies, but in all cases, authorship must be based on substantial contributions in a combination of one or more of:

- conception and design of the research project
- analysis and interpretation of research data
- drafting or making significant parts of the creative or scholarly work or critically revising it so as to contribute significantly to the final output.

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Researchers are expected to:

- Offer authorship to all people, including research trainees, who meet the criteria for authorship listed above, but only those people.
- accept or decline offers of authorship promptly in writing.
- Include in the list of authors only those who have accepted authorship
• Appoint one author to be the executive author to record authorship and manage correspondence about the work with the publisher and other interested parties.

• Acknowledge all those who have contributed to the research, facilities or materials but who do not qualify as authors, such as research assistants, technical staff, and advisors on cultural or community knowledge. Obtain written consent to name individuals.

Included in this thesis are 3 published papers in Chapters 3, 4 and 5 which are co-authored with other researchers. My contribution to each co-authored paper is outlined at the front of the relevant chapter. The bibliographic details for these papers are:


• Chapter 5: Ibell, Paula T., Xu, Zhihong, Blumfield Timothy. J. (2012) Weed control treatments influence soil $\delta^{13}$C, foliar $\delta^{15}$N and $\delta^{13}$C in an exotic pine plantation of subtropical Australia. Plant and Soil. (DOI) 10.1007/s11104-012-1554-3


Appropriate acknowledgements of those who contributed to the research but did not qualify as authors are included in each published paper.

(Signed)
Name of Student

(Countersigned)

Supervisor: Name of Supervisor
“Sylvicultural (sic) practice is founded upon intimate knowledge of the life-histories of trees. The life history of every species is different and must be observed, investigated and recorded patiently for each, from seed to maturity decay. Whilst red and white cedar and maple spring exuberantly from the ground only to meet in frost, drought and twig borers, the very dangers to which their undue succulence exposes them, the minute Hoop Pine seedling lurks unseen beneath the weed masses, and by its ability to endure in babyhood an almost overwhelming shade, and later to resist the blight of frost and drought which lays low its fast-growing competitors, succeeds to ultimate dominance of the forest...All these processes and a myriad more must be isolated before silvicultural command over species may be established, and in no State of Australia are the difficulties greater or the sylvics more complex than in the sub-tropical State of Queensland.”

Edward Harold Fulcher Swain, Acting Director of Forests, Queensland Forestry Department, 1918.
(Taylor 1994)
Chapter 1 Introduction

The current emphasis on exotic pine plantation management is achieving higher economic returns with the expectation of more responsible environmental performance. However, there are still efficiencies to be gained in plantation management by tailoring silvicultural treatments to improving growth on specific sites and maintaining soil nutrient capital over the long term. For example, understanding how various silvicultural techniques influence nutrient and water competition, C and N cycling and/or tree eco-physiological processes at different sites could identify important limitations to tree growth at some sites.

In addition, silvicultural practices provide a suite of options for forest plantation managers to influence resource availability. However, the direct contributions of various silvicultural treatments on C, N and water relationships are relatively unknown in the F1 hybrid pine plantations of Southeast Queensland. Further studies, therefore, may yield valuable information on how weed control and fertilisation influences resource availability and affects tree growth in this region.

Developing a better understanding of how silvicultural techniques influence C, N and water use in plantation soils is important because it allows forest managers to direct their increasingly limited resources more effectively. This may be achieved by identifying a series of decision making scenarios (silvicultural treatments) and testing them empirically across a range of different sites. These experiments offer the quantification of the short and long-term effects of those treatments on tree growth processes and nutrient cycles. By linking tree growth and competition dynamics (weeds) to other environmental variables (soil, tree physiology and tree water use), we can start to identify the processes influencing tree growth under each scenario, and select the best management option to overcome the growth limiting factors at each site.
This thesis aimed to investigate how early establishment silvicultural treatments influenced both C and N cycling and tree eco-physiological responses in an F1 hybrid exotic pine plantation in subtropical Australia in 2- and 8-year old plantations. Chapter 2 reviews literature relevant to these processes and aimed to identify known benefits of silviculture on tree performance, C and nutrient cycling and competition dynamics. It also reviews how tree physiological variables influence growth at early establishment, post-establishment, juvenile and later stages of plantation growth, as well as reviewing contemporary research on the use of carbon (δ\(^{13}\)C) and nitrogen (δ\(^{15}\)N) isotopes in soil processes and plant physiology.

The experimental sites and experimental design have been included in each of the chapters for each experiment. Chapter 3 is the first of the four data chapters and investigates the effect of weed control and fertilisation on soil C and N cycling and other soil macro-nutrients (P and K) at 7-8 years after establishment. It also investigates how weed control and fertilisation influenced weed biomass and what effect the presence or absence of organic residues resulting from weeds had on soil fertility indicators including soil labile C (hot-water extractable organic C (HWEOC)), and N pools (hot-water extractable total N (HWETN), potentially mineralizable N (PMN), nitrate (NO\(_3\)-N) and ammonium (NH\(_4^+\)-N) and gravimetric soil moisture content (MC). In addition, the influence of treatments on soil carbon (δ\(^{13}\)C) and nitrogen (δ\(^{15}\)N) isotope compositions were investigated and related to labile C and N pools and weed composition to better understand how silviculture would influence the rate of C and N cycling using both δ\(^{13}\)C and δ\(^{15}\)N in the soil.

Chapter 4 links the effects found in the soil in Chapter 3 to the foliage of trees. It investigates the relationships between δ\(^{13}\)C and δ\(^{15}\)N in the soil (organic matter and N cycling), N assimilation and water use in the trees, and proposes how δ\(^{13}\)C and δ\(^{15}\)N
data help to explain the processes occurring as a result of the different silvicultural treatments.

Chapters 5 and 6 investigate early establishment tree growth up to 2 years after establishment, and relate growth to relative weed cover on two soil types in the subtropics. In addition, foliar N concentration, $\delta^{15}$N and $\delta^{13}$C are used to identify how treatments influence tree N assimilation, soil N cycling and tree water use. A diurnal physiological survey is also undertaken, in the two-year-old trees, on each soil type, to identify what physiological processes (including photosynthesis ($A_n$), stomatal conductance ($g_s$), transpiration ($E$), photosynthetic N use efficiency (PNUE), intrinsic water use efficiency or photosynthesis/stomatal conductance ($WUE_i$) and xylem pressure potential ($\Psi_{XPP}$)), were influencing (or limiting) tree growth at each site under the prevailing environmental conditions. Figure 1.1 indicates a simplified flowchart of the proposed linkages among soil and plant variables subjected to different weed control and fertilisation treatments as proposed in this thesis.

Finally, Chapter 7 summarises all the results from each Chapter and discusses the implications of this research for future research and plantation management in general. It also gives a summarised overview in two flowcharts outlining the identified (1) soil and (2) plant processes, resulting from silvicultural treatments in an F1 hybrid pine plantation, in the subtropics of southeast Queensland, as identified by this thesis.
Figure 1.1: A simplified flowchart encompassing the linkages among soil and plant variables subjected to early establishment silviculture.
Chapter 2 A review of literature related to silviculture and its influence on edaphic, tree ecophysiology and growth

Pinus species are widely grown throughout the world and are valued for their fast growth rates, timber strength and ability to tolerate nutrient poor sites. Their suitability as exotic species, outside their natural environment is enhanced by the absence of pest and diseases and tolerance to seasonal wet and dry conditions. Commercially, Pinus spp. are used widely for furniture, structural and building purposes. Australia has 2 million ha of forest plantations with 50% of this planted with exotic pine species. And the other 50% planted with hardwood species (CoA 2012). Approximately 136,000 ha of this is grown in Queensland. At the time of commencement of this research, Forestry Plantations Queensland (FPQ) (formerly known as DPI Forestry) managed approximately 190,000 ha of timber plantations, of which 136,000 ha was exotic pine (FPQO 2010). As of June 2012, the exotic pine resource in Queensland was sold to Hancock Queensland Plantations Pty Ltd under a 99 year land lease agreement, in association with the Department of Natural Resources and Mines (FPQO 2010).

Regional climate dictates species selection of exotic pines throughout Australia. For example Pinus radiata D. Don and Pinus taeda L. are grown in the temperate and elevated regions of southeastern Australia, while Pinus elliottii Engelm. var. elliottii and Pinus caribaea Morelet var. hondurensis (Sènècl.) W.H.G. Barett & Golfari., and their progeny are grown in the subtropical and tropical regions of Queensland (Nickles 1996). Exotic pine plantations throughout Australia have been through multiple rotations, which brings new challenges to the industry.

These challenges include maintaining acceptable growth rates while increasing sustainable management practices (Turner et al. 1999). In addition, there is a greater reliance on timber sourced from plantations and increasing pressure on the plantation
industry to use forestry practices that have minimal impact on the environment. However, the more intensive management regimes (Simpson et al. 2004) that produce shorter rotations may also have impacts on soil fertility and tree water use.

The impacts of intensive management and multiple rotation plantations are not yet fully understood. For example, factors such as soil fertility and tree water use are critical factors influencing tree growth. It is well recognised that water and nutrients are the two most limiting factors to plantation growth over the long-term (Wagner et al. 1999; Evans 2000). However, how silvicultural management strategies influence growth by reducing the competition for water and nutrients, and how this influences soil fertility, nitrogen (N) and carbon (C) cycles is not yet fully understood. In this regard, we are not yet fully conversant with how early establishment, plantation management (silviculture) impacts on soils and the physiology of the F1 hybrid trees grown in Southeast Queensland during a second rotation (Hogberg and Read 2006).

Plantation forests are important for a number of reasons. They not only provide a timber resource for domestic and export use but they also provide greenbelts between urban areas with amenity and recreation land uses. Current management in plantation operational areas requires the maintenance of buffers on all types of watercourses, which can improve water quality. Plantations incidentally provide refuge, food and nesting sites for birds and other animals. Plantations at regional scales have the ability to ameliorate the effects of global climate change because of their inherent ability to sequester C in their stems and soils.

The fact that timber is now predominantly sourced from plantation resources also has important implications for the processing industry. The plantation industry has adapted to harvesting smaller trees in larger volumes, while competing land uses such as agricultural and housing have influenced the development of plantations in east Australia away from the more productive agricultural areas (Huang et al. 2008a). In addition, the
potential for harvestable timber from plantations per unit area is greater when compared to subtropical native forest, hardwood operations.

2.1 Background

Pine plantations have been grown along the southeast coast of Queensland since the early 1930’s. The introduction of plantation forestry into Queensland was pioneered by E.H.F. Swain and colleagues from the Queensland Forestry Department (Taylor 1994). At this time Swain identified the need to establish timber plantations for future use because of the unprecedented rate at which native trees were being cut for timber. Swain spent time studying in the United States of America (USA) and on his return, introduced the idea of planting pine species from the US onto the poorer coastal sites in Queensland. A series of exotic pine experiments, including *Pinus elliottii* var *elliottii*, was established at Imbil in Southeast Queensland. Empirical data were investigated from early pine growth experiments to understand how *Pinus elliottii* var *elliottii* performed under the local conditions and how its growth could be improved (such as with fertilisation). Currently, exotic pine plantations provide Queensland with three quarters of its domestic timber supply.

In the early 1960’s, *Pinus elliottii* Engelm. var. *elliottii* (maternal) and *Pinus caribaea*. var. *hondurensis* (Sénécl.) W.H.G Barrett & Golfari. (paternal) parents were inter-crossed to form a series of F₁ hybrids. These selections were based on individuals from each species that demonstrated superior growth, form and other desirable phenotypic characteristics (Dale and Teasdale 1995; Nickles 1996). In the 1990’s these crosses formed the basis of a family clonal, forestry program which was later reproduced using vegetative methods (Haines and Walker 1993). A second and third screening of these families of elite clones included screening for desirable wood qualities (density and
spiral grain presence) in association with desirable growth attributes such as form, growth rate and branching characteristics (Harding and Copley 2000).

2.2 The exotic pine plantation industry in Queensland

In the 1990’s Forestry Plantations Queensland implemented a planting program using a series of clones from the *Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis* family selections. This research focused on clones that performed well in certain landscape conditions (such as on wetter or dryer sites) (Prasolova *et al.* 2003), and those that showed greater consistency in strength grading, wood density and form ratings with reductions of the occurrence of spiral grain tendencies (Harding and Copley 2000). One of the major benefits of these trials was the ability to test for adaptations to site conditions. By selecting genotypes that maximised water use efficiency (WUE)(the ratio between photosynthesis and water loss), trees were able to be screened to match site conditions and to maximise resource use and growth on poorer sites. For example, drought can be a significant problem influencing the survival and growth of trees in plantations. Genotypes that can adjust their physiology to adapt to drought stress are considered advantageous (Nambiar and Brown 1997).

More recently, the last few decades have seen management strategies implemented that further increase plantation productivity, wood quality and environmental protection. These strategies include but are not limited to:

- The selection and propagation of improved genetic materials (which have focused on improving vigour, form, wood quality and branching characteristics);
- The adoption of biotechnology in the propagation of trees;
- The implementation of silvicultural practices at early establishment;
- The implementation of nutrition programs to improve site specific tree growth;
• Stand management including pre-commercial and commercial thinning practices, pruning and density management to hasten rotation age and improve wood quality; and

• Protection and planning for wildfires including strategic weed control, hazard reduction burning and fire management planning.

Despite improvements in tree uniformity and the contraction of rotation age, the application of site-specific silvicultural practices may further increase tree growth. Site-specific silviculture may include encouraging the build up of C and nutrient resources in soils with low natural organic matter, or reducing weed competition for water on drier sites. These are just two examples of principles that may be applied to increase growth rates during early establishment.

Initially in Beerburrum, Southeast Queensland pine plantations were grown on a forest type referred to as ‘wallum scrub’. Wallum has diverse floral associations, with generally poor sub-soil drainage and nutrition. These lands were considered unproductive and unsuitable for large-scale agriculture. In Queensland, the exotic pine plantings rejuvenated the work-force, after the 2nd World War. Now with many of these plantations in their second rotations, management needs can be tailored to vary with site edaphic and drainage conditions. Despite ongoing research into species selection, and silvicultural benefits to tree growth in the exotic pine plantations, there is still limited research done to understand what physiological mechanisms facilitate or limit tree growth in response to certain environmental conditions or silvicultural management in the Queensland hybrid pines. Previous research undertaken on the eco-physiology of the exotic pines has investigated how genetics, environmental conditions and water use efficiency vary in different F$_1$ hybrid clones (Xu et al. 2000; Prasolova et al. 2003; Tutua et al. 2008). However, there is little published work that integrates the effects of edaphic
site factors such as soil fertility (Simpson et al. 2004) with tree physiology, nutrition or tree growth, at early plantation establishment. This information may provide preliminary data to investigate how the genetic potential for growth is limited by the environment and may offer further information on how to best manipulate the environment to reduce such limitations. By assessing a variety of different silvicultural treatments on different soil types in the subtropical regions, we may better understand how individual sites respond to silvicultural practices and which management techniques are most appropriate to increase tree growth, by increasing tree nutrient and water resource use efficiency.

2.3 Limitations to growth in plantations

While the main aim of plantation forestry is to maximise timber growth for commercial purposes, plantation silviculture can increase the efficiency of resources invested for stem/wood growth, maximising biomass accumulated within the merchantable product. Therefore silvicultural management also plays an important role in maximising water and nutrients allocated to the merchantable product (Gholz et al. 1990). One of the first accounts of the use of silviculture to improve declining yields was in a second rotation, *Pinus radiata* plantation in South Australia. In these plantations, there was a 30 % reduction in growth attributed to both the removal of organic residues after harvesting and competition for water and nutrient from weeds and grasses (Keeves 1966). This was rectified by implementing a no burning policy to harvesting slash and maintaining the harvesting debris across the site, as well as the implementation of post-planting weed control. In Queensland, various research has also identified how the removal or burning of harvesting debris can negatively influence site fertility (Blumfield and Xu 2003), and tree growth over the long-term (Tutua et al. 2008). Other research has identified the importance of weed control and fertiliser, in the inter-rotational and early establishment
periods on tree-survival and growth (Xu et al. 1995a, b, c; Simpson et al. 2004; Dickenson et al. 2005; Huang et al. 2008a, b, c).

In addition to the competition from weeds, there is often significant spatial variability across management units. To better understand how pine tree growth in plantations are limited by site-specific environmental stresses (water or nutrients) we first need to understand how trees respond to site variations such as water and nutrient gradients. This can be achieved by looking at the interrelationships at different sites, between C assimilation (growth), soil nutrient cycling and water use (Gholz et al. 1990).

2.4 Silviculture for maximising nutrient and water resources for C gain

Water and nutrient availability is fundamental to the growth and survival of trees in a plantation environment because of the intimate relationship between C assimilation, water and nutrient availability (Allen et al. 1990; McMurtrie et al. 1990). For example, water moves into the trees from the soil, controlled by gradients created from the loss of water via the stomata in the leaves (transpiration) (Sperry et al. 2002). Transpiration reduces in the leaves when water demand exceeds the soils ability to recharge the plant with water from the soil or where atmospheric demands reduce the plants ability to remain turgid. Depending on whether the water loss is greatest through transpiration or soil water deficit, leaves close their stomata in response to either increasing concentrations of abscisic acid in the leaves or roots, or reduced turgidity in the leaves, (Kozlowski and Pallardy 1997). Reduced xylem pressure potential ($\Psi_{XPP}$) may facilitate the closure of stomata and also limit C assimilation due to a decreased supply of CO$_2$.

When transpiration slows, diffusion of CO$_2$ to the plant also decreases (Farquhar et al. 1989). When CO$_2$ decreases in a leaf’s cells, or where a plant is critically dehydrated the tree’s ability to convert sunlight energy is limited and can result in reduced photosynthesis (Flexas and Medrano 2002). Reduced photosynthesis results in less
assimilates being available for leaf expansion and development and hence reduces growth. Similarly, nutrient uptake is facilitated by the movement of sap up the xylem through transpiration from the leaves (cohesion tension theory), and as the flow of nutrient ions and compounds at the root hairs decreases, biochemical reactions that lead to plant growth may be inhibited. Nutrients from the soil are used in the conversion of C and energy from the sun (photosynthetically active radiation), to sugars through the process of photosynthesis. The ability of nutrients to be recycled within the plant is an important nutrient conserving mechanism which can affect C allocation within the tree (Landsberg and Gower 1997).

Nitrogen (N) is an important nutrient that forms a basic constituent of chlorophyll. Chlorophyll is an important pigment involved in the harvest (Photosystem 1) and REDOX (Reduction-Oxidation) reactions (oxidation of water to O₂ and H⁺) within the photosynthetic electron transport system (Photosystem 11). Therefore, N deficiencies can reduce the C assimilation (Evans 1989). It could be expected therefore, that increased chlorophyll per unit leaf area may lead to increased gross assimilation rates, however there are costs associated with increasing plant size or morphological characteristics including greater respiration, water and nutrient demands (Wright et al. 2003).

Photosynthesis can also be limited by other factors such as drought or shading. This has been shown by Gholz et al. (1990a) where increasing availability of water led to increased leaf area, and consequently increased gross photosynthesis and transpiration rates. A plant’s potential to grow is therefore not only influenced by the energy available for the plant to convert C and nutrients to photosynthetic materials but is also influenced by water and nutrient limitations (Mason and Milne 1999; Watt et al. 2003). Therefore, a balance of water and nutrients in the presence of light energy creates the building blocks of plant growth. In addition, it is the integration among photosynthesis, N assimilation
and light energy that allows C to be converted and stored as fixed carbon, and processed for growth by respiration. Therefore, photosynthesis, respiration, N assimilation and water in the presence of light energy are intimately related (Hopkins and Hüner 2009).

So while silviculture has potential to increase the efficiency of resource acquisition, tree growth depends on the interaction of all the available resources (Binkley 2004). Resource use may therefore be measured by identifying how much resource is used for every unit of growth (Binkley 2004). This is because the simultaneous conversion of nutrients and water in the presence of light energy to growth can be determined or limited by the plant’s ability to access those resources (Wright et al. 2003).

Determining resource use however requires techniques sensitive enough to measure C, N and/or water assimilation. Various authors (Reiter et al. 2005; Landsberg and Gower 1997) recognise the importance of predicting how C is assimilated within a tree, but they concur, the processes are not well understood because there is a lack of knowledge on the how carbohydrates are allocated and what controls this allocation. Furthermore, modelling of C, N, water use and light processes can be used to estimate how plant interactions respond to various stimuli. Therefore, there needs to be observations made in the field (or laboratory), comparing benchmarks (controls) and treatments to indicate the direction growth takes to the various management practices. The aim of this thesis is to therefore, assess various resources required for growth (water, carbon and nitrogen) and investigate how their availability varies with different silvicultural practices in pine plantations in Southeast Queensland. The following section aims to review the effects of silviculture on soil C and N cycling, tree physiology, tree water use and tree growth and the techniques used to measure these variables, with reference to Pinus spp.
2.5 Soil nutrient cycling and sustainable plantation management

One of the overall goals of sustainable forestry practices is to make plantations self-sustaining in the replenishment of on-site nutrients (Schroth and Sinclair 2003). In the quest for sustainable forest management in plantations, three essential processes have been identified relative to soil nutrition. These include:

1. The sources of nutrients and the processes affecting their inputs;

2. The transformations of nutrients such as recycling and mobilization; and

3. The potential for and processes leading to, nutrient loss.

Nutrient uptake by plants is primarily from the soil solution, or as a result of exchange from sites on clay particles and soil organic matter decomposition. These however represent only a small fraction of the available nutrients ha\(^{-1}\) (Landsberg and Gower 1997). Plant roots facilitate reactions between ionic solutions and the plant, resulting in metabolic uptake. There is also a myriad of processes that exist in the soil medium that affect plant growth and nutrient availability. In addition, anthropogenic disturbance of soils can also change the balance between C, nutrients and water availability (Landsberg and Gower 1997).

Nutrient cycling is a complex process with many factors. For example, mean daily temperature throughout the year can influence annual nutrient cycling in humid environments. Where temperatures are high and water is not limiting, biological processes can be continuous throughout the year. Constantly high temperatures can lead to continual growth which increases annual net production in both the sub-tropic and tropical environments. This may result from either, increased annual nutrient mineralisation or nutrient uptake, when compared to temperate environments. Cycling of
nutrients can also increase due to more active litterfall, herbivory and decomposition on the forest floor. Leaf litters and organic residues are decomposed by a variety of arthropods and microorganisms (bacteria and fungi), which recycle nutrients back into the ecosystem. The nutrients released as a result of decomposition, are important for nutrient cycling and ecosystem function (Jordon 1985). The products remaining in the soil that result from decomposition are called humus. Humus mixed with the mineral soil contains an important structural matrix which acts as a reservoir for nutrients to support plant growth. It is this component of the soil which can degrade with management and cultivation and hence its maintenance is critical to sustainable forestry practices.

In subtropical environments, the majority of nutrient cycling occurs in the wet season under suitable conditions (rainfall, soil moisture and warm temperatures). When nutrients are released too rapidly from an ecosystem there can be losses through leaching and other processes. On the other hand, slow decomposition rates may result during periods of water deficit and reduce nutrient availability which seasonally slows plant growth. In southeast Queensland, there is a distinct dry season which often occurs in association with low temperatures, leading to slower plant growth.

**2.5.1 Soil fertility dynamics**

Management practices that affect the succession of plants also affect soil quality (Landsberg and Gower 1997). These effects can be monitored by measuring various soil indicators (N and P mineralisation; organic matter or C content; soil pH; bulk density etc). Soil monitoring is used to determine the ability of the soil to carry out a process or role and is therefore, a useful tool to measure soil sustainability (Knoepp et al. 2000; Rees et al. 2001). The difficulty lies in the interpretation of these indicators, as often they reflect differences depending on environmental conditions. Management units
within pine plantations are often mapped prior to site preparation using 50 x 50 m grids to characterize the site’s edaphic (soil) characteristics. Soil-type therefore, may be a reasonable factor to stratify soils and to investigate the effect of silvicultural treatments on soil fertility.

2.5.2 Organic matter decomposition

Organic matter decomposition may undergo several processes before the resultant nutrients are available for plant uptake by the roots. Organic and humic substances contain important resources for microbial decomposition. In dry seasons, when primary production of leaf biomass decreases, decomposition continues which lowers C reservoirs compared to forests with greater moisture (Jabbagy and Jackson 2000, 2001). This process contributes to lower primary production in these environments.

2.5.3 Soil organic matter

Soil organic matter (SOM) acts as important source and storage pool for C and N in the soil-plant continuum (Mendham et al. 2003). Organic matter is the remnant components of plants decaying and contains relative proportions of minerals to the original plant, in a lattice of biodegradable plant fibre and lignin cells. When an organic matter component is added to the soil, most of the inorganic nutrient elements are leached to the soil. The quality and quantity of soil organic matter at a site is important in maintaining a soil’s fertility (Rees et al. 2001; Mendham et al. 2003). Organic matter is divided into a number of fractions including light, particulate C, microbial biomass C and mineralisable C fractions, and the enzyme and carbohydrate fractions (Rees et al. 2001). It is the variations in these fractions that can be assessed as measures of the SOM quality and processes. SOM also provides soils with potential for water retention, soil aggregation, air filtration and protection against erosion. The quality of SOM can be affected by
management practices. For example, a study looking at residue retention at establishment in 2\textsuperscript{nd} rotation hoop pine plantations found the quality of the SOM increased due to the presence of foliage residues in the windrows (Mathers \textit{et al.} 2003). Soils mineral composition, topography, prevailing climate and management affect how much organic matter is retained and how much is lost (Rees \textit{et al.} 2001). The rate of decomposition of SOM is also influenced by the soil C to N ratio (Silva and Anand 2011). This ratio is generally related to a site’s soil and vegetation characteristics. In a study on microbial biomass concentrations and diversity, vegetation control was shown to decrease the C-to-N ratio and affect the corresponding microbial C activity (Li \textit{et al.} 2004).

\subsection*{2.5.4 Soil total organic C}

The organic C in soils is derived from plants (Kuzyakov and Domanski 2000) via litter fall and rhizodeposition (Chen \textit{et al.} 2003). Plant litter decays by exposure to microbial activity, rainfall, increasing temperatures (Rees \textit{et al.} 2001), management practices affecting soils and vegetative cover (Jobbagy and Jackson 2000, 2001). Each of these factors has the potential to affect the quality and distribution of organic C in soils and the related litter profiles (Turner \textit{et al.} 1999; Turner and Lambert 2000). The time taken for the different fractions of organic matter to breakdown varies, but is influenced by fraction size, soil microbial activity, soil moisture and climate (Turner and Lambert 2000; Rees \textit{et al.} 2001; Chen \textit{et al.} 2003). One method used to monitor the response of SOM to management is the measure of total organic C (TOC). For example, plantations up to 10 years of age had demonstrated a loss of TOC in the 0–50 cm layer of a soil profile with the net accumulation of C not occurring till 10–20 years after establishment (Turner and Lambert 2000). Soil microbiological activity is also affected by management activities (Chen \textit{et al.} 2003) and can be monitored to reflect changes in
nutrient and SOM cycling (Li et al. 2004). Seasonal fluctuations in temperature and water availability may influence soil microbial biomass C, N, P and S (He et al. 1997; Chen et al. 2003). However, management practices such as residue retention, site preparation, harvesting, burning and fertilisation, can also influence soil nutrition and SOM (He et al. 1997; Bubb et al. 1999; Chen et al. 2003; Ghani et al. 2003; Chen and Xu 2005) and subsequently affect the availability of nutrients to the plant (Turner and Lambert 2000; Chen et al. 2004; Chen and Xu 2005), therefore influencing C cycling and stand productivity.

2.5.5 Total soil N

N is a major component of many biological organisms and is fundamental to their structure and functioning. The N, available for plant use, depends on the degree of mineralisation of organic materials in the rhizosphere, losses through leaching (Smethurst and Nambiar 1989) and site disturbances such as forest harvesting, site preparation and burning (Vitousek and Matson 1985; Matson et al. 1987; Landsberg and Gower 1997; Chen and Xu 2005). In southeast Queensland, the availability of N is a limiting factor in plantation growth (Bubb 1996). N and P are generally deficient in the majority of terrestrial ecosystems (Schachtman et al. 1998). This deficiency can be magnified by weed competition for available site nutrients (Nambiar and Brown 1997) or increased tree growth (Sword et al. 1998).

Plants generally take up N as ammonium (NH$_4^+$) or nitrate (NO$_3^-$). Plant metabolic assimilation of soil N to other compounds (such as with ammonium (NH$_4$), to nitrate (NO$_3^-$) or nitrites (NO$_2^-$)), is possible due to their conversion by a host of bacteria, fungi and actinomycetes. In a study looking at residue retention, site preparation and herbicide treatments in intensively managed loblolly pine plantations, microbial activity was fundamental in controlling N availability and losses (Vitousek and Matson 1985). This
study also reported that 90% of N was immobilized in the residue and in the nil herbicide treatment over 28 days, whereas residue removal and herbicide application treatment retained only 70% of N. Vitousek and Matson (1985) concluded that the soil nitrate pool was greater in the first two planting seasons following site preparation and that the removal of organic substrates (harvesting slash, stumps and leaf, branch and cone litter), reduced immobilization of on-site N in subsequent years. In a study at a 6-year old slash pine plantation in sub-tropical Australia, it was found that the retention of harvesting residues increased total soil C and N when compared with a treatment that removed harvesting residues (Chen and Xu 2005). Another study in the same region found that residue retention in windrows in a 2nd rotation hoop pine plantation increased the retention of N, compared to the previous management technique of heaping and burning residues (Blumfield and Xu 2003; Blumfield et al. 2004). There were however concerns that cleared inter-rows still suffered from N losses by leaching and denitrification.

2.5.6 Potentially mineralisable nitrogen (PMN)

When plant and animal debris decay, their N components are mineralised into inorganic N compounds such as NH$_4^+$ or NO$_3^-$ (Vitousek and Matson 1984). Soil N mineralisation occurs in the ecosystem only when biological conditions are suitable (Haynes and Goh 1978). Major factors affecting the rate of mineralisation of N include the availability of water, soil temperature, aeration and attributes of the organic matter (including the C-to-N ratio), phenolic and lignin constitution and microbial activity (Nambiar and Brown 1997). The use of the potentially mineralisable N (PMN) as an index of N availability compares a seven day incubation period of soil samples to freshly extracted samples. The incubation facilitates the mineralization of organic forms of N by microbial biomass, in anaerobic conditions (Keeney 1980). This method is considered as one of the most
appropriate laboratory methods for PMN analysis (Keeney 1980) and can identify the potential of the soil to produce inorganic N products from labile pools.

For example, in-situ net N mineralisation rates across a range of conifer and hardwood forests in the temperate zones across the USA were found to increase linearly with annual net primary production. Increased N mineralisation rates were attributed to the variation in soil types rather than forest types (Reich et al. 1997). In another example, cultivation with a disc plough in a 2nd rotation hoop pine plantation at establishment increased the mean seasonal, net N mineralisation from ~30 to 53 kg ha\(^{-1}\). Cultivation also resulted in increases of nitrate leaching from ~10 to 73 kg ha\(^{-1}\) and nitrification from 28-43 kg ha\(^{-1}\) (Blumfield et al. 2005). These results suggest that N fluxes can result from different management activities such as those applied at early plantation establishment.

2.5.7 N transformations

The major form of mineral N available for plant growth is through soil N mineralisation. N mineralisation involves two processes, ammonification and nitrification. Ammonification is the process whereby heterotrophic bacteria and fungi decompose organic forms of N, and convert it to ammonium (NH\(_4^+\)). Ammonium is then available for plant uptake at the roots but may also be transformed by other potential pathways in the soil. For example, ammonium may be adsorbed onto the soil colloids, assimilated into microbial biomass (immobilization) or converted to nitrite and then nitrate by autotrophic micro-organisms (nitrification). Nitrate can also be taken up by plant roots, immobilised, or in some instances lost through leaching or conversion to N oxides and N\(_2\) gases (denitrification) (Haynes and Goh 1978).
2.5.7.1 Nitrogen Immobilisation

Where ammonia has been produced as a result of soil N mineralisation, it can be locked up during soil microbial growth and production. This results in inorganic N not available for plant growth. The immobilisation of N in weeds can also be used as a method to minimise leaching losses in plantation management, particularly in more tropical forest ecosystems (Matson et al. 1987; Smethurst and Nambiar 1989). In addition, vegetation control can decrease microbial C and C-to-N ratios because of the loss of vegetation being cycled to the soil (Li et al. 2004).

2.5.7.2 Nitrification and denitrification

Ammonium produced by soil N mineralisation does not always accumulate in soils because nitrifying bacteria (nitrosomonas and nitrobacters) convert ammonium to nitrite and then to nitrate. In agriculture or forestry, N can be given to crop plants as ammonium or nitrate fertiliser or as urea. Nitrate is negatively charged and readily leachable, which means it has the potential to cause negative off-site, water quality issues. Methods such as residue retention in intensively managed loblolly plantations in North Carolina, have been shown to prevent N losses by leaching, denitrification and erosion (Vitousek and Matson 1985). Site characteristics, such as low pH and P, have also been shown to restrict nitrification in Pinus radiata on podzolised sands in South Australia (Carlyle et al. 1990). Denitrification causes a permanent loss of N from N sinks; however the loss is considered a small component of the total annual mineralisation processes (Vitousek and Matson 1985).

Various methods can be used to quantify N losses. One example is the $^{15}$N isotope tracer method where $^{15}$N-labeled fertiliser is applied to macroplots to allow an estimation of the $^{15}$N pools retained within a plot area (Matson et al. 1987). Various authors have used this method to estimate N losses (Vitousek and Matson 1985; Matson et al. 1987),
competition effects by weeds, decomposition times of $^{15}$N treated residues (Blumfield and Xu 2002; Blumfield et al. 2004) and the effects of fertilisation on tree crops (Bubb et al. 1999). Vitousek and Matson (1984) found that after harvesting and clearing of a plantation site, 83% of the $^{15}$N retained was immobilized by microbial biomass, with only 13% of the $^{15}$N taken up in the plant. Although these results were specific to the site, they led to the implementation of residue retention after harvesting in these areas which was seen as an important advance towards long-term nutrient sustainability.

2.5.8 Soil C isotope composition ($\delta^{13}$C) and N ($\delta^{15}$N) isotope composition

This review has outlined how organic matter forms an important source of the C and N substrate, and that its decomposition can be increased by the oxidation and the breaking up of organic particles in the soil through management. However, in addition to the above-mentioned indices, soil C and N pools are also composed of a proportion of stable C ($\delta^{13}$C) and N ($\delta^{15}$N) isotopes. These allow processes influencing C and N processes to be recognised by the responses of the isotopes to the disturbance. $\delta^{13}$C and $\delta^{15}$N are sensitive to the changes that influence C and N cycles, and the residence times of nutrient pools (Wedin et al. 1995; Cadisch et al. 1996; Emmett et al. 1998; Templer et al. 2007). Therefore, their use in soils can effectively represent changes in the quantity and quality of organic inputs, the rate of N mineralisation and the presence of the associated decomposing microorganisms. As a result they can be used as an index of the mechanisms influencing C and N cycling (Falxa-Raymond et al. 2012; Templer et al. 2007; Koba et al. 2003; Hogberg et al. 1995).

More recently, there is research linking variations in soil $\delta^{13}$C to the presence of different communities of decomposers such as fungi and bacterial communities. For example, where soil $\delta^{13}$C is low, $\delta^{13}$C can indicate that soils maybe composed of both a mix of bacteria and fungi in their microbial compositions (Hobbie et al. 1999; Hobbie et
Soils low in $\delta^{13}$C, have also been linked to faster N cycling (less N immobilisation) and higher N losses, which can lead to increased soil $\delta^{15}$N (Hogberg and Read 2006).

Soils enriched with $\delta^{13}$C represent soils with an increased presence of labile C (incorporating dead fungal and bacterial cells) and increased quantities of organic matter returned to the soil (Ehleringer et al. 2002). This pool of increased microbial activity can result in increasing N in organic N forms which effectively reduces nitrification and is reflected as lower $\delta^{15}$N in the inorganic N pools (Hogberg et al. 1995). These ecosystems, can be described as slow N cycling and have been associated with the presence of mychorrizae fungi to facilitate increased N availability to the plant (symbiosis) (Silva and Anand 2011; Koba et al. 2003; Kitayama and Iwamoto 2001). While slower N cycling contributes to lower soil $\delta^{15}$N (Silva and Anand 2011), mychorrizal associations can result in lower foliar $\delta^{15}$N because mychorrizal fungi fractionate heavily during dis-association of N to the plant (Robinson 2001).

Soil $\delta^{13}$C has also been linked to photosynthetic plant types growing above the soils. The organic residues of different photosynthetic plant types can vary in their $\delta^{13}$C and therefore, soils can reflect the organic matter residues returned to them (Kohn 2010; Cheng et al. 2008; Wedin et al. 1995).

**2.5.9 Soil phosphorus**

The storage and uptake of C in an ecosystem is limited by P supply (Townsend et al. 2002) and this is because P is a significant part of enzymes, proteins, photosynthesis and energy during the DNA replication (Benton Jones 1998). P anions are dihydrogen phosphate ($H_2PO_4^-$) or monohydrogen phosphate ($HPO_4^{2-}$), although inorganic forms may come with Al, Fe, or Ca phosphate. P availability is limited by pH and is most available at neutral pH ranges between pH 6 and 7. Accordingly, pH determines the
availability of P (Benton Jones 2001). P can be equally divided into organic and inorganic forms and is mineralized to a mobile form prior to plant uptake; typically P occurs with aluminium and iron phosphates in acid soils and with calcium phosphates in alkaline soils. P may be in the soil but in a form unavailable to plants. Up to 80% can be locked up due to adsorption, or immobilised in organic forms. P limitation is recognised as occurring in old, weathered soils and tropical soils where soils are high in iron or aluminium oxides. In addition, losses of P through vegetation management or land-use change may have long-term consequences for productivity (Townsend et al. 2002). Available P has been shown to correlate with plant biomass. The majority of P available in the soil pool is either from recycling of leaf litters (in forests) or through root deposition (in pastures and grasslands) (He et al. 1997; Chen et al. 2003).

As with soil N, decomposition of organic matter by soil microbes is responsible for the immobilisation and mobilization of P (He et al. 1997; Frossard et al. 2000; Chen et al. 2003) and hence microbial P can be a suitable indicator of P availability. The release of P from the inorganic form (P₀) is fundamental to P cycling in forest ecosystems (Saggar et al. 1998). Various authors attribute the seasonal flux of mobile P in soils to soil moisture and the input of organic matter (He et al. 1997; Chen et al. 2003) and while Chen et al. (2003) showed air temperature affected microbial mineralisation of P, He et al. (1997) found no correlation between biomass P and the ambient air temperature. Carlyle et al. (1998) found that mineralisation of N increased by 13% with increasing P mineralisation in podzolised soils in South Australia. P taken up by plants and roots varied significantly in foliar concentrations of 1 year-old slash pine in a study comparing weed control and no weed control treatments, with the former showing greater foliar P concentrations. Their research also found that the P concentration in the weed free treatment increased on the 116th and 187th day from 0.25 to 0.97 mmol per plant, while nil weed control showed no significant difference in foliar P concentration throughout the
study. In addition, because P is considered to be a relatively immobile nutrient in plants and soils, a greater proportion of P is taken up with increased root surface area, when compared to increased root volume (Schachtman et al. 1998). With the increasing reliance on synthetic fertilizers (particularly N and P) to maintain high productivity in agriculture and forestry, poor fertilizer management (such as overuse, run-off or leaching) has potential to degrade water quality (Vitousek and Matson 1984; Frossard et al. 2000), which highlights why it is important to manage N and P resources more efficiently.

2.5.10 Potassium and magnesium

Potassium (K) is important for stomatal opening and closing, osmoregulation, cell expansion and energy-related metabolism (Sebanek 1992; Kozlowski and Pallardy 1997; Proe et al. 2000). Both K and magnesium (Mg) are highly mobile and primarily acquired through internal cycling and recycling of leaf litters (Sword et al. 1998). Magnesium is important for metabolism and ribosome maintenance and forms an important part of chlorophyll molecules (Kozlowski and Pallardy 1997). The application of a P fertiliser and herbicides in loblolly pines, growing on infertile coastal sites, can also increase foliar K and Mg (Sword et al. 1998). However the increase in foliar K resulting from different herbicide applications and P fertilisation rates was short-lived because as the stand matured, growth rates slowed and K deficiencies became apparent, reflecting the sites inability to continue to provide for increased K demands (Sword et al. 1998).

2.6 Silviculture and optimizing tree growth

The previous sections outline how there has been a considerable volume of applied research documenting the effects of competition control, and fertilisation on tree growth, and foliar nutrition in pine plantations. A number of authors have investigated the benefits of weed control and fertilisation in plantations (Smethurst and Nambiar 1989;
Haywood et al. 1997; Nambiar and Brown 1997; Mason and Milne 1999; Adams et al. 2003; Wagner et al. 1999, 2006) while Dickenson et al. (2005) and Huang et al. (2008b, c) summarised that weed control in 2 m strips were required to maximise plantation vigour. Conversely, while there was an increase in vigour with strip weed control compared to nil weed control, Smethurst and Nambiar (1989) found strip weed control facilitated a 50-80% reduction in total mineral soils N concentrations at the 0-15 cm soil depth when compared to total weed control. Despite this, the comparison of total weed control and strip weed control showed little effect on net N mineralisation in the 0–15 cm soil zone. They concluded that the use of strip weed control compared to the total weed control treatments in the first growing season reduced leaching by 45% but also reduced stem biomass at 20 months by 46% compared to stem biomass in the total weed control treatments, which they concluded was in part due to reduced foliar N concentrations of up to 14% (Smethurst and Nambiar 1989).

Research on Pinus radiata D. Don in New Zealand identified the long-term benefits in tree growth gained by early weed control and fertilisation, were significant from five years old through to mid-rotation. Samuelson et al. (2004) found significant differences in tree growth in loblolly plantations in Bainbridge, USA using fertilisation at mid-rotation despite no significant differences at mid-rotation between the treated weed control plots and untreated plots. Samuelson et al. (2004) also found increases in above- and below-ground biomass of up to 200% by integrating silvicultural management treatments (i.e. weed control, irrigation, pest control and fertiliser treatments). Increased stem-wood productivity and leaf area index [LAI] were also demonstrated at the site and were attributed to the lower partitioning of resources to the roots and shoots (woody components).
2.6.1 Fertilisation and irrigation

As a silvicultural strategy, fertilisation aims to maximise biomass production. Traditionally N, P and K are applied at early establishment (and copper on water-logged soils) in the Southeast Queensland, exotic plantations. Fertilisation may also be applied at mid-rotation if nutrient limitations are diagnosed through foliar analysis. Fertiliser management strategies in pine plantations aim to synchronize the timing of fertiliser applications with potential limitations to tree growth. Liming may also be used to release unavailable site resources and neutralise soil pH. The more efficient use of a sites resources, can potentially increase growth and help to reduce timber rotation length. For example, when fertilisation and irrigation treatments were maintained up to nine years after planting in a Pinus taeda plantation in North Carolina USA, Albaugh et al. (2004) found that the treatments resulted in increased height, basal area, leaf area index, stem mass accumulation and current annual stem mass increment and that the increases were greater with fertilisation than with irrigation.

The authors concluded that while optimum nutrient amendments could reduce the rotation age of commercial pine operations, it could also reduce timber quality by decreasing basic density. Albaugh et al. (2004) also found that stem specific gravity and density of the growth rings, taken at 3, 4 and 5 years, also decreased with fertilisation by 7.5%, whereas with irrigation there was no effect. For example, increasing nutrients (through fertilisation) had the potential to increase stem volume, total biomass and leaf area index by >100%, while irrigation achieved only a 25% increase. Fertilisation increased stem volume growth efficiency (stem growth per unit leaf area index) by 21%, irrigation increased it by 19% and the combination of both fertilisation and irrigation increased stem volume growth efficiency by 30%. These increases in growth were attributed to an increased allocation of resources to needles and photosynthetic capacity, because biomass partitioning alone did not explain the increase in total biomass
productive efficiency (fertilisation (91%), irrigation (29%) and fertilisation and irrigation combined (129%)).

An investigation by McMurturie et al. (1990) in Pinus radiata plantations in Canberra, Australia, found that fertigation and irrigation amendments increased projected leaf area index from 5 to 7 m² m⁻² and canopy N (dry-weight) from 9 to 17 mg g⁻¹ in the second growing season after the treatment application. The authors found that increases in projected leaf area index, during periods of positive net photosynthesis, were dependent on climate and soil water balance. They also found that annual canopy net photosynthesis ranged from 18 T C per ha⁻¹ for control to 38 T C per ha⁻¹ respectively in the irrigated and fertilized stands. Further simulations found 67% of the difference in tonnage for C ha⁻¹ could be explained by the increase in active growth by irrigation, while 23% was attributed to the increase in leaf area in the irrigated fertilized stands and 10% of the variation was explained by the differences in photosynthesis and attributed to increased N nutrition. McMurturie et al. (1990) highlight how the integrated effects of nutrition and water are important factors limiting exotic pine growth.

2.6.2 Weed control and fertilisation

Nambiar and Brown (1997) found that the use of Round up® (Glyphosate) doubled tree biomass in six species of Acacia at 30 months old, alongside a range of Eucalypts on former Imperata spp. grasslands in Indonesia. In contrast, results from physical cultivation practices including ploughing and harrowing showed no effect. In addition, foliar N uptake by total biomass (including weeds), using strip weed control was 49% higher with a corresponding reduction of N apportioned to pine trees from 15.5 to 9.0 kg N ha⁻¹. These effects were further compounded where no weed control was used. Smethurst and Nambiar (1989) concluded that weeds directly competed for N and could create N deficiencies in young Pinus radiata plantations. Furthermore, complete weed
control and the addition of ammonium nitrate fertiliser not only increased foliar N, N uptake and growth of trees but had the potential to lead to serious tree form issues.

Will et al. (2002) compared two Pinus taeda sites in Georgia (USA) and found that both fertilisation and weed control increased current annual increments (CAI) at one site but not another. They also found that the effects of fertilisation on leaf biomass increased with age while the effects of competition control on leaf biomass decreased with age. Finally they found that fertilisation increased growth efficiency (the ratio of stem production to leaf area) between the ages 7-13 years, but it reduced from age 13 years. However because growth efficiency also decreased with increasing tree size (confounding the results with tree age) they concluded the importance of maximising leaf biomass at the early stages of tree development to increase stem growth per unit of foliage. This research also highlights how responses to weed control and fertilisation can be specific to site conditions.

Cain (1989) investigated weed control treatments in even-aged plantations of Pinus taeda and Pinus echinata (Mill) (shortleaf pine) in the upper coastal plains of Arkansas, USA. The treatments included four levels of weed control: woody weed control (WC); herbaceous weed control (HC); total weed control (TC); and control (C) (with no weed control treatment) applied up to 4-5 years after planting. Trees were then thinned at age 5 years to 1235 trees ha\(^{-1}\). Diameter growth decreased in HC plots between 5-13 years compared to WC and this was suggested to be the result of woody weed competition during 5-13 years. At 13 years, pine tree volumes were 48% greater in the plots with total competition control (282 m\(^3\) ha\(^{-1}\)), compared to the control plots (160 m\(^3\) ha\(^{-1}\)), while the means of WC and HC were not significantly different from each other.

Martin and Jokela (2004) found that stemwood periodic annual increment (PAI), decreased by 275% between 5 and 8 years in Pinus taeda plantations on spodosol soils in north-central Florida, USA. They attributed this reduction in stemwood growth rate to
the onset of inter-tree competition and for nutrients. They also found that fertilisation and competition control between 16 and 18 years, continued to increase height, basal area, stemwood and biomass accumulation, foliar N and leaf area index. In addition, these treatments decreased growth of tree ring earlywood/latewood ratios and accelerated the transition from juvenile to mature wood.

2.7 Silviculture and tree physiological processes

The previous sections show what variables and treatments influence plantation silviculture. This section aims to review how the changes to tree growth occur. Plant growth and plantation productivity are primarily influenced by plant nutrient status, water relations and environmental influences. While there is numerous research quantifying the advantages of weed control and fertilisation treatments on plantation pine productivity (Colbert et al. 1990; Watt et al. 2003; Samuelson et al. 2004) and physiological responses to silviculture (Thompson and Wheeler 1992; Robinson et al. 2001; Munger et al. 2003), research is less common in the F$_1$ hybrid pine grown in the subtropics. There has been some work undertaken in the F$_1$ hybrid pine identifying the mechanisms influencing growth on wet and dry sites, in association with family selections in Southeast Queensland (Xu et al. 2000; Prasolova et al. 2001, 2003). These studies have identified how WUE and N varied with clone and environmental conditions in pine grown at different sites.

Research looking at the efficiency of the conversion of C accumulation and water use can allow us to quantify how the relationships between C gain and water flux vary with different management options. Because water constitutes over 90% of a plant’s composition, it is important for biochemical processes including photosynthesis, nutrient uptake and structural turgidity. Silviculture offers methods to reduce the competition for on-site water resources particularly because irrigation is considered to be neither a
practical nor an economic way of alleviating water stress in commercial pine plantations (Manogaran 1973).

Ecophysiological approaches to water and nutrient studies in plants were developed in the 1960s in combination with studies into transpiration and photosynthesis, while isotope analyses are contemporary techniques that allow the interpretation of C and water fluxes within the plant (Ehleringer et al. 1993; Bowling et al. 2002). When this information is compared with tree growth variables, it can help explain the physiological mechanisms influencing tree growth. In addition, when compared to soil isotopes it may also offer insights into how C and N cycling in the soil influences tree growth.

The theoretical C balance of a plant community can be determined by the difference between uptake (C fixed by photosynthesis and biomass) minus respiration (Waring et al. 1998; Landsberg et al. 2003; Allen et al. 2005). The efficiency of the conversion of CO₂ and water to carbohydrates can be measured as the total carbohydrate produced per unit of photosynthetically active radiation (PAR) absorbed (Nambiar and Brown 1997; Binkley et al. 2004). This relationship can also be referred to as ‘growth efficiency’ and it is strongly influenced by the nutrient and water status of the plant. In another example, Carlyle (1998) identified that leaf area index was highly correlated to available N where the combination of predawn water potential, N uptake and LAI explained up to 95% of the variation in tree growth across a variety of treatments in Pinus radiata plantations. Hence, the integration of nutrient, water and growth variables could better explain variations in tree growth.

2.7.1 Carbon assimilation

Pine plantations in subtropical areas are relatively fast growing and this makes them inherently effective for carbon sequestration. A new plantation of Pinus elliottii var elliottii Engelm released up to 15.6 Mg C/ha up to 3 years after planting, thereafter they
became carbon sinks as a result of increasing leaf area. At canopy closure sites continued to sequester carbon with a net carbon uptake of between 4 and ~8 Mg C ha\(^{-1}\) yr\(^{-1}\) depending on seasonal conditions (Brancho et al. 2012). For example, in the same study drought negatively influenced water availability, leaf area index and radiation-use efficiency which led to a 25% reduction in net carbon uptake.

Carbon assimilation occurs during plant photosynthesis and combines available CO\(_2\), nutrients, light energy and water. Carbohydrates formed during photosynthesis provide energy for further biochemical reactions which form the cellulose, enzymes, proteins, amino acids, hormones and organic acids required for primary and secondary growth in plants. When these processes are optimal, plant growth is maximized. However, because these processes work simultaneously, where CO\(_2\), nutrients, light energy or water is limiting, there may be a reduction to optimal plant functioning and hence growth (Wright et al. 2003). In addition, trees require energy for both tree growth and maintenance processes.

Although various authors have investigated the more complex interactions between plant physiological processes and resource use (Carlyle 1998; Jokela and Martin 2000; Mora 2003; Ludovici et al. 2002; Jokela et al. 2004; Martin and Jokela 2004; Allen et al. 2005), gas exchange measurements can provide valuable information on the primary processes of C acquisition such as CO\(_2\) exchange and its incorporation into organic compounds. However, little physiological information exists on how C assimilation changes with management, in the exotic pine trees of southeast Queensland.

Studies on physiological processes and resource use conclude how water loss in plants via transpiration occurs in response to changes in the humidity at the leaf surface (atmospheric water vapour pressure deficit or VPD) and how soil water deficits can affect transpiration, respiration and photosynthesis (Gholz et al. 1990, Brancho et al. 2012). One method of assessing how C assimilation is influenced by water loss is
through the monitoring of stomatal adjustment which can indicate both supply and demand relationships at the leaf level (Mitchell and Hinkley 2003). Another is through the assessment of water potential within the tree which is related to water availability within the soil (Kramer and Boyer 1995).

2.7.2 Water use

Water is required for photosynthesis, nutrient and carbohydrate transport and it is fundamental in maintaining plant structural turgor. When terrestrial plants are grown under controlled light and nutrient concentrations, the efficiency of resource acquisition per unit biomass can be affected by the size of the plants (Givnish 1988). While both large and small plants divert resources for the development and maintenance of transport and storage systems such as xylem and phloem, larger plants (such as trees) with more complex vascular systems, use greater resources per unit biomass than competing smaller plants. Transport systems also include the cuticle and stomatal cells and intercellular gas spaces (Osmond 1987). When resources are limited, growth rate is consequently reduced. This is an example of how the efficiency of resources in the plant can be less efficient in larger plants per unit light (mol of photons) and N absorbed or water transpired (per g) compared to other species in competition for these resources (Osmond 1987, Ludovici et al. 2002).

2.7.2.1 Water use efficiency

Water use efficiency (WUE) represents C uptake per unit of water loss, where changes in WUE can be related to either, water deficit or transpiration (per unit leaf area) (Sinclair and Ludlow 1985) or both, although there are a number of different interpretations of the measure of WUE. WUE has been described as a process whereby plants exhibit either, decreasing photosynthesis and/or transpiration and stomatal conductance rates to water loss (Sheriff et al. 1986). Because gas diffusion pathways are linked, WUE can also
describe transpiration efficiency (WUE$_T$), (intrinsic transpiration efficiency or instantaneous WUE) or intrinsic water use efficiency (WUE$_i$). WUE$_T$ is referred to as the ratio of plant biomass to the amount of water lost through transpiration whereas WUE$_i$ is the ratio of net photosynthesis (A) to stomatal conductance ($g_s$) ($A/g_s$) (Farquhar et al. 1980; Von Caemmerer and Farquhar 1981; Condon et al. 2002).

\[ WUE_T = \frac{A}{T} \]  
\[ WUE_i = \frac{A}{g_s} \]

Equation 1  
Equation 2

Where:

T is transpiration rate;

A is photosynthesis; and

$g_s$ is stomatal conductance. (Farquhar et al. 1980)

For example, Korol et al. (1999) concluded that intrinsic transpirational efficiency (the ratio of CO$_2$ assimilated and water transpired at a given water pressure) increased with decreasing water availability, while Guehl et al. (1995) reported that another measure of transpiration efficiency (the ratio of biomass production/ plant water loss), decreased with reduced foliar and whole plant N concentration. Guehl et al. (1995) also found that intrinsic WUE (as measured by gas exchange) and time-integrated WUE (foliar $\delta^{13}$C), decreased with lower foliar and whole plant N concentration. However, when time-integrated WUE (foliar $\delta^{13}$C) is used alone, a decrease in WUE may result from either decreased photosynthesis or transpiration, hence other measures of physiological processes should be used in conjunction with foliar $\delta^{13}$C to determine the direction of change and/ or magnitude in time-integrated WUE.
To determine tree photosynthetic capacity, requires measurement of photosynthetic efficiency at a whole tree level, this process requires destructive sampling or leaf area index (LAI) calculation which can be resource intensive and impractical. On the other hand, while WUE$_T$ can be a time consuming method when dealing with larger tree crops, WUE$_i$ is measured on an instrument, on a single leaf basis, and representative of the tree. An example of an instrument suitable for measuring gas exchange is the LICOR 6400 which measures photosynthesis and a range of other related variables. In addition, because C, O and H form the structure of plant cells and have roles in most metabolic processes, measuring CO$_2$ and water in the plants can provide methods of quantifying the interactions between C and O use during plant biochemical processes (Sebanek 1992; Farquhar et al. 1993).

2.7.2.2 Foliar C isotope composition ($\delta^{13}$C)

The stable isotope analysis techniques allow long-term C and water flux trends to be investigated. The use of stable isotope analysis in the study of plants requires the comparison to standards such as atmospheric CO$_2$. Stable isotopic analysis can be used to examine variations in plant physiological processes including photosynthesis, transpiration and stomatal conductance (Ehleringer and Cook 1989; Farquhar et al. 1993). This is because isotopic fractionation and discrimination occur during physiological processes in plants (Ehleringer and Cook 1989). Thereby, differences in $^{13}$C/$^{12}$C ratios occur due to the process of fractionation during CO$_2$ assimilation, where lighter isotopes of $^{12}$CO$_2$ are preferentially taken up and the heavier isotopes are discriminated against.

For example, $^{12}$CO$_2$ molecules from the atmosphere are lighter and they diffuse through the stomata for photosynthesis more readily than $^{13}$CO$_2$. In addition, the lighter isotopes have bonds that are more easily broken and therefore are more readily available.
for uptake in larger volumes. As a result $^{13}\text{CO}_2$ is discriminated against, resulting in lower $^{13}\text{C}/^{12}\text{C}$ ratios or greater C isotope discrimination ($\Delta$) in plant materials. Subsequently, this discrimination continues during other biochemical and physiological growth processes (Ehleringer \textit{et al.} 1993; Lajtha and Michener 1994, Cabrera-Bosquet \textit{et al.} 2012), resulting in differences in fixed $\delta^{13}\text{C}$ in plant cells (Farquhar \textit{et al.} 1989; Ehleringer \textit{et al.} 2002). The variation between the $^{12}\text{C}$ and $^{13}\text{C}$ isotopes fixed in plant cells therefore provides an index of gas exchange as it relates to the CO$_2$ available to plants (Lajtha and Michener 1994). Measures of C isotopes ($\delta^{13}\text{C}$) are negative values and correlate positively with instantaneous WUE as measured through gas exchange, the less negative the $\delta^{13}\text{C}$ the greater WUE. More recent work with foliar $\delta^{13}\text{C}$ has shown links between foliage carbon pools (soluble carbohydrates and waxes) with foliage, soil and ecosystem respiration (Mortazavi \textit{et al.} 2012).

\textbf{2.7.3 Plant water status}

Water potential measures the thermodynamic potential of water as it moves through the soil plant atmosphere continuum (Boyer 1995; Kramer and Boyer 1995; Osmond 1987). Water in under tension in plants compared to the atmosphere and is therefore expressed in units of pressure (MPa). Because water in plants and soils contains solutes not found in pure water, water potential is expressed as a negative value per unit water. Water absorption by roots is linked to the rate of transpiration (Doley 2004). This is because the stomata are sensitive to changes in atmospheric water vapour deficit and soil water deficits (Ewers \textit{et al.} 1999). A decrease in cell water content and an increase in cell solute concentration can lead to changes in cell metabolic activity (Kramer and Boyer 1995). Increases in solute concentrations lower the chemical potential of water, creating a more negative tension or pressure inside the cells. The reduction in plant water potential also affects stomatal and mesophyll conductance.
A plant’s water potential may decrease with the addition of solutes to the available water, increased adsorption or tension of soil water to soil particles (matric potential) or by a reduction of water pressure in plant cell (turgor pressure). Water potential may also increase with the hydration of surfaces (reducing matric potential), dilution of solutes with water or by the increase of cell turgor (Kramer and Boyer 1995). Water status changes within plants on a daily basis, dependent upon the frictional resistances imposed on available water (Boyer 1995). Where competition for water exists such as in the presence of weeds, water becomes more quickly unavailable which can be particularly important to tree survival at the early stages of tree establishment.

At a whole-plant level, water potential varies within a plant. Water potentials are often less negative closer to the roots because there is less frictional resistance, and more negative at the growing tips. As water potential decreases plants may show a reduction in transpiration (Gholz et al. 1990; Hari et al. 2000) and C assimilation particularly at the growing tips and stem of plants (Boyer 1995). Nambiar and Brown (1997) make the clear distinction that optimum use of water resources in plantations requires an accurate understanding about mechanisms of supply and demand at different stages of the plantations’ life cycle. It has been identified that plant water use is affected by leaf area in general and by planting density at canopy closure (Gholz et al. 1990; Nambiar and Brown 1997). Therefore, in the absence of other limiting factors, the higher an individual tree’s leaf area, the more water is transpired, culminating in greater growth until canopy closure.

The measure of plant water stress can be carried out on leaves or twigs with a Scholander Pressure chamber (Tyree and Hammel 1972). Equipment such as pressure chambers have been developed for the measurement of water potential in the field. However, at a stand level, interpretation of such data is still precarious (Farquhar et al. 1980). The nature of the sampling work with a pressure chamber requires that leaves are
left on the plant with measures taken at predawn (as an indicator of capacity to recover or recharge), at midday (measured from the upper part of canopy and fully exposed to the sun). These sampling precautions allow data to be reproduced in the field with some accuracy and are necessary to reliably detect variations in water stress between trees (Boyer 1995).

Water potential using the pressure chamber integrates the soil water deficit, hydraulic resistance to water through the plant, and the atmospheric evaporative forces such as humidity, wind and temperature. The measure of water potential provides a quantitative index of how water stressed a plant is at the time of measurement. Water potential has two major components which include pressure potential ($P$) and osmotic potential ($\Pi$) and which are expressed by the following equations:

\[ \psi_{cell} = P - \Pi \]  
\[ \text{Equation 3} \]

Where:

$\psi_{cell}$ – is the Osmotic pressure minus turgor pressure of the cell;

$P$ - Turgor pressure (or pressure exerted by the cell wall) of the cell;

$\Pi$ - Osmotic pressure (or pressure of the cell solution) of the cell; or

\[ \psi_{o} = \psi_{\rho} - \psi_{\pi} \]  
\[ \text{Equation 4} \]

Where:

$\psi_{o}$ - Osmotic potential minus the turgor potential of the sample;

$\psi_{\pi}$ - Osmotic potential of the sample;

$\psi_{\rho}$ - Turgor potential of the sample.
As water availability declines through the upper soil horizon, plant turgor can decline in response to soil water availability. In response, plant growth can reduce across the tree and leaves may senesce influencing the relationships between water and C assimilation. In both trees and herbaceous plants, turgor is critical for structure or form. Where turgor is inadequate stomatal opening, cell elongation and structure may be adversely affected (Boyer 1995). Where turgor drops below a certain threshold, cell plasmolysis can occur, and if not reversed can eventually lead to the cell’s death. Stomata also close in response to increasing soil water deficit, further reducing the ability of the plant to conduct CO₂ for the process of photosynthesis and therefore, water stress can result in an either physical or biochemical limitation to tree growth.

Stomatal conductance responds to changes in atmospheric vapour deficit which can influence water deficit. As atmospheric deficits increase, the plant responds by decreasing stomatal and mesophyll conductance (Gholz et al. 1990; Hari et al. 2000) which reduce total CO₂ conductance. Stomata have been shown to respond to biochemical signalling (ABA) from the leaf apoplast or roots when there is an imbalance of either mesophyll or root tip water supply. Other triggers to stomatal closure may be internal pH, solute or cell volume changes (Boyer 1995). However, conifers in general have a delayed response to ABA concentrations when compared with angiosperms (McAdams et al. 2011).

Leaf water status equilibrates when soil water supply is recharged or when water availability is not in excess of water demand. Extreme water deficits may result in tracheid cavitation which can have negative impacts on tree growth (Tyree and Ewers 1991) and wood quality (Chan 2007). Sinclair and Ludlow (1985) suggest that cell volume and relative leaf water content changes are what trigger physiological process to
slow and inhibit growth while, Schulze (1986 a, b) attributes water movement at the root tips to decreasing gas exchange and hence reduced growth. However, water potential can also vary with resistance within the plant stems (hydraulic conductivity) and while there is less frictional resistance to water flow at the roots, this resistance increases at the growth tips because of the cohesion between water molecules to each other, and their adhesion to the xylem wall.

Research by Robinson et al. (2001) found that while there were correlations between net photosynthesis ($A_n$) and available soil N in jack pine (Pinus banksiana Lamb.) forests with increasing competitor density, they did not find any relationship between $A_n$ and soil water. On the other hand, Myers (1988) found that with certain treatments in the dry season, the water stress integral (or the cumulative measure of predawn water potential over time), was related to soil water content. Where soil water content was not limiting, water stress integral was related more closely to nutrient status. Chan (2007) related moisture content of Pinus radiata in New Zealand and found that stem water stress could lead to stem cavitation in extreme seasonal cases which had implications for wood quality in plantation trees. Therefore it can be concluded that water, as well as nutrient and light have important consequences on tree growth, productivity and wood quality in plantations (Nambiar 1995).

2.7.4 Canopy and radiation interception

The size of the tree and arrangement of leaves of a tree determine how much light energy is converted for C assimilation, nutrient uptake, transport and storage (Kozlowski and Pallardy 1997; Nambiar and Brown 1997). The potential for photosynthesis depends on exposure to shade or light (actual interception). Plants from high light environments have a greater capacity to utilise photosynthetically active radiation (PAR) per unit dry weight, however physiological limitations to this. For example, leaves from shaded
environments do not have the same density of photosynthetic apparatus per unit leaf area as leaves growing in high light areas (Givnish 1988; Sebanek 1992). In addition, at planting out stage, inadequate hardening or exposure to extremes in sunlight, temperature, frost or wind, can result in poor tree survival.

Increasing canopy leaf area has the potential to intercept greater PAR, which can lead to an increased potential for photosynthesis (Allen et al. 2005). However, whole-tree C assimilation is also influenced by canopy architecture and the light attenuation within the canopy, therefore photosynthetic capacity may change with canopy position. Various authors have shown correlations between PAR interception and both leaf area index (LAI) and current annual index (CAI) in various plantation species (Gholz et al. 1990; Samuelson et al. 2004). Allen et al. 2005 found positive correlations between intercepted PAR and above-ground net primary production (ANPP) in sweetgum and sycamore stands. However, a plant’s ability to maximise intercepted radiation is a function of H$_2$O and nutrient availability.

2.7.5 Nutrient use efficiency

Nutrient use efficiency (NUE) is described as the quantity of dry matter produced per gram nutrient assimilated (Chapin III 1980). NUE has two components:

1. The efficiency of nutrient acquisition by the roots of the plant; and

2. The efficiency of nutrient utilization within the plant (Schroth and Sinclair 2003).

NUE is high where plants achieve high growth rates for each unit of nutrient taken up (Schlesinger et al. 1989). NUE can be expressed through comparisons with respiration or photosynthesis per gram of nutrient used. Nutrients affect tree growth by influencing the rate of radiation conversion in plants (Nambiar and Brown 1997).
efficiency of specific nutrients (i.e. N), can be described as the sum of the nutrient taken up, by the average proportional weight of nutrient concentrations in the foliage, wood components or leaf litters (Harrington et al. 2001). The integrated relationship between N and photosynthesis can be described as photosynthetic NUE (PNUE) and describes the rate of photosynthesis for every unit of N used.

A study by Schlesinger et al. (1989) showed higher nutrient use efficiency with *Pinus ponderosa* compared to the broadleaved *Artemisia tridentata*, shrub, when they were grown under identical nursery conditions. The conifers showed a higher ability to re-absorb nutrients before leaf abscission and had slower relative growth rates. The slower relative growth rate of the pine species indicated that conifers, which are typically from poor sites, have an inherent ability to use nutrients for growth more efficiently (Schlesinger et al. 1989).

2.7.5.1 Foliar nutrition

In plantations, foliar nutrient concentrations are used for the assessment of nutritional status after planting (Moorehead 1998). Various studies have used this method to show how nutrient concentrations vary in pine trees in response to certain stimuli or genetics (Sheriff et al. 1986; Nambiar 1995; Xu et al. 1995 a, b, c; Haywood et al. 1997; Bekele et al. 1999; Harrington et al. 2001; Allen et al. 2005). Furthermore, Bekele et al. (1999) consider the analysis of foliar nutrient concentrations as one method that integrates many factors which affect plant nutrition. The functional relationships that exist between N and other nutrients, identified through foliar analysis are therefore critical to identify how we can achieve a more efficient resource use. The benefits of fertilisation to a plantation can also be reduced by increasing the biomass of non-commercial vegetation which, compete for nutrients, water and light more vigorously (Wagner et al. 2006).
Nitrogen, P and K nutrition are important in fundamental processes of plant growth. Nitrogen is used extensively in the maintenance of chlorophyll, and P is used as an energy source in photosynthesis. Bekele et al. (1999) identified that net C assimilation per unit leaf area showed a greater response to a combined N and P treatment, followed by the P and then finally the N fertilisation in a Pinus radiata plantation, despite Landsberg and Waring (1997) having previously identified that foliar nutrient concentrations were not closely linked in conifers. The combination of N and P fertilisers also increases leaf area index (LAI) and litter-fall, when compared to individual applications of either N or P and when other resources are not limiting (Ewers et al. 1999; Harrington et al. 2001). Yu (1999) found that the effects of fertilisation can take 2-3 years after application to show as increased leaf area while Martin and Jokela (2004) found that increasing fertilisation in 15 years old Pinus taeda plantations, resulted in higher growth rates which was partially attributed to nutrient limitations at that stage of the plantations development.

2.7.5.2 Conifer needle morphology

Conifer needles are evergreen, elongated and have a thick waxy cuticle. These morphological adaptations assist in water conservation. Management can influence needle growth because its effect on soil nutrient, water and light availability. For example, Zutter et al. (1999) found individual fascicle mass increased with herbaceous and woody weed control at age 2 years on twelve Pinus taeda sites established in the Competition Omission Monitoring Project (COMP) at locations in Louisiana, Georgia and Virginia. While woody weed control increased N, P and K concentrations on less than one third of the sites, herbaceous weed control increased N concentrations on half of the sites. Needle P concentrations on the other hand declined or were neutral with weed
control. Zutter et al. (1998) attribute the P dilution effect as a result of increased individual fascicle mass in the crown biomass due to increased N availability.

2.8 Hypotheses

This series of experiments contained within this thesis aim to identify how the addition of increased N, P and K and trace elements would influence soil nutrition and weed growth compared to the standard fertilizer applications. This study also aimed to identify how different levels of weed control would affect tree growth, foliar nutrient compositions and the interactions among the physiological growth processes including tree water use efficiency, photosynthesis, soil and foliar $\delta^{13}$C and $\delta^{15}$N in relation to tree WUE and C and N cycling. It is hypothesized that while weed control and fertilisation may increase tree growth, they may also be influencing the surrounding weeds in the inter-rows which may increase competition factors such as water stress or decrease available nutrients to the plantation trees. While the aim of silvicultural practices such as fertilisation and weed control increase nutrient and water resource availability, there may be other environmental or physiological factors limiting tree growth. For example, site characteristics may also influence these relationships and hence site-specific treatments may be beneficial to overcome the variability of growth limiting factors on different sites. The following section outlines the objectives and hypotheses for each data chapter of this thesis.

Chapter 3 – Effects of weed control and fertilisation on soil carbon and nutrient pools in an exotic pine plantation of subtropical Australia. In this chapter I hypothesized that:

1. Weed biomass and weed composition could be influenced by weed control and fertilisation treatments.

2. Soil C and nutrient pools could be influenced by weed control and fertilisation treatments.
3. Soil $\delta^{13}$C and $\delta^{15}$N could be influenced by changes in soils C and N processes occurring as a result of weed control and fertilisation treatments.

**Chapter 4** – The influence of weed control on foliar $\delta^{15}$N, $\delta^{13}$C and tree growth in an 8 year-old exotic pine plantation of subtropical Australia. In this chapter, I hypothesized that:

1. Establishment silviculture (including weed control and fertilisation treatments) would influence C cycling as indicated by (soil $\delta^{13}$C) and nutrient transformations (particularly N), 8 years after establishment.

2. The natural abundance of $^{15}$N (soil $\delta^{15}$N) may be an effective tool for assessing the effects of establishment silviculture on soil N transformations and tree N uptake, and;

3. Foliar $\delta^{15}$N (as an indicator of silvicultural effects of soil N transformations and tree N uptake) is related to tree WUE as indicated by foliar $\delta^{13}$C, and tree growth in an 8-year-old F$_1$ hybrid pine plantation of subtropical Australia.

**Chapter 5** – The effects of weed control and fertilisation at early establishment on tree nitrogen nutrition and water use in an exotic F$_1$ hybrid pine plantation (grown on a Yellow Earth soil type). In this chapter, I hypothesized that:

1. Establishment weed control and fertilisation treatments, influence foliar N concentrations and tree growth (in the first 2 years of plantation establishment), by altering the availability of nutrients (particularly N), tree WUE and water status ($\Psi_{XPP}$);

2. The natural abundance of $^{15}$N ($\delta^{15}$N) may be an effective tool for quantifying the effects of establishment silviculture on plant N competition, uptake and tree growth during establishment;
Chapter 6 - The effects of weed control and fertilisation on tree water use at early establishment in an exotic F₁ hybrid pine plantation (grown on a Grey Podzolic soil type) of subtropical Australia. In this chapter, I hypothesized that:

1. Soil N transformations (as shown by foliar N concentration and foliar δ¹⁵N) would be influenced by weed control and fertilisation treatments, in the first 2 years of plantation establishment; and

2. Weed control and fertilisation influence tree growth by altering water relations (Ψₓᵣᵣ) and tree physiological parameters WUE under experimental conditions on a Grey Podzolic soil type in a 2-year-old, F₁ hybrid pine plantation of subtropical Australia.

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Statement of contribution to co-authored published paper

This paper includes a co-authored published paper. The bibliographic details of the published paper including all authors are:


My contribution to the published paper involved:
Acting as the principle and corresponding author, assisting with the establishment of the experimental design, collection of the soil, weed biomass samples, preparation of samples for soil nutrition (total N, P and K concentrations), C and N total stable isotope composition and inorganic C and N sample preparation, preparation and measurement of weed biomass and soils for statistical analysis, the comprehensive statistical analysis and preparation of data into tables, and providing written drafts outlining the direction, scope and structure of the analysed data.

(Signed)

Name of student:

(Coauthorsigned)

Corresponding author of published paper: Name of corresponding author

(Coauthorsigned)

Supervisor: (Name of Supervisor)
Chapter 3 **Effects of weed control and fertilisation on soil carbon and nutrient pools in an exotic pine plantation of subtropical Australia**

3.1 **Abstract**

Soil carbon (C) and nutrient pools under different plantation weed control and fertilizer management treatments were assessed in a 7-year-old, F$_1$ hybrid (*Pinus elliottii* Engelm. var. *elliottii* (maternal) and *Pinus caribaea* var. *hondurensis* (Sènècl.) W.H.G Barrett & Golfari.) plantation in southeast Queensland, Australia. This research aimed to investigate how early establishment silvicultural treatments would affect weed biomass, soil C, nitrogen (N) and other nutrient pools; and soil C ($\delta^{13}$C) and N isotope composition ($\delta^{15}$N) to help explain the key soil processes regulating the soil C and nutrient pools and dynamics. Soils were sampled in June 2006 in both the planting row and in the inter-planting row at three depths (0–5, 5–10 and 10–20 cm). The variables investigated in this study included total and labile C and N pools; soil $\delta^{13}$C and $\delta^{15}$N; total phosphorus (P); extractable potassium (K); moisture content and weed biomass. The luxury weed control treatments significantly reduced weed biomass and its organic residues returned to the soil in the first 7 years of plantation development. This resulted in significant variations at some depths and positions in soil $\delta^{13}$C, $\delta^{15}$N, extractable K, hot water extractable organic C (HWEOC), hot water extractable total N (HWETN), potentially mineralizable N (PMN) and soil moisture content (MC). Luxury weed control in the absence of luxury fertilisation also significantly decreased extractable K. There was a significant interaction between soil depth and sampling position for soil total C, total N, HWEOC and HWETN. Weed biomass correlated positively with soil total N, $\delta^{13}$C, PMN, MC, HWEOC and HWETN. Luxury weed control treatments significantly reduced weed biomass leading to a reduction of soil organic matter. Soil $\delta^{13}$C and $\delta^{15}$N, together with the other soil labile C and N pools, were sensitive and
useful indicators of soil C dynamics and N cycling processes in the exotic pine plantation of subtropical Australia.

3.2 Introduction

The early-establishment period of forest plantation development provides an opportunity for plantation managers to maximise growth by controlling competition and maximising access to nutrient and water resources (Neary et al. 1990). Weed control and fertilisation are important management practices that allow plantation managers to achieve production outcomes (Mead 2005; Wagner et al. 2006). The success and extent of practices applied at early establishment depend largely on the management objectives and the controlling economic factors (Keeves 1966; Wagner et al. 2006). Despite the reasons for the plantation management decisions, sustaining and investigating the soils productive capacity has become a priority which is now formally endorsed around the world by the plantation certification, forestry standards and global climate change research (Weil and Magdoff 2004; Xu and Chen 2006). The effects of weed control and fertilisation to maximise growth and encourage the efficient use of nutrients could therefore be summarised not only by their contribution to the plantation productivity but also by how they affect soil processes during the early-age, establishment phase (Smethurst and Nambiar 1989; Woods et al. 1992), as has been done in the past with other forest management practices (Vitousek and Matson 1984; Xu et al. 2008, 2009). Contemporary research on this subject shows a complexity of results due to the nature of soils (Jobbagy and Jackson 2001). It is well accepted globally that land-use change, such as the conversion of abandoned pastures to forest plantations, or establishment of a second rotation plantation can have significant influences on soil C and nutrient dynamics (Chen et al. 2004; Echeverria et al. 2004). Plantation establishment, whether native or exotic pine plantations, has been shown to initially reduce soil C status when
established on abandoned or improved pastures (Paul et al. 2002) although this was
dependent on the species grown and stage of development (Guo and Gifford 2002;
Chen et al. 2004). Previous land-use and management practices have also been shown
to influence N transformations in soil and their associated δ15N natural abundances
(Watson and Mills 1998; Burton et al. 2007; Huang et al. 2008; Pan et al. 2008, 2009)
while deforestation and agricultural pursuits can reduce soil organic matter (SOM)
recycling and alter SOM chemical composition (Solomon et al. 2002; Mathers et al.
2003; Ussiri and Johnson 2007).

Management of plantation soils can lead to the maintenance, increase or decrease
of SOM decomposition rates (Swift 2001; Weil and Magdoff 2004). For example,
maintaining SOM inputs into soils ensures that soils are capable of storing nutrient
resources in stable, less mineralizable forms (Swift 2001; Jandl et al. 2007). SOM is
responsible in part, for the binding of soil particles, increasing their structure and
porosity which leads to an increase in the soils ability to cycle nutrients and hold plant
available water (Ghani et al. 2003; Chantigny 2003). One concept of SOM is that it is
divided into a number of fractions which includes labile, intermediate and passive
pools. N availability, microbial biomass community structure, gross N mineralization
and C:N ratio can each be influenced by the presence of the light-fraction organic
matter which forms a part of the labile C fraction (Cookson et al. 2005). This is
because the labile C and N fraction are mobile within the soil and provide ammonium
which mediates microbial N transformations. Labile C fractions as measured by hot
water extractable organic C (HWEOC) are a useful indicator of soil fertility because
they are responsive to short-term management practices (Sparling et al. 1998; Ghani et
al. 2003). Labile C has also been identified as indicators of soil productivity, microbial
activity and sustainable land management practices (Franzluebbers et al. 1996; Vance
2000). This research has focused on both total and labile C and N, along with soil δ13C
and \( \delta^{15} \) as indicators of soil C dynamics and N cycling processes in an exotic pine plantation of subtropical Australia. Soil \( \delta^{13} \)C can be altered through changes in microbial composition during decomposition of SOM (plant, root and microbial and by greater contributions of C\(_4\) photosynthetic plant compositions to the soil (Balesdent et al. 1987; Ehleringer et al. 2000) and so the status of soil organic C and \( \delta^{13} \)C can provide an understanding of C cycling resulting from forest management practices (Xu et al. 2008, 2009). Paul et al. (2002) found from comparing a number of studies on soil C and land-use that weed control and fertilisation could influence the rate of soil C decomposition when pastures or ex-cropping lands were converted to forest plantations. Simpson et al. (2004) looked at the effects of weed control and residue retention over time and found that residue retention could improve tree growth and weed control could influence soil fertility during second rotation, on coastal, sandy soils of low fertility. They also surmised that luxury weed control was neither financial nor environmentally acceptable as a current management practice.

Despite this results presented here offer a unique opportunity to understand how soil \( \delta^{13} \)C and \( \delta^{15} \)N dynamics change with C and N pools as well as other nutrient variables as a result of effects of weed control and fertilisation. To build on previous studies, this study therefore aimed to investigate the manner in which weed control and fertilisation practices at early establishment influenced soil C pools, including \( \delta^{13} \)C, N pools and \( \delta^{15} \)N in a 7-year-old exotic pine plantation. This study also aimed to quantify the effects of weed control and fertilisation on the other nutrient pools (extractable K and total P). Approximately 64% of the 135, 000 ha of exotic pine plantations in southeast Queensland is grown on coastal soils, which are typically low in both N and P. Considering the length of time to harvest (up to 25 years), this study aimed to highlight how early establishment weed control and fertilisation treatments would influence soil C dynamics and N cycling processes on these sites. The hypotheses that
were tested included: (1) weed biomass and weed composition could be influenced by weed and fertilisation treatments; (2) soil C and nutrient pools could be influenced by weed control and fertilisation treatments; and (3) soil δ^{13}C and δ^{15}N could be influenced by changes in soil C and N processes occurring as a result of weed control and fertilisation treatments.

3.3 Materials and methods

3.3.1 Site description

This experiment was established in 1999 by Forestry Plantations Queensland (FPQ). It was developed as a complete randomized block design. The experimental plots are located across compartments 207, 208 and 217 in Toolara State Forest, in southeast Queensland, Australia (26°1.556'S, 152°48.81'E). The region has a subtropical climate with an average annual rainfall of 1,222 mm. The mean monthly rainfall and maximum temperatures for Toolara Forest Station are shown in Fig. 3.1.

![Figure 3.1: Mean monthly rainfall and mean maximum temperatures for Toolara Forestry Station near the experimental site.](image)

The local area experiences an average, daily relative humidity between 54% and 76%. Relative humidity varies in the summer from 70-90% at 9am to 60-80% at 3pm.
and in winter from 60-70% at 9am to 30-50% at 3pm (BoM 2013). Regional soil types are classified as Kandosols and Hyrdrosols (Isbell 1996). Localized soil types vary from Grey Podzolics through to Yellow Earths but are generally dominated by Grey Podzolics. Soil particle size analysis indicated that texture was a predominantly sandy-clay-loam soil type while pH was relatively acid at 4–4.3 (Table 3.1).

**Table 3.1:** Particle size analysis and pH in the top 20 cm soil profile of the experimental site in a 7-year-old plantation of the F1 hybrid between Slash pine and Caribbean pine in southeast Queensland, Australia. Values are means (n=4).

<table>
<thead>
<tr>
<th>Particle size</th>
<th>Depth (cm)</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-5</td>
<td>5-10</td>
<td>10-20</td>
</tr>
<tr>
<td>Clay &lt;2 µm (%)</td>
<td>11.0 ± (2.7)a</td>
<td>12.0 ± (1.9)</td>
<td>12.5 ± (2.2)</td>
</tr>
<tr>
<td>Silt 2-50 µm (%)</td>
<td>9.0 ± (0.9)</td>
<td>10.0 ± (0.6)</td>
<td>9.0 ± (2.2)</td>
</tr>
<tr>
<td>Sand 50-2000 µm (%)</td>
<td>79.0 ± (2.3)</td>
<td>78.0 ± (1.5)</td>
<td>78.0 ± (0.0)</td>
</tr>
<tr>
<td>pH (0.01 $M$ CaCl$_2$)</td>
<td>3.98 ± (0.05)</td>
<td>4.10 ± (0.02)</td>
<td>4.30 ± (0.02)</td>
</tr>
</tbody>
</table>

a Standard errors are indicated in brackets

The dimensions of the experimental plots were 10 rows x 16 trees, at 5 m x 2.4 m spacing and planted at 833 trees ha$^{-1}$. The gross plots area is approximately 0.19 ha. Sixteen plots were selected for this research out of the total experimental area (9.7 ha). The plots represent four treatments: (1) routine fertilizer plus routine weed control (RF+RWC); (2) routine fertilizer plus luxury weed control (RF+LWC); (3) luxury fertilizer plus routine weed control (LF+RWC); and (4) luxury fertilizer plus luxury weed control (LF+LWC) and were replicated four times each.
3.3.2 Site preparation and planting

All plots were strip ploughed in December 1998. The cuttings were set in October 1998 and planted out when soil moisture was suitable in May 1999. Ten high growth performance clones (containerized cuttings) of *Pinus elliottii* var. *elliottii × Pinus caribaea* var. *hondurensis* F$_1$ hybrid were used in each plot.

3.3.3 Weed control and fertilizer treatments

Routine weed control treatments were applied after planting in accordance with FPQ routine practice in coastal exotic plantations, which stipulates that weed cover should not exceed an average of 20% during the first 9 months in the planting rows. The luxury weed control treatment was applied across the whole plot. Table 3.2 shows a summary of the weed control and fertilizer treatments. Luxury weed control treatment differed from the routine application by frequency of application and extra nutrients. The fertilizer treatments were applied as a band application in July 1999. Routine fertilizer was applied as mono-ammonium phosphate (MAP) at the rate of 226 kg ha$^{-1}$ and was reported to provide 10% N and 21.9% P. In addition to the MAP, the luxury fertilizer treatment included a special blend of K and micro-nutrients at a distance of approximately 20 cm from the base of each tree. The luxury fertilizer treatment was intended to encourage maximum growth rates without the growth deformities as a result of excessive N fertilisation (Woods *et al.* 1992).

3.3.4 Soil sampling and analyses

Soils were sampled in June 2006 at 7 years old, in both the planting row (PR) and in the inter-planting row (IPR) to three depths (0–5, 5–10 and 10–20 cm). Soil was collected using a 10 cm diameter soil auger at five random locations within each plot and bulked for each soil depth. This equals one composite soil sample at each depth for each plot,
totalling 4 composite soil samples at each depth for each treatment. Soil samples were refrigerated after sampling and maintained at ~4° C until processing. Field moist samples were used for ammonium (NH$_4^+$-N), nitrate (NO$_3^-$-N) and potentially mineralizable N (PMN) measurements using the KCl extraction and incubation method of Keeney (1980). Analysis was carried out using a SmartChem SC200 discreet chemistry analyser. Soil moisture content (MC) was performed by oven drying field moist samples at 70°C to a constant dry weight (Rayment and Higginson 1992). The NH$_4^+$-N and NO$_3^-$-N results were adjusted for water content. Hot water extractable organic carbon (HWEOC) and hot water extractable total nitrogen (HWETN) extracts (hot water extracted labile forms of C and N) were prepared using the method of Sparling et al. (1998) and Chen and Xu (2005) where 5.0 g (dry weight equivalent) of fresh soil was mixed with 30 mL of distilled water in polypropylene tubes and incubated in a hot water bath at 70°C for 18 hours. At the completion of the incubation the tubes were inverted on an end over end shaker for 5 minutes and then placed in a centrifuge at 2000 rpm for 20 minutes. The tubes were centrifuged for another 10 minutes at 10,000 rpm before filtering through Whatman 42 filter papers into 70 mL containers. Finally the extract was passed through a 0.45 µm filter membrane before 25 mL of the extract was decantered for analysis using a Shimadzu TOC-V$_{CSH/CSN}$ total organic C and total N analyser.
Table 3.2: Summary of weed control and fertilizer treatments applied at early establishment of an exotic pine plantation in subtropical Australia

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Time</th>
<th>Weed control</th>
<th>Chemical applied and rate*</th>
<th>Fertilizer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Woody weed control</td>
<td>Six months prior to planting</td>
<td>All</td>
<td>D50 (Estericide 800/Amicide 500) at 10 L ha(^{-1}) and Grazon® (Triclopyr and Picloram) 1.5 L ha(^{-1})</td>
<td></td>
</tr>
<tr>
<td>Pre-plant</td>
<td>1 month prior to planting</td>
<td>All</td>
<td>7.2 L ha(^{-1}) Round-up® (Glyphosate) plus 10 L ha(^{-1}) of Simazine®</td>
<td></td>
</tr>
<tr>
<td>Pre-plant</td>
<td>1 month prior to planting</td>
<td>Luxury</td>
<td>7.2 L ha(^{-1}) Round-up®</td>
<td></td>
</tr>
<tr>
<td>Post-plant</td>
<td>4(^{a}), 9(^{b}) and 12(^{c}) months</td>
<td>Routine</td>
<td>(^{a}) 2.4 L ha(^{-1}) of Round-up® plus 10 L ha(^{-1}) of Simazine®</td>
<td>226 kg ha(^{-1}) Mono-ammonium phosphate (MAP) being 10% N and 21.9% P or 50 kg ha(^{-1}) of P</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(^{b}) 3.6 L ha(^{-1}) of Round-up®</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(^{c}) 3.6 L ha(^{-1}) of Round-up®</td>
<td></td>
</tr>
<tr>
<td>Post-plant</td>
<td>2(^{a}), 4(^{b}), 6(^{c}), 9-10(^{d}), 13(^{e}) months</td>
<td>Luxury</td>
<td>(^{a}) 9.0 L ha(^{-1}) of Round-up®</td>
<td>As routine fertilizer plus a basal dressing of 5 kg ha(^{-1}) Cu, 5 kg ha(^{-1}) Zn, 5 kg ha(^{-1}) B and 50 kg ha(^{-1}) of K as Muriate of potash (applied 50 kg ha(^{-1}) of K or at 120 g per tree)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(^{b}) 2.4 L ha(^{-1}) of Round-up® plus 10 L / ha(^{-1}) of Simazine®</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(^{c}) 3.6 L ha(^{-1}) of Round-up®</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(^{d}) 3.6 L ha(^{-1}) of Round-up®</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(^{e}) 3.6 L ha(^{-1}) of Round-up® and at 9.2 L ha(^{-1}) Round-up® (in blocks 3 and 4)</td>
<td></td>
</tr>
</tbody>
</table>

*All treatments included Pulse at 3 mL L\(^{-1}\)
All other analysis required soil sub-samples to be ground on a puck and mill grinder including total C and N, $\delta^{13}$C, $\delta^{15}$N, total P and extractable K. Total C and N, $\delta^{13}$C and $\delta^{15}$N were determined on a GVI Isoprime Mass Spectrometer (Manchester, UK) with a Eurovector elemental analyser (Milan, Italy). Total P was analysed using a perchloric / nitric acid digestion (Olsen and Sommers 1982). The supernatant was measured by colorimetric determination on a UV - 160A Shimadzu, UV Visible Recording, Spectrophotometer at 880 nm. Extractable K was carried out using an acetic acid extraction method and determined using a flame atomic absorption spectrophotometer (ASS) (Avanti, GBC Sigma) (Knudsen et al. 1982). A series of soil reference samples for total P and extractable K was sent for analysis to two external, independent laboratories to check the accuracy of P and K analysis and used as reference samples. All other analyses were carried out at Griffith University, Nathan, Queensland.

3.3.5 Understorey biomass sampling

Five 0.25 m$^2$ quadrats were used to collect understorey biomass from each of the four treatment replicates. The biomass was collected from the inter-row sampling position using the method of Mannetje and Haydock (1963). The samples were stored at 4°C until sub-sampling and then separated into plant types and pine litter (including debris) and dried in an oven at 70°C to a constant dry weight prior to weighing each sample. The mass of the weed biomass and pine litter/ debris from the five quadrats were averaged per plot and converted from grams per sampling area to tonnes ha$^{-1}$. Treatment means were then calculated and analysed. When accounting for total understorey biomass two divisions of the understorey components were made. These were (1) pine litter/ debris which included leaf litter, bark and branch, cones and duff (horizon above the mineral soil layer) and (2) weed biomass sorted in generalized life
forms. These life forms included dried litter (predominantly blady grass litter), herbaceous weeds (*Bidens* spp., etc), native grasses (barbed wire grass), (green) blady grass (*Imperata cylindrica*), pasture grasses (*Paspalum* spp., etc), *Lomandra* spp., native shrubs (*Acacia* spp., *Hakea* spp., *Doodenia* spp.), exotic shrubs (*Baccharis* spp.), pine seedlings (*Pinus* spp.), grass trees (*Xanthorrhoea* spp.), vines (various) and swamp grasses.

### 3.4 Statistical analyses

Statistical analysis was carried out using combinations of factorial and general ANOVAs and Fisher’s least significant difference (LSD) for pair-wise comparisons (treatment and treatment x position). Bonferroni analysis was used where significant means were compared to more than two means (depth, depth x position and interactions). Analysis was done using GenStat version 11.1 (VSN International Ltd. 2008). Statistical analysis included three factors, sampling positions, sampling depths and treatments. Sampling positions were divided into planting row (PR) and inter-planting row (IPR), with three sampling depths (0–5, 5–10 and 10–20 cm) and four treatments (RF+RWC, RF+LWC, LF+RWC and LF+LWC). Correlations were undertaken between the weed biomass and the soil variables and were assessed for pooled depths (0–5, 5–10 and 10–20 cm) and pooled positions (PR and IPR) at each depth using the Spearman correlation coefficient. Primer 6 (Clarke and Gorley 2005) was used to summarise the patterns between the composition of weed biomass and environmental variables. This included tests such as multidimensional scaling (MDS), Anosim (permutation-based hypothesis testing between groups) and SIMPER (to assess the differences between the weed biomass compositions within each treatment). Principal component analysis (PCA) was used to identify the inter-relationships between soil variables at the 0-5 cm depth at both positions because it was expected
this would be the most dynamic soil depth. Soil variables were range standardised and
the weed biomass data were log transformed prior to multivariate analysis.

3.5 Results

3.5.1 Weed biomass and composition

Multi-dimensional scaling of weed compositions by biomass indicated that the four
treatments formed two significantly different groups. Group 1 (RF+RWC and
LF+RWC) consisted predominantly of a mix of dried and green blady grass (*Imperata
spp.*), shrubs and native grass biomass while Group 2 (RF+LWC and LF+LWC)
consisted of a mixture of native grass, pine seedlings and herbaceous weeds (Table
3.3).

Group 1 consisted of RF+RWC and LF+RWC treatments which had
approximately 8.38 and 6.45 t ha\(^{-1}\) of weed biomass respectively (Table 3.4). Group 2
consisted of RF+LWC and LF+LWC treatments which had approximately 0.03 and
0.06 t ha\(^{-1}\) of weed biomass respectively. The Anosim global R-test revealed that weed
compositions were significantly different and that it was the LF+RWC treatment that
varied in composition from the RF+LWC and LF+LWC treatments (p<0.05). In
addition to weed biomass each treatment had a layer of pine needle litter and woody
biomass (branches and cones) which attributed approximately ~6 t ha\(^{-1}\) of understorey
cover. The exception was for the RF+LWC treatment which had ~11 t ha\(^{-1}\) although
this was shown to be not significantly different from the other treatments (Table 3.4).
Table 3.3: Weed biomass components separated into generalised life-forms under different weed management practices 7 years after establishment of an exotic pine plantation. Groups (1 and 2) represent different weed composition groups.

<table>
<thead>
<tr>
<th>Grouping</th>
<th>Treatment</th>
<th>Biomass major components</th>
<th>Individual Contribution %</th>
<th>Cumulative percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Group 1</td>
<td>RF+RWC</td>
<td>Dried blady grass litter</td>
<td>41.70</td>
<td>41.70</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shrub</td>
<td>22.32</td>
<td>64.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Native grass</td>
<td>21.51</td>
<td>85.54</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Blady grass</td>
<td>7.45</td>
<td>92.99</td>
</tr>
<tr>
<td></td>
<td>LF+RWC</td>
<td>Dried blady grass litter</td>
<td>57.01</td>
<td>57.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Shrub</td>
<td>17.69</td>
<td>74.69</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Native grass</td>
<td>14.28</td>
<td>88.97</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Blady grass</td>
<td>11.03</td>
<td>100.00</td>
</tr>
<tr>
<td>Group 2</td>
<td>RF+LWC</td>
<td>Native grass</td>
<td>48.37</td>
<td>48.37</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pine seedling</td>
<td>42.40</td>
<td>90.77</td>
</tr>
<tr>
<td></td>
<td>LF+LWC</td>
<td>Native grass</td>
<td>82.62</td>
<td>82.62</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Herbaceous weed</td>
<td>10.50</td>
<td>93.12</td>
</tr>
</tbody>
</table>

Table 3.4: Understorey components were divided into weed biomass and pine litter/debris under different management practices 7 years after establishment of an exotic pine plantation.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Understorey components</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertilizer</td>
<td>Weed control</td>
</tr>
<tr>
<td>RF</td>
<td>RWC</td>
</tr>
<tr>
<td>RF</td>
<td>LWC</td>
</tr>
<tr>
<td>LF</td>
<td>RWC</td>
</tr>
<tr>
<td>LF</td>
<td>LWC</td>
</tr>
</tbody>
</table>
Where values are followed by different lower-case letters this indicates that means are significantly different from each other (p<0.05).

Standard errors are indicated in brackets.

Principal component analysis (PCA) was used to investigate the inter-relationships within soil variables. In the planting row at the 0–5 cm depth, PC 1, 2, 3 and 4 explained 82.2% of the total variation in the soil variables. PC1 at this position and the soil depth contributed to the 38.9% of the total variation and consisted of predominantly soil total C, N and NH$_4^+$-N. PC2 contributed to the 20.0% of the variation and consisted of NO$_3^-$-N, HWEOC and HWETN. PC3 contributed 12.8% and consisted of soil NO$_3^-$-N, PMN and total P. PC4 contributed 10.5% and consisted of C:N ratio and total P.

At the 0–5 cm depth in the inter-planting row, results indicated soil $\delta^{13}$C, $\delta^{15}$N, NH$_4^+$-N, NO$_3^-$-N all increased with soil depth while C:N ratio, total P, extractable K, and PMN decreased with depth (Table 3.5). Soil total P varied significantly between the two sampling positions at the 0-5 cm depth in the LF+LWC treatment (p≤ 0.05) and at the 5-10 cm depth in the RF + RWC treatment (p<0.05) (Table 3.6). In both cases, soil total P was higher in the planting row. HWEOC showed a significant effect of sampling position in the RF+RWC (p<0.05), LF+RWC (p≤ 0.05) and LF+LWC (p<0.05) treatments at the 0-5 cm depth. HWETN showed a similar response for position and both HWEOC and HWETN were higher in the inter-planting row (Table 3.7). Soil moisture content was significantly higher in the inter-planting row at 5-10 cm in the LF+RWC treatment while NH$_4^+$-N was significantly different between IPR and PR sampling position at the 5-10 cm depth in the RF+LWC treatment (Table 3.6).
3.5.2 Effects of treatments on soil variables

There was a significant interaction between the luxury fertilizer and luxury weed control treatment for soil extractable K in the planting row at the 0-5 cm depth. There were significant main effects of the fertilizer treatments at the 0-5 and 5-10 cm depth on soil $\delta^{13}$C in the planting row ($p<0.05$) (Table 3.6). There were also significant main effects of the weed control treatments at the 0-5 cm depth in the planting row, on soil total HWEOC and HWETN; total N and $\delta^{13}$C, and in the inter-planting row on HWEOC, HWETN and moisture content, soil $\delta^{13}$C and $\delta^{15}$N, extractable K, PMN at the 0-5 cm depth ($p<0.05$) (Tables 3.7 and 3.8). Moisture content and PMN were significantly different at the 5-10 cm depth in the planting row for ($p<0.05$) where both MC (Table 3.7) and PMN (Table 3.8) were higher in the routine weed control treatments. Weed control treatments were significant at the 5-10 cm depth in the inter-planting row for HWEOC, moisture content, soil $\delta^{13}$C, $\delta^{15}$N, extractable K and PMN ($p<0.05$) (Tables 3.6 and 3.8 respectively).
Table 3.5: Carbon (C) and nitrogen (N) isotope compositions ($\delta^{13}$C and $\delta^{15}$N), C:N ratio, total phosphorus (P), extractable potassium (K), ammonium (NH$_4^+$-N), nitrate (NO$_3^-$-N), potentially mineralizable nitrogen (PMN) and moisture content (MC) (%) at each soil depth in the soil profile from pooled soil depths under at early establishment of an exotic pine plantation. Soil depths were from 0-5, 5-10 and 10-20 cm.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>$\delta^{13}$C (%)</th>
<th>$\delta^{15}$N (%)</th>
<th>C:N ratio</th>
<th>P (mg kg$^{-1}$)</th>
<th>K (cmol kg$^{-1}$)</th>
<th>NH$_4^+$-N (mg kg$^{-1}$)</th>
<th>NO$_3^-$-N (mg kg$^{-1}$)</th>
<th>PMN (mg kg$^{-1}$)</th>
<th>MC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-5</td>
<td>-26.77 a</td>
<td>1.893 a</td>
<td>39.27 b</td>
<td>68.09 b</td>
<td>0.061 b</td>
<td>1.285 a</td>
<td>0.421 a</td>
<td>7.997 b</td>
<td>7.581 a</td>
</tr>
<tr>
<td>5-10</td>
<td>-26.47 b</td>
<td>2.282 a</td>
<td>36.66 b</td>
<td>58.45 b</td>
<td>0.054 b</td>
<td>1.547 b</td>
<td>0.500 ab</td>
<td>7.337 ab</td>
<td>7.673 a</td>
</tr>
<tr>
<td>10-20</td>
<td>-26.13 c</td>
<td>3.472 b</td>
<td>31.73 a</td>
<td>31.75 a</td>
<td>0.046 a</td>
<td>1.694 b</td>
<td>0.532 b</td>
<td>6.317 a</td>
<td>7.977 a</td>
</tr>
</tbody>
</table>

*Where values are followed by different lower-case letters for each soil depth this indicates that sampling depths are significantly different from each other (p<0.05).*
Table 3.6: Total phosphorus (P), hot-water extractable total organic carbon (HWEOC), hot water extractable total nitrogen (HWETN), nitrate (NO$_3^-$-N), and moisture content (MC) in the 0-10 cm soil profile under different management practices at early establishment of an exotic pine plantation. Treatments are: routine fertilizer plus routine weed control (RF+RWC); routine fertilizer plus luxury weed control (RF+LWC); luxury fertilizer plus routine weed control (LF+RWC); and luxury fertilizer plus luxury weed control (LF+LWC). Sampling positions are from the planting row (PR) or the inter-planting row (IPR). Values are means (n=4).

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Fertilizer</th>
<th>Weed control</th>
<th>Total P (mg kg$^{-1}$)</th>
<th>HWEOC (mg kg$^{-1}$)</th>
<th>HWETN (mg kg$^{-1}$)</th>
<th>NO$_3^-$-N (mg kg$^{-1}$)</th>
<th>MC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>0-5 cm</td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
<td>IPR</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
<td>IPR</td>
</tr>
<tr>
<td>0-5 cm</td>
<td></td>
<td></td>
<td></td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
<td>IPR</td>
</tr>
<tr>
<td>RF</td>
<td>RF</td>
<td>RWC</td>
<td>89.95</td>
<td>71.5</td>
<td>313.8 a B</td>
<td>459.5 a A</td>
<td>10.30 a B</td>
</tr>
<tr>
<td>RF</td>
<td>RF</td>
<td>LWC</td>
<td>68.3</td>
<td>61.1</td>
<td>259.2 b</td>
<td>324.3 b</td>
<td>9.08 b</td>
</tr>
<tr>
<td>LF</td>
<td>LF</td>
<td>RWC</td>
<td>76.3</td>
<td>49.4</td>
<td>347.3 a B</td>
<td>501.2 a A</td>
<td>13.12 a B</td>
</tr>
<tr>
<td>LF</td>
<td>LF</td>
<td>LWC</td>
<td>76.7 A b</td>
<td>44.1 B</td>
<td>249.5 b B</td>
<td>314.6 b A</td>
<td>8.04 b B</td>
</tr>
<tr>
<td>5-10 cm</td>
<td></td>
<td></td>
<td></td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
<td>IPR</td>
</tr>
<tr>
<td>RF</td>
<td>RF</td>
<td>RWC</td>
<td>71.1 A</td>
<td>46.8 B</td>
<td>268.1</td>
<td>312.3 a</td>
<td>8.04 B</td>
</tr>
<tr>
<td>RF</td>
<td>RF</td>
<td>LWC</td>
<td>66.4</td>
<td>56.6</td>
<td>272.7</td>
<td>236.1 b</td>
<td>11.15</td>
</tr>
<tr>
<td>LF</td>
<td>LF</td>
<td>RWC</td>
<td>67.8</td>
<td>50.5</td>
<td>317.2</td>
<td>293.3 a</td>
<td>11.64</td>
</tr>
<tr>
<td>LF</td>
<td>LF</td>
<td>LWC</td>
<td>66.7</td>
<td>41.1</td>
<td>222.5</td>
<td>240.2 b</td>
<td>6.41</td>
</tr>
</tbody>
</table>

a Where values are followed by different lower-case letters for each soil depth this indicates that treatment means are significantly different from each other (p<0.05).

b Where values are followed by different capital letters this indicates that sampling position means are significantly different (p<0.05).
Table 3.7: Total carbon (C), total nitrogen (N) and hot-water extractable total organic C (HWEOC) and total N (HWETN) at pooled soil depths and different sampling positions in the soil profile at early establishment of an exotic pine plantation. Soil depths are sampled from 0-5, 5-10 and 10-20 cm. Sampling positions are from the planting row (PR) or the inter-planting row (IPR). Values are means (n=16).

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Total C (%)</th>
<th>Total N (%)</th>
<th>HWEOC (mg kg⁻¹)</th>
<th>HWETN (mg kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
<td>IPR</td>
</tr>
<tr>
<td>0-5</td>
<td>1.41 c</td>
<td>2.02 d</td>
<td>0.036 bc</td>
<td>0.050 d</td>
</tr>
<tr>
<td>5-10</td>
<td>1.30 bc</td>
<td>1.41 c</td>
<td>0.035 bc</td>
<td>0.038 c</td>
</tr>
<tr>
<td>10-20</td>
<td>0.76 a</td>
<td>0.80 ab</td>
<td>0.024 a</td>
<td>0.025 ab</td>
</tr>
</tbody>
</table>

Where values are followed by different lower-case letters for each soil depth and position this indicates that sampling depth and position are significantly different from each other (p<0.05).

The interaction of between luxury fertilisation and luxury weed control was significant for both soil C:N ratio in the inter-planting row at the 5-10 cm depth (which reduced the C:N ratio) and for extractable K in the planting row at 0-5 cm depth, where extractable K was lowest as a result of routine fertilisation and luxury weed control (Table 3.8).
Figure 3.2: Relationships between: (a) total carbon (C) (%) and total nitrogen (N) (%) (n=92, p<0.001); and (b) between hot water extractable C (HWEOC) and hot water extractable total N (HWETN) (n=92, p<0.001) at pooled soil sampling depths and positions under different weed control and fertilisation treatments.

Figure 3.3: Relationships between: (a) total carbon (C) (%) and nitrogen (N) isotope composition ($\delta^{15}$N) (‰) (n=92, p<0.001); and (b) total N (%) and $\delta^{15}$N (n=92, p<0.001) at pooled soil sampling depths and positions under different weed control and fertilisation treatments.
**Table 3.8**: Total nitrogen (N), carbon (C) and N isotope compositions ($\delta^{13}$C and $\delta^{15}$N), extractable potassium (K), potentially mineralizable N (PMN) and C:N ratio in the 0-10 cm soil profile under different management practices at early establishment of an exotic pine plantation. Treatments are: routine fertilizer plus routine weed control (RF+RWC); routine fertilizer plus luxury weed control (RF+LWC); luxury fertilizer plus routine weed control (LF+RWC); and luxury fertilizer plus luxury weed control (LF+LWC). Sampling positions are from the planting row (PR) or the inter-planting row (IPR). Values are means (n=4).

<table>
<thead>
<tr>
<th>Fertilizer</th>
<th>Weed control</th>
<th>Total N (%)</th>
<th>$\delta^{13}$C (%)</th>
<th>$\delta^{15}$N (%)</th>
<th>Extractable K (cmol kg$^{-1}$)</th>
<th>PMN (mg kg$^{-1}$)</th>
<th>C:N ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>0-5 cm PR</td>
<td>IPR</td>
<td>PR IPR</td>
<td>PR IPR</td>
<td>PR IPR</td>
<td>PR IPR</td>
</tr>
<tr>
<td>RF</td>
<td>RWC</td>
<td>0.039 a</td>
<td>0.057</td>
<td>-26.9 ba</td>
<td>-26.8 a</td>
<td>2.05</td>
<td>1.60</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td>0.063 a</td>
<td>0.068</td>
</tr>
<tr>
<td>RF</td>
<td>LWC</td>
<td>0.032 b</td>
<td>0.043</td>
<td>-27.3 bb</td>
<td>-27.2 b</td>
<td>2.22</td>
<td>1.85</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td>0.043 b</td>
<td>0.045</td>
</tr>
<tr>
<td>LF</td>
<td>RWC</td>
<td>0.044 a</td>
<td>0.056</td>
<td>-25.9 aa</td>
<td>-26.4 b</td>
<td>1.67</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
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<td>0.065 a</td>
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<tr>
<td>LF</td>
<td>LWC</td>
<td>0.031 b</td>
<td>0.044</td>
<td>-26.9 ab</td>
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<td>2.82</td>
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</tr>
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<td>0.063 a</td>
<td>0.066</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5-10 cm PR</td>
<td>IPR</td>
<td>PR IPR</td>
<td>PR IPR</td>
<td>PR IPR</td>
<td>PR IPR</td>
</tr>
<tr>
<td>RF</td>
<td>RWC</td>
<td>0.035</td>
<td>0.048</td>
<td>-26.7 b</td>
<td>-26.5 a</td>
<td>2.28</td>
<td>1.79</td>
</tr>
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<td></td>
<td>0.056</td>
<td>0.058 a</td>
</tr>
<tr>
<td>RF</td>
<td>LWC</td>
<td>0.039</td>
<td>0.032</td>
<td>-26.8 b</td>
<td>-26.8 b</td>
<td>2.42</td>
<td>3.37</td>
</tr>
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<td></td>
<td>0.055</td>
<td>0.040 b</td>
</tr>
<tr>
<td>LF</td>
<td>RWC</td>
<td>0.038</td>
<td>0.038</td>
<td>-26.0 a</td>
<td>-25.9 a</td>
<td>1.72</td>
<td>1.77</td>
</tr>
<tr>
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<td></td>
<td>0.062</td>
<td>0.059 a</td>
</tr>
<tr>
<td>LF</td>
<td>LWC</td>
<td>0.031</td>
<td>0.034</td>
<td>-26.6 a</td>
<td>-26.8 b</td>
<td>2.74</td>
<td>2.18</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>0.050</td>
<td>0.055 b</td>
</tr>
</tbody>
</table>

Where values are followed by different lower-case letters for each soil depth this indicates that treatment means are significantly different from each other (p<0.05).
Figure 3.4: Relationships between: (a) hot water extractable organic carbon (HWEOC) (mg kg⁻¹) and nitrogen (N) isotope composition (δ¹⁵N) (‰) (n=92, p<0.001); and (b) hot water extractable total N (HWETN) (mg kg⁻¹) and δ¹⁵N treatments (n=92, p<0.001) at pooled soil sampling depths and positions under different weed control and fertilisation.

3.5.3 Correlations of soil variables and weed biomass

At pooled sampling positions and soil depths, there were significant positive correlations between soil total C and N (Fig. 3.2a) and between HWEOC and HWETN (Fig. 3.2b) (Table 3.9). Significant negative correlations existed between soil total C and δ¹⁵N (Fig. 3.3a), soil total N and δ¹⁵N (Fig. 3.3b); between HWEOC and δ¹⁵N (Fig. 3.4a); and between HWETN and δ¹⁵N (Fig. 3.4b). There were also significant correlations between soil total C and extractable K, and between soil total N and extractable K (Fig. 3.5a and 3.5b) when the sampling positions and depths were pooled (Table 3.9).
Figure 3.5: Relationships between: (a) total carbon (C) (%) and extractable potassium (K) (cmol kg\(^{-1}\)) (n=92, p<0.001); and (b) total nitrogen (N) (%) and extractable K (cmol kg\(^{-1}\)) (n=92, p<0.001) at pooled soil sampling depths and positions under different weed control and fertilisation treatments.

Figure 3.6: Relationships between: (a) total carbon (C) (%) and hot water extractable organic C (HWEOC) (mg kg\(^{-1}\)) (n=32, p<0.001); and (b) total nitrogen (N) (%) and hot water extractable total N (HWETN) (mg kg\(^{-1}\)) (n=32, p<0.001) at the 0–5 cm soil sampling depth under different weed control and fertilisation treatments.
Table 3.9: Spearman correlation coefficients between soil total carbon (C), nitrogen (N), C:N ratio, C and N isotope compositions (δ\textsubscript{13}C and δ\textsubscript{15}N), ammonium (NH\textsubscript{4}\textsuperscript{+}-N), nitrate (NO\textsubscript{3}\textsuperscript{-}-N), potentially mineralizable N (PMN), moisture content (MC), hot-water extractable organic C (HWEOC) and total N (HWETN), total phosphorus (P), extractable potassium (K) and weed biomass analyzed for pooled positions and pooled soil depths, under different management practices at early establishment of an exotic pine plantation (n=30).

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>C/N</th>
<th>δ\textsubscript{13}C</th>
<th>δ\textsubscript{15}N</th>
<th>NH\textsubscript{4}\textsuperscript{+}-N</th>
<th>NO\textsubscript{3}\textsuperscript{-}-N</th>
<th>PMN</th>
<th>MC</th>
<th>HWEOC</th>
<th>HWETN</th>
<th>P</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>0.96***</td>
<td>0.35***</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>C/N</td>
<td>0.57***</td>
<td>0.35***</td>
<td>0.57***</td>
<td>-0.29**</td>
<td>-0.27**</td>
<td>-0.26*</td>
<td>-0.50***</td>
<td>0.43***</td>
<td>0.12</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>δ\textsubscript{13}C</td>
<td>-0.29**</td>
<td>-0.27**</td>
<td>-0.26*</td>
<td>-0.29**</td>
<td>-0.27**</td>
<td>-0.26*</td>
<td>-0.50***</td>
<td>0.43***</td>
<td>0.12</td>
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<tr>
<td>δ\textsubscript{15}N</td>
<td>-0.50***</td>
<td>0.43***</td>
<td>-0.51***</td>
<td>0.10</td>
<td>0.05</td>
<td>0.10</td>
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<td>NH\textsubscript{4}\textsuperscript{+}-N</td>
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<td>0.20</td>
<td>-0.21*</td>
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<td>0.10</td>
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</tr>
<tr>
<td>NO\textsubscript{3}\textsuperscript{-}N</td>
<td>0.02</td>
<td>0.03</td>
<td>-0.05</td>
<td>-0.09</td>
<td>0.13</td>
<td>0.20</td>
<td></td>
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</tr>
<tr>
<td>PMN</td>
<td>0.41***</td>
<td>0.46***</td>
<td>0.09</td>
<td>-0.04</td>
<td>-0.21*</td>
<td>0.42***</td>
<td>-0.44***</td>
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</tr>
<tr>
<td>MC</td>
<td>0.47***</td>
<td>0.54***</td>
<td>-0.01</td>
<td>0.06</td>
<td>0.15</td>
<td>0.43***</td>
<td>0.18</td>
<td>0.47***</td>
<td></td>
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<tr>
<td>HWEOC</td>
<td>0.76***</td>
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<td>0.43***</td>
<td>-0.23*</td>
<td>-0.68***</td>
<td>0.00</td>
<td>-0.23*</td>
<td>0.43***</td>
<td>0.18</td>
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<tr>
<td>HWETN</td>
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<td>0.72***</td>
<td>0.34***</td>
<td>-0.22*</td>
<td>-0.65***</td>
<td>-0.04</td>
<td>-0.27**</td>
<td>0.38***</td>
<td>0.08</td>
<td>0.96***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>0.44***</td>
<td>0.39***</td>
<td>0.41***</td>
<td>-0.28**</td>
<td>-0.28**</td>
<td>-0.04</td>
<td>-0.27**</td>
<td>0.38***</td>
<td>0.08</td>
<td>0.96***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>K</td>
<td>0.69***</td>
<td>0.68***</td>
<td>0.34***</td>
<td>-0.15</td>
<td>-0.28**</td>
<td>-0.02</td>
<td>-0.29*</td>
<td>0.47***</td>
<td>0.50***</td>
<td>0.53***</td>
<td>0.48***</td>
<td>0.40***</td>
<td></td>
</tr>
<tr>
<td>Weed biomass</td>
<td>0.20</td>
<td>0.23*</td>
<td>0.02</td>
<td>0.32**</td>
<td>-0.10</td>
<td>0.21</td>
<td>-0.29*</td>
<td>0.46***</td>
<td>0.40***</td>
<td>0.25*</td>
<td>0.21*</td>
<td>0.10</td>
<td>0.29**</td>
</tr>
</tbody>
</table>

*, ** and *** indicate significance at P < 0.05, P < 0.01 and P < 0.001 respectively.
Correlations also existed between the soil variables at the 0-5 cm depth when sampling positions were pooled, particularly between soil moisture content and soil total C (total N / extractable K and NH$_4^+$-N); PMN, soil total C and total N were each correlated to HWEOC (Fig. 3.6a); and HWETN (Fig. 3.6b); and soil moisture content was correlated to soil total C (Fig. 3.7a), total N (Fig. 3.7b) and extractable K (Table 3.10). At the 5-10 cm depth with pooled sampling positions, soil total C and total N were highly correlated to soil extractable K (HWEOC/HWETN) while PMN was also correlated with soil moisture content (Table 3.11). At the 10-20 cm depth, soil total C and N were correlated to extractable K (HWEOC/HWETN/ soil total P and soil moisture content) while soil $\delta^{13}$C was correlated to soil total P/total C/HWEOC and HWETN) (Table 3.12).

Figure 3.7: Relationships between: (a) total carbon (C) (%) and moisture content (MC) (%) (n=31, p<0.001); and (b) total nitrogen (N) (%) and MC (%) (n=32 p<0.001) at the 0–5 cm sampling depth under different weed control and fertilisation treatments.
Table 3.10: Spearman correlation coefficients between soil total carbon (C), nitrogen (N), C:N ratio, C and N isotope compositions ($\delta^{13}$C and $\delta^{15}$N), ammonium (NH$_4^+$-N), nitrate (NO$_3^-$-N), potentially mineralizable N (PMN), moisture content (MC), hot-water extractable organic C (HWEOC) and total N (HWETN), total phosphorus (P), extractable potassium (K) and weed biomass analyzed for pooled positions at the 0-5 cm soil depth, under different management practices at early establishment of an exotic pine plantation (n=29).

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>C/N</th>
<th>$\delta^{13}$C</th>
<th>$\delta^{15}$N</th>
<th>NH$_4^+$-N</th>
<th>NO$_3^-$-N</th>
<th>PMN</th>
<th>MC</th>
<th>HWEOC</th>
<th>HWETN</th>
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<td>Weed biomass</td>
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<td>-0.12</td>
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<td>-0.16</td>
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*, ** and *** indicate significance at P < 0.05, P < 0.01 and P < 0.001 respectively.
Table 3.11: Spearman correlation coefficients between soil total carbon (C), nitrogen (N), C:N ratio, C and N isotope compositions ($\delta^{13}$C and $\delta^{15}$N), ammonium ($\text{NH}_4^+$-N), nitrate ($\text{NO}_3^-$-N), potentially mineralizable N (PMN), moisture content (MC), hot-water extractable organic C (HWEOC) and total N (HWETN), total phosphorus (P), extractable potassium (K) and weed biomass analyzed for pooled positions at the 5-10 cm soil depth, under different management practices at early establishment of an exotic pine plantation (n=31).

<table>
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<th>$\text{NO}_3^-$-N</th>
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<th>MC</th>
<th>HWEOC</th>
<th>HWETN</th>
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<td>-0.40*</td>
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<td>PMN</td>
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<td>0.49**</td>
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<td>0.28</td>
<td>0.08</td>
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<td>0.27</td>
<td>-0.41*</td>
<td>0.56***</td>
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<td>0.42*</td>
<td>0.29</td>
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*, ** and *** indicate significance at P < 0.05, P < 0.01 and P < 0.001 respectively.
Table 3.12: Spearman correlation coefficients between soil total carbon (C), nitrogen (N), C:N ratio, C and N isotope compositions ($\delta^{13}$C and $\delta^{15}$N), ammonium (NH$_4^+$-N), nitrate (NO$_3^-$-N), potentially mineralizable N (PMN), moisture content (MC), hot-water extractable organic C (HWEOC) and total N (HWETN), total phosphorus (P), extractable potassium (K) and weed biomass analyzed for pooled positions at the 10-20 cm soil depth, under different management practices at early establishment of an exotic pine plantation (n=30).

<table>
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<th>NH$_4^+$-N</th>
<th>NO$_3^-$-N</th>
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<th>MC</th>
<th>HWEOC</th>
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</tr>
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<td>-0.23</td>
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</tr>
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<td>0.42*</td>
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<td>-0.15</td>
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<td>0.25</td>
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</table>

* *, ** and *** indicate significance at P < 0.05, P < 0.01 and P < 0.001 respectively.
When weed biomass (t ha\(^{-1}\)) was correlated to the soil variables, at pooled soil depths and sampling positions, weed biomass was significantly and positively correlated to soil total N, \(\delta^{13}C\), PMN, moisture content, HWEOC, HWETN and extractable K, but negatively correlated to soil NO\(_3^−\)-N (Table 3.9). At the 0-5 cm depth with the pooled sampling positions, weed biomass was positively correlated to total N, soil \(\delta^{13}C\), PMN, moisture content, HWEOC and HWETN but was not correlated to soil NO\(_3^−\)-N (Table 3.10). At the 5–10 cm depth with the pooled sampling positions, weed biomass was positively correlated to PMN, moisture content, HWEOC and extractable K, but was negatively correlated to NO\(_3^−\)-N (Table 3.11). At the 10-20 cm depth with the pooled sampling positions, only soil moisture content was significantly and positively correlated to the weed biomass (Table 3.12).

### 3.6 Discussion

#### 3.6.1 Treatment effects on weed biomass and composition

Results indicated that weed biomass and weed composition were influenced by weed control and fertilisation treatments as hypothesized (Hypothesis 1). The use of routine weed control treatments with luxury fertilisation showed the greatest potential to encourage a biomass composition of C\(_4\) weeds. The composition of C\(_4\) grasses alone can result in greater soil organic matter (SOM) residues (Cheng et al. 2008) and increased \(\delta^{13}C\) of plant residues recycling into the soil organic matter fractions (Balesdent et al. 1987). Cheng et al. (2008) discuss how C\(_4\) plants have a higher C:N ratio in their biomass compared to C\(_3\) plants due to the increased RUBISCO levels in the C\(_4\) plants. The variation in C:N ratios of C\(_4\) plants allow them to fix more C per unit weight and therefore produce more biomass for cycling to the soils. Other studies have also found that herbicide applications have the potential to reduce C and N cycling as a
result of decreased residues returned to the soil and the reduction of the quality of those residues (Vitousek et al. 1982; Locke and Bryson 1997). In addition to the weed biomass, each treatment also had a layer of pine needle litter and woody biomass which would also be a significant contributor to the nutrient recycling. Although this layer was not significantly different between treatments there was a trend for it to be higher in the routine fertilizer and luxury weed control treatment which changes the predominant source of residues returned to the soils in these treatments. These results suggest that the choice of weed control management has the potential to influence the amount of weed biomass while luxury fertilisation has the potential to influence the composition of weeds growing and the subsequent residues returned to the soil over the 7-year period.

3.6.2 Treatment and sampling effects on soil C pools, $\delta^{13}\text{C}$ and other related soil variables

Results indicated that weed control and fertilisation treatments influenced soil C pools (Hypothesis 2) and $\delta^{13}\text{C}$ (Hypothesis 3). Routine weed control, when compared to luxury weed control treatments, resulted in a significant increase in weed biomass. This increase was associated with a significant increase in soil $\delta^{13}\text{C}$ at the 0-5 and 5-10 cm depths in the inter-planting row and at the 0–5 cm depth in the planting row. A number of reasons are offered to explain why soil $\delta^{13}\text{C}$ would differ as a result of weed control treatments and soil-sampling position. Ehleringer et al. (2000) proposed that the most regularly observed trend contributing to the progressive increase of $\delta^{13}\text{C}$ in the SOM was due to the increased soil microbial activity. Ehleringer et al. (2002) indicate that soil bacteria and fungi constitute an important component for nutrient cycling, and that they are usually enriched in $\delta^{13}\text{C}$ compared to the substrates which they decompose. This leads to the increased soil $\delta^{13}\text{C}$, where soil microbes are present. It has been established that soil microbial processes are controlled not only by pH, temperature and
soil moisture but also the quality and quantity of available substrates (Franzluebbers 2004; He et al. 2005, 2006). The presence and degree of this activity is limited primarily by the soil total C and N pools available within the substrates (Mathers et al. 2003) and this has been shown to decrease with soil depth due to the depletion of C compounds (Schlesinger 1977). The results for HWEOC and HWETN also support an increase in microbial activity in soils under these treatments. The hot water method used for labile C extraction removes a component of microbial cells and the method has been shown to correlate with microbial biomass C (Sparling et al. 1998). The HWEOC results show a similar trend to soil δ^{13}C concentrations in the 0-10 cm soil depths in the inter-planting row and in the 0-5 cm depths for the planting row. The variation at sampling depth and position could be due to the presence or absence of weed roots in the weed control treatments. The increase in HWEOC and δ^{13}C in the routine weed control treatments seems to indicate an increase of microbial activity as a result of the increased litter, roots and detritus available for decomposition, although further investigation of microbial activity is warranted to confirm this.

On the other hand, Balesdent et al. (1987) attribute relative proportions of ^{12}C/^{13}C in organic matter, to the plant material it is derived from, resulting in the labelling of organic matter δ^{13}C content dependent on its origins from either C_3 or C_4 vegetation types. The less negative or δ^{13}C enrichment in soils under the routine weed control treatments could also be related to the organic matter being enriched with δ^{13}C from C_4 residues growing in these treatments. The results presented here show that the most significant contribution to soil C and N dynamics was as a result of the increased above-ground residues from the routine weed control treatments even though the experiment was only 7 years old at sampling. Wedin et al. (1995) found that δ^{13}C changes were small but significant after 2 years when four grass species were introduced into an oak
savannah. The grass litter in their study reportedly lost 70% of its initial mass over the two years. In addition, the δ\textsubscript{13}C signatures shifted for both C\textsubscript{4} and C\textsubscript{3} grasses during decomposition by -1.5‰ and +0.6‰ respectively. Wedin et al. (1995) concluded that the shifts in δ\textsubscript{13}C were the result of soil organic C mixing with residual C from fungal and microbial activity formed on litters from both C\textsubscript{3} and C\textsubscript{4} sources. Oelbermann and Voroney (2007) found a shift in soil δ\textsubscript{13}C from that typically recorded for C\textsubscript{4} vegetation (long term pasture site) to one representative of C\textsubscript{3} vegetation after 13 years of intercropping with predominantly C\textsubscript{3} plants.

Cheng et al. (2008) found that increasing residual inputs from the introduced Spartina alterniflora (a C\textsubscript{4} plant) onto Yangtze River wetlands in China after 8 years, had shown a clear shift from the original Scirpus mariqueter (a C\textsubscript{3} plant) δ\textsubscript{13}C values to that typical of a C\textsubscript{4}, δ\textsubscript{13}C isotopic signature. These examples of how δ\textsubscript{13}C is affected by vegetative litter sources can alter the soil organic matter δ\textsubscript{13}C values over relatively short time frames, give evidence to support the reasoning that residual inputs from the C\textsubscript{4} grass litters could have decomposed enough in 7 years for the soil organic C to be enriched by the C\textsubscript{4} δ\textsubscript{13}C. This is also supported by significant positive correlations of total weed biomass to soil δ\textsubscript{13}C, total N, HWEOC, HWETN, PMN and soil moisture content, suggesting that as weed biomass (plant residues) increased so did the magnitude of these variables. Although results showed only small shifts in δ\textsubscript{13}C isotope signatures (~0.05- 0.1‰) in the soil under routine weed control treatments, the differences were statistically significant. Unfortunately the determination of δ\textsubscript{13}C values for each plant type was outside the scope of this research, the predominant species (Pinus spp. and Imperata spp.) photosynthetic groups have been reported in other literature (Chmura and Aharon 1995). There was also a change in δ\textsubscript{13}C with soil depth (in the upper soil layers). Changing δ\textsubscript{13}C with depth is explained by Cheng et al.
(2008) and Jobbagy and Jackson (2000) as an effect of increased root biomass and residues from their decomposition in the upper soil layers. Jobbagy and Jackson (2000) also suggest that SOM accumulation with depth was not only a function of the above-ground vegetation contributing to the residues but also the interaction between soil texture, type of C present and precipitation.

Soil $\delta^{13}C$ in the planting row was also influenced by the main effect of fertilizer at the 0–5 and 5–10 cm depths. At this position and these depths the $\delta^{13}C$ was more enriched as a result of luxury fertilisation ($\sim+0.35$). The effect of luxury fertilisation on $\delta^{13}C$ was limited to the planting row where it was applied. Schlesinger (1997) and Alvarez (2005) suggest that nitrate fertilisation can increase soil C but only when the residues of the increased plant biomass are returned to the soil. Girvan et al. (2004) found that the use of fertilizers had the potential to increase microbial biomass and facilitate shifts in the microbial communities. If this were so we would expect a similar response to fertilizer treatments from HWEOC in the planting row, and this was not the case.

3.6.3 Treatment and sampling effects on soil N pools, $\delta^{15}N$ and other related soil variables

Results indicated that weed control and fertilisation treatments also influenced soil N pools (Hypothesis 2) and $\delta^{15}N$ (Hypothesis 3). Routine weed control was also associated with the significant differences found in soil moisture content, PMN, and HWETN at the 0–5 cm depth in the inter-planting row and total N in the planting row. PMN is influenced by soil moisture and temperature and therefore their increase may lead to greater N mineralization. Routine weed control provided a soil mulching effect which could have decreased evaporation and reduced temperature variation from the soil surface prior to the time of sampling. Routine weed control resulted in more
favourable conditions for soil N accumulation and as a result greater nutrient cycling was facilitated. PMN, NH$_4^+$-N and HWETN showed similar trends at the 0-5 cm depth (although NH$_4^+$-N was not significant) with higher concentrations in the inter-planting row in the routine weed control treatments. PMN was also significant at the 5–10 cm depth at both sampling positions between weed control treatments. A number of studies have linked the reductions of some labile soil organic matter fractions, to a decline in microbial N supplies (Cookson and Murphy 2004; Cookson et al. 2005). The question remains if this could also be reason for the decrease in HWETN as a result of luxury weed control treatments. When weed biomass (t ha$^{-1}$) was correlated to the soil variables at the 0-5 cm depth, results indicated that the weed biomass showed significant relationships with soil total N, PMN and HWETN and soil moisture content. This suggests that total and labile N variables varied as a result of weed biomass. Smethurst and Nambi (1989) and Woods et al. (1992) recognised the pros and cons of N immobilization by weeds in plantations. Principle components analysis at both sampling positions in the 0–5 cm soil depth also indicated a significant contribution of labile N (NO$_3^-$-N and NH$_4^+$-N), $\delta^{15}$N and HWETN to the variation in soil nutrient patterns.

Results indicated a trend that was consistent with higher concentrations of $\delta^{15}$N and NO$_3^-$-N as a result of luxury weed control treatments. Both these variables showed significant negative relationships to HWEOC, HWETN and PMN at pooled depths and positions. NO$_3^-$-N showed a similar trend to soil $\delta^{15}$N where both variables increased in the inter-planting row with luxury weed control but unlike soil $\delta^{15}$N, NO$_3^-$-N was not significantly different between the weed control treatments. This could have been the result of soil spatial variability encountered during sampling and because N
transformations are influenced by many factors (Hogberg 1997; Hogberg and Johannisson 1993).

As the luxury weed control treatments produced very low weed biomass, there were very few weeds in these treatments to assimilate N. Large pools of NO$_3^-$-N in soils have the potential to be lost out of the soil profile. This is because NO$_3^-$-N is a mobile compound and if it is not taken up by microbes, plants or roots it can be lost by denitrification, volatilization or leached from the soil (Nadelhoffer and Fry 1994). Higher $\delta^{15}$N in the luxury weed control treatments coincided with higher nitrate accumulations and demonstrated the potential for their loss. Soils can become enriched in $\delta^{15}$N as a result of the fractionation that occurs during ammonium volatilization, nitrification and denitrification. Huygens et al. (2008) found that fractionation could not alone explain large $\delta^{15}$N variation patterns but concluded that $\delta^{15}$N enriched microbial compounds were related to high $\delta^{15}$N in the soils. The increase of $\delta^{15}$N with depth results from the accumulation of organic materials enriched in $\delta^{15}$N, compared to above-ground inputs which are generally low in $\delta^{15}$N (rainfall and plant litter). This along with the variations in above-ground weed biomass could explain why the variation of $\delta^{15}$N was limited to the top 10 cm of the inter-planting row. These results highlight the influence of early vegetation management on the N cycling processes in coastal sandy soils after 7 years of plantation establishment.

3.7 Conclusion

Luxury weed control treatments significantly reduced weed biomass leading to a reduction in soil organic matter accumulation. The reduction of soil organic matter in the top 0-10 cm of soil influenced the availability of various nutrients, soil labile C and N pools and soil moisture. In the absence of weed biomass, there was a decrease in labile C pools and soil $\delta^{13}$C, with negative correlations among soil $\delta^{15}$N, HWEOC and
HWETN. Routine weed control practices led to a larger pool of weed residues and the subsequent active cycling of C and N pools as indicated by the increased HWEOC, HWETN, PMN and δ¹³C. This study has implicated the consequences of early-age plantation management techniques to C and N cycling in soils and their on-going effects to long-term soil fertility, in an exotic pine plantation of subtropical Australia. The uses of δ¹³C and δ¹⁵N in association with other labile nutrient indices (HWEOC, HWETN, PMN) have proven useful indicators of litter recycling and potential soil microbial processes; N transformations; and N losses and nutrient cycling pathways as a result of the effects of weed control treatments after 7 years of plantation development.

3.8 References


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Statement of contribution to co-authored published paper

This paper includes a co-authored published paper. The bibliographic details of the published paper including all authors are:


My contribution to the published paper involved:

Acting as the principle and corresponding author, assisting with the establishment of the trial design, collection of the soil, weed biomass and foliage samples, preparation of samples for soils and foliar nutrition (total N, P and K concentrations), C and N total stable isotope composition and inorganic C and N sample preparation, preparation and measurement of weed biomass, soils, foliage and growth data for statistical analysis, the comprehensive statistical analysis and preparation of data into tables, and providing written drafts outlining the direction, scope and structure of the analysed data.

(Signed)

Name of student:

(Countersigned)

Corresponding author of published paper: Name of corresponding author

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Supervisor: (Name of Supervisor)
Chapter 4 The influence of weed control on foliar $\delta^{15}N$, $\delta^{13}C$ and tree growth in an 8 year-old exotic pine plantation of subtropical Australia

4.1 Abstract

The aim of weed control and fertilisation in forest plantations was to increase tree growth by reducing competition for available nutrients and water. However, treatments that influence weed biomass can also have significant impacts on soil carbon (C) and nitrogen (N) cycling which can in turn lead to changes in the dynamics of stable C ($\delta^{13}C$) and N ($\delta^{15}N$) isotope compositions in soils and tree foliage.

We examined the key C and N cycling processes influenced by routine and luxury weed control and fertilisation treatments as reflected by soil and foliar $\delta^{13}C$ and $\delta^{15}N$ and long-term tree growth in an 8-year old $F_1$ hybrid pine ($Pinus elliottii \times P. caribaea$) plantation in southeast Queensland, Australia. Weed control treatments varied by treatment frequency and intensity while fertilisation treatments varied by the application of N, phosphorus (P), potassium (K) and micronutrients. Different soil and canopy sampling positions were assessed to determine if sampling position enhanced the relationships among soil N transformations and tree N use, water use efficiency and carbon gain under the early establishment silviculture.

Routine weed control was associated with increased weed biomass returned to the soil, compared with luxury weed control. Soil $\delta^{13}C$ increased at the 0-5 cm soil sampling depth in both the inter-planting (IPR) and planting row (PR) as a result of the routine weed control treatments. In addition, soil $\delta^{13}C$ was significantly higher as a result of fertilisation treatment in the 0-5 cm soil sampling depth in the PR. Soil $\delta^{13}C$
was negatively correlated to soil $\delta^{15}$N at the 0-5 cm soil sampling depth in the IPR. Soil $\delta^{15}$N increased in the 0-5 and 5-10 cm soil sampling depths in the IPR, as a result of more frequent (luxury) weed control. Foliar $\delta^{15}$N and tree water use efficiency (WUE) (as indicated by foliar $\delta^{13}$C) were positively correlated with tree growth at age 8 years. While relationships between $\delta^{13}$C and $\delta^{15}$N in the soil and foliage varied depending on soil sampling depth and position, and with canopy sampling position where there were consistent relationships between soil $\delta^{13}$C (or $\delta^{15}$N) and foliar $\delta^{15}$N.

This study demonstrates how early establishment silviculture has important implications for soil C and N cycling and how soil $\delta^{13}$C and $\delta^{15}$N were consistent with changes in soil C cycling and N transformations as a result of weed control treatments, while foliar $\delta^{15}$N was linked to more rapid N cycling as reflected in the soil $\delta^{15}$N, which increased tree growth and tree WUE (as reflected by foliar $\delta^{13}$C).

4.2 Introduction

The use of plantation silviculture, such as weed control and fertilisation at establishment, has long been practised to increase the productivity of forest plantations. Weed control aims to reduce competition for available water and nutrients while fertilisation aims to increase nutrients to the planted tree (Neary et al. 1990; Woods et al. 1992; Xu et al. 1995 a, b, c; Chen et al. 2002, 2003). Sandy soils low in organic matter, such as the coastal sands under plantation production in the subtropics in southeast Queensland, may be exposed to rapid cycling of C and N due to the decomposition of soil organic matter during site establishment (Blumfield and Xu 2003; Huang et al. 2008a). Silvicultural management practices can lead to losses in soil organic or labile C and N due to increased cycling of C and N, and changes in soil moisture and fertility in general (Huang et al. 2008 b; Blanco and Gonzalez 2010).
Indeed, some of the most efficient silvicultural management procedures have been shown to reduce long-term soil fertility by decreasing the quality of soil organic matter and soil nutrient holding capacity (Mathers et al. 2003; Huang et al. 2008b; Xu et al. 2008).

Increased frequency of weed control can reduce weed biomass residues returned to the soil and lead to decreased labile C and N pools (Huang et al. 2008c; Ilbell et al. 2010). Increased weed competition may also influence tree nutrition (total N, P and K), growth and water use efficiency (WUE), which is important on coastal sandy soils with poor nutrition and water holding capacity (Xu et al. 1995a). Variations in soil $\delta^{13}$C and $\delta^{15}$N may provide insights into C and N cycling and functioning of microbes in the soil as a result of silvicultural management (Hogberg et al. 1995; Xu and Chen 2006). Linking tree growth, foliar nutrition and foliar $\delta^{13}$C and $\delta^{15}$N responses to changes in soil $\delta^{13}$C and $\delta^{15}$N may allow us to better understand the mechanisms influencing the biological and physiological factors underpinning tree growth in the plant-soil interface.

For example, it is generally accepted that the process of microbial immobilization regulates N losses and hence the removal of harvest residues and weed substrates can reduce important sources of C and N for immobilization (Vitousek et al. 1991; Huang et al. 2008c). Positive relationships have been observed between rates of soil N cycling and soil $\delta^{15}$N (Templer et al. 2007). More importantly, N transformations influence $\delta^{15}$N because of discrimination against the heavier $^{15}$N isotope during microbial assimilation, soil N mineralisation and nitrification which can leave the $^{15}$N abundance in the residual NH$_4^+$-N in soils increased (Hogberg 1997; Adams and Grierson 2001). Soil $\delta^{15}$N enrichment may also occur in soils when lighter N products are lost through denitrification and volatilization (Evans and Ehleringer 1993; Pu et al. 2001, 2002) or where leachates may be enriched in $^{15}$N (Amundson et al. 2003). However, while the
impact of N cycling on soil $\delta^{15}$N is important, the below-ground microbial communities present may also influence soil $\delta^{15}$N and $\delta^{13}$C (Hobbie et al. 1999; Staddon 2004; Hobbie et al. 2004). The mechanisms influencing soil $\delta^{15}$N also influence plant biochemical uptake and $\delta^{15}$N and hence it is critical to understand the inputs and losses influencing $\delta^{15}$N in the soil (Billings and Richter 2006).

Soil $\delta^{13}$C is also affected by microbial activity in the soil. Microbial biomass is an important component of nutrient cycling and is enriched in soil $\delta^{13}$C compared to the substrates they decompose (Ehleringer et al. 2002). However, the source of organic matter present can also influence soil $\delta^{13}$C (Balesdent et al. 1987; Cadisch et al. 1997). Residues returned to the soil may be from different photosynthetic plant types (C<sub>3</sub>, C<sub>4</sub> or crasularium acid metabolism (CAM)) and may vary in $\delta^{13}$C. This can lead to changes in soil $\delta^{13}$C and has been used as a tracer to identify major shifts in plant types in undisturbed soils in paleoecological studies (Silva and Anand 2011; Kohn 2010). In addition, soil $\delta^{13}$C has been shown to indicate differences of C fluxes between autotrophic and heterotrophic respiration (Bowling et al. 2008) and therefore it is important to identify the microbial taxa present in soils. However, using one isotope in isolation can reduce the effectiveness of the interpretation particularly in C and N dynamics, where soil $\delta^{15}$N and $\delta^{13}$C together have been identified as useful tools for investigating the factors influencing soil C and N cycling process (Peterson and Fry 1987; Hobbie et al. 1999).

Soil $\delta^{15}$N is reflected in foliar $\delta^{15}$N, depending on the form of N present in soils, the discrimination associated with N transformations in soils and the fractionation associated with N uptake during assimilation. Hence, the active N pool is in a constant state of flux and is more likely to influence $\delta^{15}$N in plants over the short term than total N (Hogberg and Johannissson 1993; Koba et al. 2003). Foliar $\delta^{13}$C has a different role,
and represents an index of WUE, where early stomatal closure (indicative of increased WUE) and the resulting draw-down of internal CO$_2$ during photosynthesis lead to enriched $^{13}$C in tree foliage. The relationship between foliar $\delta^{13}$C and stomatal conductance is regulated by changes in vapour pressure (D) or soil water deficit (Warren et al. 2001). Furthermore, the interpretation of foliar $\delta^{13}$C, tree $\delta^{13}$C has also been shown to vary with altitude, latitude and $\delta^{13}$C of CO$_2$ (Kohn 2010) and at more local scales with tree age and height. Changes in tree $\delta^{13}$C with canopy sampling position may also be related to changes in photosynthesis due to exposure to irradiance (Livingstone et al. 1998), N nutrition (per unit leaf area), depth in canopy, and leaf structure (mass per area) (Duursma and Marshall 2006). Changes in assimilation of N during plant uptake may also lead to variations in foliar $\delta^{15}$N (Robinson 2001) and as a result the best location to sample foliar $\delta^{13}$C and $\delta^{15}$N has not yet been comprehensively studied.

The use of $\delta^{13}$C and $\delta^{15}$N has been used to explain the processes associated with soil C and N cycling in the soil and at the roots, and related to processes occurring in the canopy such as tree nutrition, WUE and tree growth. In this study, we propose that different silvicultural treatments would influence C and N cycling. The direction of changes in soil $\delta^{13}$C and $\delta^{15}$N would be influenced by the quantity and source of plant materials returned to soil organic matter, N transformations in the soil, and the presence of microbial activity in the soil. These changes in the soil inevitably influence nutrient uptake in the trees which result in changes to tree photosynthesis and WUE. Therefore, the use of $\delta^{15}$N and $\delta^{13}$C in the soil and tree foliage may help explain the edaphic and physiological mechanisms influencing C and N cycling and tree growth as a result of early establishment silvicultural treatments. The objective of this study was to quantify the long-term effects of weed control and fertilisation at early establishment on C and N
cycling processes as reflected in foliar $\delta^{13}$C and $\delta^{15}$N, foliar nutrient concentrations and tree growth in an 8-year-old F$_1$ hybrid ($Pinus elliottii$ Engelm var. elliottii × $P. caribaea$ var. hondurensis Barr. et Golf.) in southeast Queensland of subtropical Australia. We hypothesized that (1) establishment silviculture (including weed control and fertilisation treatments) would influence C cycling (as indicated by soil $\delta^{13}$C) and nutrient transformations (particularly N), 8 years after establishment (2) the natural abundance of $^{15}$N (soil $\delta^{15}$N) may be an effective tool for assessing the effects of establishment silviculture on soil N transformations and tree N uptake, and (3) that foliar $\delta^{15}$N (as an indicator of silvicultural effects of soil N transformations and tree N uptake) is related to tree WUE (as indicated by foliar $\delta^{13}$C) and tree growth in an 8-year-old F$_1$ hybrid pine plantation of subtropical Australia.

4.3 Materials and methods

4.3.1 Site description and experimental design

The experimental site is located in Toolara State Forest, southeast Queensland, Australia (26°1.556'S, 152°48.81'E). The region has a humid, subtropical climate with a mean annual rainfall of 1222 mm. The mean monthly rainfall and maximum temperature for Toolara Forest Station are shown in (see Figure 3.1). The majority of rainfall at Toolara State Forest occurs from December to February. The overall soil types in the area are classified as Kando sols and Hydrosols (Isbell 1996). Soil types vary from Grey Podzolics to Yellow Earths but are generally dominated by Grey Podzolics.

The design of the experiment was a randomized complete block design. Sixteen plots comprised of four replicates of each of the four treatments: (1) routine fertilizer plus routine weed control (RF+RWC); (2) routine fertilizer plus luxury weed control
(RF+LWC); (3) luxury fertilizer plus routine weed control (LF+RWC); and (4) luxury fertilizer plus luxury weed control (LF+LWC) were sampled for soils and tree foliage. Twenty-one plots were used for statistical analysis of the growth data which resulted in an unbalanced replication of the growth variables. The experimental plots were approximately 10 rows x 16 trees, at 5 m x 2.4 m spacing with a plant density of 833 trees ha$^{-1}$.

Site establishment involved strip ploughing and cultivation in December 1998. The F$_1$ pine hybrid cuttings were set in October 1998 and planted out with adequate soil moisture in May 1999 as containerized cuttings. Ten high growth performance clones of ($Pinus$ $elliottii$ var. $elliottii$ x $P$. $caribaea$ var. $hondurensis$ ) F$_1$ hybrids were planted in each plot and the foliar samples collected represented a random mix of these clones.

4.3.2 Weed control and fertilizer treatments

Luxury weed control treatments differed from the routine treatment by the frequency of applications and area sprayed. Luxury weed control was applied to the whole plot whilst routine weed control was applied in strips and limited to the planting rows. The application frequency of routine weed control was made in accordance to the Forestry Plantations Queensland weed control policy at the time for coastal exotic plantations, which stipulated that weed cover should not exceed an average of 20% during the first 9 months in the planting row. Weed control was discontinued at approximately 14 months after planting leaving less than 5% weed cover in the planting rows. It is expected that the treatments implemented at early establishment would have prolonged effects on tree growth.

The fertilizer treatments were applied in July 1999 along the planting row. The routine fertilizer treatment was applied as 226 kg ha$^{-1}$ mono-ammonium phosphate while the luxury fertilizer treatment included a blend of potassium (50 kg ha$^{-1}$), copper
(5 kg ha\(^{-1}\)), zinc (5 kg ha\(^{-1}\)) and boron (5 kg ha\(^{-1}\)) applied at approximately 20 cm from the base of each tree. Luxury fertilisation was intended to encourage maximum growth without incurring excessive N fertilisation and the associated stem deformities (Woods et al. 1992).

### 4.3.3 Understorey biomass sampling

The treatments were validated at 8 years of age using weed biomass sampling where five 0.25 m\(^2\) quadrats were used to collect understorey biomass from each of the four treatment replicates. The biomass was collected from the inter-planting row sampling position using the method of Mannetje and Haydock (1963). The samples were stored at 4°C before processing where they were separated into plant types and dried in an oven at 70°C for 24 hours prior to weighing each sample. The weed biomass from the five quadrats in each plot were averaged and converted to tonnes per ha\(^{-1}\).

### 4.3.4 Soil sampling

Soil samples were collected in June 2006 in both the planting row (PR) and in the inter-planting row (IPR) at three depths (0–5, 5–10 and 10–20 cm) using the procedures described by Ibell et al. (2010) and in Chapter 3 section 3.3.4 of this thesis. Briefly, soil was collected from five random locations within each plot in both the PR and IPR and bulked giving one composite soil sample for each soil depth (0–5, 5–10 and 10–20 cm) at each sampling position (PR and IPR) in each plot. Soil samples were refrigerated after sampling and maintained at ~4°C until processing. Soil samples were sub-sampled, sieved and oven dried at 70°C for 48 hours prior to total C and N, δ\(^{13}\)C, δ\(^{15}\)N, total P and extractable K analyses as described by Xu et al. (2008) and Ibell et al. 2010. Once samples were dried they were ground using a puck and mill grinder to ~2 mm.
4.3.5 Foliar sampling

Needle samples were collected in June 2006 at 5 canopy positions within each plot from the current year’s growth. Needle samples included 50 needles from the most recent, fully expanded needles at the tip of each branch, at 5 canopy positions within the tree crown. It was expected that foliar nutrition and $\delta^{13}$C and $\delta^{15}$N variables would be different with the canopy sampling positions which is why various canopy positions were sampled. Sampling positions included: P1 - north facing, upper-outer foliage; P2 - north facing mid-outer foliage; P3 - north facing mid-inner foliage; P4 - south facing mid-outer foliage; and P5 - north facing, lower-outer foliage. Samples were collected from 5 trees in each plot and the samples from each canopy position in each plot were bulked together. Foliar samples were then refrigerated to ~4°C until processing where they were dried at 70°C to a constant dry weight and ground using a puck and mill grinder for foliar N, P, K, $\delta^{13}$C and $\delta^{15}$N determinations as reported previously (Xu et al. 1995a, b and c; Xu et al. 2000).

4.3.6 Measurement of tree growth

Growth measurements were made by the Forestry Plantations Queensland over 8 years. Growth data were analysed from the net area of 21 plots representing the four treatments. Treatments 1 and 4 were each replicated 6 times while Treatment 2 was replicated 5 times and Treatment 3 was replicated 4 times. Measurement of tree growth included diameter at breast height over bark (DBH) (1.3 m above ground level), basal area (BA), height (H) and the periodic annual increment for DBH (DBHPAI), BA (BAPAI) and H (HPAI). Periodic annual increments were analysed for the period between age 5 and 8 years old and were calculated as outlined in Philip (1994).
**4.3.7 Soil and foliar chemical analyses**

Soil chemical analysis for ammonium (NH$_4^+$-N), nitrate (NO$_3^-$-N) and potentially mineralizable N (PMN), inorganic N, soil moisture content (MC) and hot water extractable organic C (HWEOC) and total N (HWETN) procedures and analysis techniques are outlined in chapter 3 section 3.3.4 of this thesis.

Soil and foliar total C and N were analysed on a GVI Isoprime Mass Spectrometer (Manchester, UK) with a Eurovector elemental analyser (Milan, Italy). Standards for soil $\delta^{13}$C and $\delta^{15}$N analyses obtained precisions of 0.3 ‰ and 0.1 ‰ (n = 10) respectively, while foliar $\delta^{13}$C and $\delta^{15}$N analysis both obtained precisions of 0.1 ‰ (n = 12). All analyses were carried out at Griffith University, Nathan, Queensland. Soil and foliar total P and foliar total K were prepared using nitric/ perchloric acid digestions (Olsen and Sommers 1982) and the supernatant was measured by colorimetric determination on a UV-160A Shimadzu, UV Visible Recording, spectrophotometer at 880nm. Foliar total K samples were determined using a flame atomic absorption spectrophotometer (ASS) (Avanti, GBC Sigma). A series of known reference samples were used during total P and K spectrophotometer determinations to check the accuracy of the analysis.

**4.4 Statistical analyses**

While most of the statistical analyses were performed using GenStat version 14.0 (VSN International 2010) multivariate analysis, as referred to in Ibell et al. (2010), was performed using multidimensional scaling (MDS), Anosim (Permutation-based hypothesis testing), SIMPER (to assess weed biomass compositions) and principle components analysis (PCA) in Primer 6. Multivariate analysis was used to summarize the differences between weed biomass compositions and trends in the soil variables. Weed biomass was log transformed and soil variables were range standardised prior to
multivariate analysis. The effects of treatments on foliar variables were analysed using a 3-way ANOVA with weed control, fertilisation and canopy sampling position (P1-P5) as factors, while the soils data were analysed using a 4-way ANOVA with weed control, fertilisation, sampling position (planting row and inter-planting row) and depth (0–5 cm, 5–10 cm and 10–20 cm) as factors. Due to unbalanced replication the growth data were analysed using residual maximum likelihood (REML). Fishers least significant difference (LSD) (95%) was used for treatment mean comparisons and the relationships between soil and foliar analysis were investigated using correlation coefficients. Correlations were used instead of regressions except for the growth data, because the relationships under investigation were not conclusively shown to be cause and effect but more-so inter-related. Where data were pooled it indicates that there was no loss in the interpretation between pooled and individual data.

4.5 Results

4.5.1 Weed biomass and soil C and N dynamics

Routine weed control resulted in significantly greater weed biomass (6.4 – 8.3 t ha\(^{-1}\)) compared with luxury weed control (0.03 – 0.06 t ha\(^{-1}\)). Soil total N, labile C and N pools (HWEOC and HWETN) and soil \(\delta^{13}C\) were also significantly greater as a result of routine weed control treatments in the 0–5 cm sampling depth (Table 4.1). In addition, PMN and NH\(_4^+\)-N also showed trends towards increased concentrations under the routine weed control treatments at the 0 – 5 cm sampling depth in the inter-planting row, although only PMN was significantly different (p<0.05) as a result of weed control treatments (RWC = 10.93 mg kg\(^{-1}\), LWC = 6.53 mg kg\(^{-1}\)) while NH\(_4^+\)-N was not (RWC = 1.71 mg kg\(^{-1}\), LWC = 1.20 mg kg\(^{-1}\)). When soil \(\delta^{13}C\) and soil \(\delta^{15}N\) were pooled for depth (n=48) there were no significant relationships at each soil sampling
position, however in the inter-planting row, there was a trend for increasing soil $\delta^{15}N$ with decreasing soil $\delta^{13}C$ as a result of the luxury weed control treatments (Fig. 4.1). Histograms have been added to Figure 4.1 to show the distribution frequency within each variable, as a result of weed control treatments.

**Figure 4.1:** The relationship between plot means for soil $\delta^{13}C$ (x) and soil $\delta^{15}N$ (y) at pooled soil sampling depths (0-5, 5-10 and 10-20 cm) in the inter-planting row. Symbols are ‘▲’ for routine weed control and ‘○’ for luxury weed control treatment. Histograms represent the frequency of values for the complete dataset while lines on histograms represent the trend for routine weed control (solid line) and luxury weed control (broken line) treatments.

Further analysis of this trend found significant relationships between soil $\delta^{13}C$ and soil $\delta^{15}N$ at 5–10 cm in the PR ($r = -0.50$, $p = 0.05$, $n = 16$) and at the 0–5 cm depth in the IPR ($r = -0.73$, $p = 0.001$, $n = 16$). When weed biomass was correlated to soil variables for pooled sampling positions (planting row and inter-planting row) at the 0–5
cm sampling depth there were positive correlations between weed biomass and soil total N (r = 0.39, p = 0.003, n = 29), PMN (r = 0.48, p = 0.009, n = 29), HWEOC (r = 0.55, p = 0.002, n = 29), HWETN (r = 0.50, p= 0.006, n=29) and soil δ^{13}C (r = 0.47, p = 0.01, n = 29). These relationships were only slightly improved in the IPR at 0-5 cm where weed biomass was significantly correlated to PMN (r = 0.60, p = 0.02, n = 15), HWEOC (r = 0.68, p = 0.005, n = 15),HWETN (r = 0.61, p= 0.01, n=15) and soil δ^{13}C (r = 0.56, p = 0.03, n = 15) indicating that similar trends existed irrespective of the soil depth and sampling position.

When soil sampling positions and depths were pooled (n = 90), soil δ^{15}N was negatively correlated to HWEOC (r = -0.68, p = <0.001) and HWETN (r = -0.65, p = <0.001) while NO_3^-N was also negatively correlated to PMN (r = -0.44, p = <0.001). A principle components (PC) analysis conducted for soil variables at both the inter-planting row and planting row sampling positions at the 0–5 cm sampling depths, identified PC 1, 2, 3 and 4 explained 82.2% variation in the data, with total C, N, and NH_4^+-N contributing 38.9% (PC1) while NO_3^-N, HWEOC and HWETN (PC2) contributed another 20% and PMN (PC3) and C:N ratio (PC4) explained another 23.3 % of the variation in the N dynamics at this site. The PCA analysis suggest that the differences in total C and N and ammonium pools were driving the results between the treatments, with nitrate and the labile fraction, PMN and C:N ratio playing a less but still significant role, while the correlations indicate that the relationships between the soil variables occurred in both the IPR and PR, between 0-10 cm where weed biomass positively influenced C and N total and labile pools and negatively influenced N cycling rates and soil δ^{15}N.

4.5.2 Weed control treatments, foliar nutrients, δ^{15}N and tree WUE

Foliar δ^{15}N was significantly higher in the luxury weed control treatments compared to routine weed control treatments (LWC = -1.05‰, RWC = -1.67‰, p = 0.052). There
were no significant differences as a result of the weed control and fertilisation treatments for foliar N, δ^{13}C or P concentrations (Table 4.2). There was a significant effect of canopy sampling position on foliar δ^{15}N (P1 = -0.59‰; P2 = -1.58‰; P3 = -1.52‰, P4 = -1.58‰; P5 = -1.63‰; p<0.001) where foliar δ^{15}N at P1 was significantly higher than the other sampling positions (Table 4.3). Foliar δ^{13}C and N were also significantly different as a result of sampling position where foliar δ^{13}C at P1 was significantly greater than those of all the other positions. Foliar N concentrations at P1 and P2 were significantly higher than those of P3, P4 and P5 while foliar N concentrations at canopy sampling positions P4 and P5 were not significantly different from each other (Table 4.3).
Table 4.1: Analysis of variance (ANOVA) (means, S. E.) for soil total nitrogen (N), stable carbon (C) isotope composition (δ^{13}C) and nitrogen isotope composition (δ^{15}N), hot water extractable organic carbon (HWEOC) and hot water extractable nitrogen (HWETN) at different soil sampling positions (planting row and inter-planting row) at different sampling depths (0-5 and 5-10 cm) in an 8-year-old F_1 hybrid pine plantation under different weed control and fertilisation regimes in subtropical Australia.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total N (%)</th>
<th>δ^{13}C (%)</th>
<th>δ^{15}N (%)</th>
<th>HWEOC (mg kg⁻¹)</th>
<th>HWETN (mg kg⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-5 cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
<td>IPR</td>
<td>PR</td>
</tr>
<tr>
<td>Weed control</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RWC</td>
<td>0.042 (0.005) a</td>
<td>0.057 (0.008)</td>
<td>-26.40 (0.26) a</td>
<td>-26.63 (0.19) a</td>
<td>1.85 (0.15)</td>
</tr>
<tr>
<td></td>
<td>LWC</td>
<td>0.031 (0.002) b</td>
<td>0.044 (0.007)</td>
<td>-27.14 (0.13) b</td>
<td>-27.26 (0.14) b</td>
</tr>
<tr>
<td>Fertilisation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RF</td>
<td>0.036 (0.003)</td>
<td>0.050 (0.009)</td>
<td>-27.11 (0.15) b</td>
<td>-27.05 (0.13) b</td>
<td>2.13 (0.16)</td>
</tr>
<tr>
<td></td>
<td>LF</td>
<td>0.037 (0.005)</td>
<td>0.050 (0.006)</td>
<td>-26.43 (0.26) a</td>
<td>-26.84 (0.25)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>5-10 cm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weed control</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RWC</td>
<td>0.036 (0.003)</td>
<td>0.043 (0.006)</td>
<td>-26.3 (0.18) a</td>
<td>-26.2 (0.27) a</td>
<td>2.0 (0.22)</td>
</tr>
<tr>
<td></td>
<td>LWC</td>
<td>0.035 (0.005)</td>
<td>0.033 (0.005)</td>
<td>-26.7 (0.11) b</td>
<td>-26.8 (0.15) b</td>
</tr>
<tr>
<td>Fertilisation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RF</td>
<td>0.037 (0.005)</td>
<td>0.040 (0.007)</td>
<td>-26.8 (0.12) b</td>
<td>-26.7 (0.16) b</td>
<td>2.35 (0.32)</td>
</tr>
<tr>
<td></td>
<td>LF</td>
<td>0.034 (0.003)</td>
<td>0.036 (0.003)</td>
<td>-26.3 (0.17) a</td>
<td>-26.4 (0.30)</td>
</tr>
</tbody>
</table>

^a Where values are followed by different lower-case letters for each soil depth this indicates that treatment means are significantly different from each other (p<0.05).

^b Standard errors are indicated in brackets.
There was a significant interaction between fertilisation and canopy sampling position where foliar K concentrations at P1 for both fertilizer treatments (RF P1 = 0.768%; LF P1 = 0.970%; \( p<0.001 \)) were significantly higher than those from the other canopy sampling positions. Foliar K concentrations at P2 in the luxury fertilizer treatment (LF P2 = 0.475%) was also significantly different from those of the other canopy positions in the routine fertilizer treatment (RF P3 = 0.310%; RF P4 = 0.347%; RF P5 = 0.311%) and P5 in the luxury fertilisation treatment (LF P5 = 0.351%). There were no significant differences in foliar P concentrations among the different canopy positions between the fertilisation and weed control treatments (Table 4.3).

4.5.3 Relationships between soil C and N dynamics, foliar \( \delta^{15}N \) and tree growth

There were significant negative correlations between soil \( \delta^{13}C \) and foliar \( \delta^{15}N \) at the 0-5 cm (Fig. 4.2, 1 – 5 and Table 4.4) and 5-10 cm soil sampling depths at each canopy sampling position (Fig. 4.2, 1 - 5 and Table 4.4) in the inter-planting row. This relationship was also present at canopy sampling positions 1, 3 and 4 and the 10-20 cm soil sampling depth (Fig. 4.2, 1, 3 and 4 and Table 4.4) in the inter-planting row. The strongest correlation between soil \( \delta^{13}C \) and foliar \( \delta^{15}N \) was at P3 and P4 for both 0-5 and 5-10 cm depths (Fig. 4.2 0-5 cm soil sampling depth at foliar sampling positions 3, 4, 5-10 cm soil sampling depth at foliar sampling positions 3 and 4 and Table 4.4).
Table 4.2: Analysis of variance (ANOVA) for foliar carbon (C) isotope composition ($\delta^{13}C$), nitrogen (N) isotope composition ($\delta^{15}N$) and nutrient concentrations at different canopy positions in an 8-year-old F_1 hybrid pine plantation under different weed control and fertilisation regimes in subtropical Australia.

<table>
<thead>
<tr>
<th>Factors</th>
<th>DF</th>
<th>$\delta^{13}C$ (%)</th>
<th>$\delta^{15}N$ (%)</th>
<th>Total N (%)</th>
<th>Total K (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F value</td>
<td>P</td>
<td>F value</td>
<td>P</td>
</tr>
<tr>
<td>Fertilisation (F)</td>
<td>1</td>
<td>0.14</td>
<td>0.711</td>
<td>0.07</td>
<td>0.791</td>
</tr>
<tr>
<td>Weed control (WC)</td>
<td>1</td>
<td>0.00</td>
<td>0.989</td>
<td>4.63</td>
<td>0.052</td>
</tr>
<tr>
<td>F x WC</td>
<td>1</td>
<td>0.15</td>
<td>0.701</td>
<td>0.00</td>
<td>0.949</td>
</tr>
<tr>
<td>F x WC x Replication (R) (Error A)</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Position (P)</td>
<td>4</td>
<td>36.22</td>
<td>&lt;0.001</td>
<td>81.83</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>F x P</td>
<td>4</td>
<td>0.18</td>
<td>0.947</td>
<td>0.20</td>
<td>0.937</td>
</tr>
<tr>
<td>WC xP</td>
<td>4</td>
<td>1.15</td>
<td>0.343</td>
<td>1.98</td>
<td>0.113</td>
</tr>
<tr>
<td>F x WC x P</td>
<td>4</td>
<td>0.70</td>
<td>0.595</td>
<td>1.13</td>
<td>0.355</td>
</tr>
<tr>
<td>F x WC x P x R (Error B)</td>
<td>48</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>79</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.3: Main effect of canopy sampling position on foliar carbon (C) isotope composition ($\delta^{13}C$), nitrogen (N) isotope composition ($\delta^{15}N$), total N and phosphorus (P) concentrations for pooled treatments for the five canopy positions (P1: north-facing, upper-outer foliage; P2: north-facing mid-outer foliage; P3: north-facing mid-inner foliage; P4: south-facing mid-outer foliage; P5: north-facing, lower-outer foliage) in an 8-year-old F$_1$ hybrid pine plantation in subtropical Australia.

<table>
<thead>
<tr>
<th>Canopy position</th>
<th>$\delta^{13}C$ (%)</th>
<th>$\delta^{15}N$ (%)</th>
<th>Total N (%)</th>
<th>Total P (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>-29.0 (0.16) a $^{ab}$</td>
<td>-0.59 (0.16) b</td>
<td>1.06 (0.02) a</td>
<td>0.15 (0.01) a</td>
</tr>
<tr>
<td>2</td>
<td>-29.6 (0.14) b</td>
<td>-1.58 (0.15) a</td>
<td>1.04 (0.02) a</td>
<td>0.14 (0.01) a</td>
</tr>
<tr>
<td>3</td>
<td>-30.1 (0.12) c</td>
<td>-1.52 (0.15) a</td>
<td>0.84 (0.03) c</td>
<td>0.15 (0.01) a</td>
</tr>
<tr>
<td>4</td>
<td>-29.9 (0.11) c</td>
<td>-1.58 (0.14) a</td>
<td>0.96 (0.02) b</td>
<td>0.14 (0.01) a</td>
</tr>
<tr>
<td>5</td>
<td>-30.0 (0.09) c</td>
<td>-1.63 (0.15) a</td>
<td>0.93 (0.02) b</td>
<td>0.14 (0.01) a</td>
</tr>
</tbody>
</table>

$^{a}$ Means followed by different letters indicate significant differences between the canopy sampling positions (P<0.05).

$^{b}$ Standard errors are indicated in brackets

Despite there being only one significant positive correlation between soil $\delta^{15}N$ (at the 0-5 cm soil depth) and foliar $\delta^{15}N$ (at P4 canopy sampling position) (Fig. 4.3, 0 - 5 cm soil sampling depth at foliar sampling positions 4), there was a trend for consistently higher foliar $\delta^{15}N$ in the luxury weed control treatments at each sampling position, in the upper soil layers (Fig. 4.3). There were moderate to strong positive relationships between foliar $\delta^{13}C$ and foliar $\delta^{15}N$ at P1 ($r = 0.74$, $p = 0.002$, $n = 16$), P2 ($r = 0.52$, $p = 0.040$, $n = 16$), P3 ($r = 0.58$, $p = 0.018$, $n = 16$) and P5 ($r = 0.57$, $p = 0.022$, $n = 16$) (Fig. 4.3), and between foliar N concentration and foliar $\delta^{13}C$ at P3 ($r = 0.71$, $p = 0.002$, $n = 16$) and P4 ($r = 0.62$, $p = 0.011$, $n = 16$). Histograms have been added to Fig. 4.4 to show the distribution frequency within each variable, as a result of weed control treatments.
Figure 4.2: Each panel shows the relationship between soil $\delta^{13}$C (x) and foliar $\delta^{15}$N (y) at each foliar sampling position (1 - 5) and soil sampling depth 0-5, 5-10 and 10-20 cm depths in the inter-planting row. Symbols are ‘x’ for routine weed control and ‘○’ for luxury weed control treatment.
Figure 4.3: Each panel shows the relationship between soil $\delta^{15}$N (x) and foliar $\delta^{15}$N (y) at each foliar sampling position (1 - 5) and soil sampling depth 0 - 5, 5 -10 and 10- 20 cm depths in the inter-planting row. Symbols are ‘x’ for routine weed control and ‘o’ for luxury weed control treatment.
Figure 4.4: The relationship between foliar $\delta^{15}$N (x) and foliar $\delta^{13}$C (y) at pooled foliar sampling positions. Symbols are ‘▲’ for routine weed control and ‘○’ for luxury weed control treatment. Histograms represent the frequency of values for the complete dataset while lines on histograms represent the trend for routine weed control (solid line) and luxury weed control (broken line) treatments.
Table 4.4: Correlations between foliar carbon isotope composition ($\delta^{13}$C) and nitrogen isotope composition ($\delta^{15}$N) at different sampling canopy positions (P1, P2, P3, P4 and P5) and soil carbon isotope composition ($\delta^{13}$C) and nitrogen isotope composition ($\delta^{15}$N) at soil sampling depths 0–5, 5–10 and 10–20 cm in the inter-planting row, sampled at age 8 years in a F$_1$ hybrid pine plantation under different weed control and fertilisation regimes in subtropical Australia (n=15).

<table>
<thead>
<tr>
<th>Foliar canopy position</th>
<th>Soil sampling position</th>
<th>0 - 5 cm inter-planting row</th>
<th>5 - 10 cm inter-planting row</th>
<th>10 - 20 cm inter-planting row</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Soil variable</td>
<td>$\delta^{13}$C (%)</td>
<td>$\delta^{15}$N (%)</td>
<td>$\delta^{13}$C (%)</td>
</tr>
<tr>
<td></td>
<td>$\delta^{13}$C (%)</td>
<td>-0.10</td>
<td>-0.66**</td>
<td>-0.11</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N (%)</td>
<td>0.24</td>
<td>-0.50*</td>
<td>-0.24</td>
</tr>
<tr>
<td></td>
<td>$\delta^{13}$C (%)</td>
<td>-0.29</td>
<td>-0.81***</td>
<td>-0.29</td>
</tr>
<tr>
<td></td>
<td>$\delta^{15}$N (%)</td>
<td>0.08</td>
<td>-0.81***</td>
<td>0.08</td>
</tr>
</tbody>
</table>

$^a$ Asterisks *, ** and *** indicate significance at p<0.05, 0.01 and 0.001 respectively.
Table 4.5: REML analysis for tree diameter at breast height (DBH), periodic annual increment (PAI) of DBH (DBHPAI), basal area (BA), PAI of BA (BAPAI), height (H) and PAI of H (HPAI) of an 8-year-old F₁ hybrid pine plantation under different weed control and fertilisation regimes in subtropical Australia.

<table>
<thead>
<tr>
<th>Factors</th>
<th>DF</th>
<th>DBH (cm) F value</th>
<th>DBH (cm yr⁻¹) F value</th>
<th>BA (m² ha⁻¹) F value</th>
<th>BAPAI (m² ha⁻¹ yr⁻¹) F value</th>
<th>H (m) F value</th>
<th>HPAI (m yr⁻¹) F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replication (R)</td>
<td>6</td>
<td>23.18</td>
<td>3.72</td>
<td>28.18</td>
<td>7.66</td>
<td>2.93</td>
<td>5.92</td>
</tr>
<tr>
<td>Weed control (WC)</td>
<td>1</td>
<td>229.8</td>
<td>4.97</td>
<td>277.9</td>
<td>89.85</td>
<td>19.09</td>
<td>1.15</td>
</tr>
<tr>
<td>Fertilisation (F)</td>
<td>1</td>
<td>0.06</td>
<td>0.813</td>
<td>0.07</td>
<td>10.41</td>
<td>0.61</td>
<td>2.46</td>
</tr>
<tr>
<td>WC X F</td>
<td>1</td>
<td>0.09</td>
<td>0.767</td>
<td>1.72</td>
<td>0.961</td>
<td>0.17</td>
<td>1.15</td>
</tr>
<tr>
<td>WC X F X R (Error)</td>
<td>12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Regressions for tree growth identified that the slopes of the luxury weed control
treatments were significantly different from the other treatments for each growth
variable (Figures 4.5 a-d). The models best explaining each growth variable were
logistic for diameter at ground level ($R^2 = 0.97$, $p = < 0.001$, $n = 273$) (Fig. 4.5 a), height
($R^2 = 0.99$, $p = < 0.001$, $n = 336$) (Fig. 4.5 b) and basal area ($R^2 = 0.98$, $p = < 0.001$, $n = 147$) (Fig. 4.5 c), and exponential for diameter at breast height ($R^2 = 0.97$, $p = < 0.001$, $n = 147$) (Fig. 4.5 d). Tree growth as measured by DBH, BA and H were significantly
greater as a result of the LWC treatments (Table 4.5) but not as a result of fertilisation
treatments at 8 years old. BAPAI (as measured from age 5 to 8 years) was greater for
LWC compared to RWC (Table 4.6). BAPAI was also greater as a result of luxury
fertilisation when compared to the routine fertilisation treatment for the same period
(Table 4.6). DBH, BA and H were positively correlated to foliar $\delta^{13}C$ at P1 (Table 4.7).
DBH and BA were also positively correlated to foliar $\delta^{13}C$ at P3. DBH, BA and H were
significantly and positively correlated to foliar $\delta^{15}N$ at each of the 5 canopy positions
with the strongest correlation at P1.
Figure 4.5: Regressions of a. diameter at ground level; b. height; c. basal area (m² ha⁻¹), and d. diameter at breast height, to age in years, for the different weed control and fertilisation treatments in an F₁ hybrid plantation between planting and year 8.
Table 4.6: REML analysis (means, S.E.) for tree diameter at breast height (DBH), periodic annual increment (PAI) of DBH (DBHPAI), basal area (BA), PAI of BA (BAPAI), height (H) and PAI of H (HPAI) of an 8-year-old F₁ hybrid pine plantation under different weed control and fertilisation regimes in subtropical Australia.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>DBH (cm)</th>
<th>DBHPAI (cm yr⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>BAPAI (m² ha⁻¹ yr⁻¹)</th>
<th>H (m)</th>
<th>HPAI (m yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weed control</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RWC</td>
<td>17.1 (0.23) b</td>
<td>1.59 (0.04) a</td>
<td>19.8 (0.62) b</td>
<td>3.20 (0.05) b</td>
<td>13.4 (0.19) b</td>
<td>1.56 (0.04) a</td>
</tr>
<tr>
<td>LWC</td>
<td>19.6 (0.17) a</td>
<td>1.50 (0.02) b</td>
<td>25.7 (0.38) a</td>
<td>3.33 (0.03) a</td>
<td>14.4 (0.10) a</td>
<td>1.52 (0.03) a</td>
</tr>
<tr>
<td>Fertilisation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RF</td>
<td>18.3 (0.47) a</td>
<td>1.50 (0.02) b</td>
<td>22.8 (1.18) a</td>
<td>3.06 (0.07) b</td>
<td>14.0 (0.22) a</td>
<td>1.51 (0.03) a</td>
</tr>
<tr>
<td>LF</td>
<td>18.4 (0.46) a</td>
<td>1.59 (0.04) a</td>
<td>22.9 (1.14) a</td>
<td>3.47 (0.08) a</td>
<td>13.8 (0.23) a</td>
<td>1.56 (0.04) a</td>
</tr>
<tr>
<td>Interaction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RF+RWC</td>
<td>17.0 (0.26)</td>
<td>1.53 (0.03)</td>
<td>19.5 (0.68)</td>
<td>2.99 (0.52)</td>
<td>13.4 (0.22)</td>
<td>1.52 (0.04)</td>
</tr>
<tr>
<td>RF+LWC</td>
<td>19.6 (0.26)</td>
<td>1.47 (0.02)</td>
<td>25.8 (0.56)</td>
<td>3.41 (0.02)</td>
<td>14.5 (0.10)</td>
<td>1.51 (0.04)</td>
</tr>
<tr>
<td>LF+RWC</td>
<td>17.1 (0.46)</td>
<td>1.65 (0.08)</td>
<td>20.1 (1.20)</td>
<td>3.12 (0.07)</td>
<td>13.4 (0.36)</td>
<td>1.60 (0.06)</td>
</tr>
<tr>
<td>LF+LWC</td>
<td>19.6 (0.25)</td>
<td>1.53 (0.03)</td>
<td>25.5 (0.53)</td>
<td>3.53 (0.03)</td>
<td>14.3 (0.14)</td>
<td>1.52 (0.05)</td>
</tr>
</tbody>
</table>

*a Means followed by different letters indicate significant differences between the main effects or interactions of treatments (P<0.05).
Table 4.7: Correlations between foliar carbon isotope composition (δ\textsuperscript{13}C) or nitrogen isotope composition (δ\textsuperscript{15}N) at different canopy positions (P1-P5) and tree growth as diameter at breast height (DBH), basal area (BA) and tree height (H) of an 8-year-old F\textsubscript{1} hybrid pine plantation under different weed control and fertilisation regimes in subtropical Australia.

<table>
<thead>
<tr>
<th>Canopy sampling position</th>
<th>Foliage variables</th>
<th>( \delta^{13}C )</th>
<th>( \delta^{15}N )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree growth variables(^a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>DBH (cm)</td>
<td>0.56 *</td>
<td>0.82 ***</td>
</tr>
<tr>
<td></td>
<td>BA (m\textsuperscript{2} ha\textsuperscript{-1})</td>
<td>0.55 *</td>
<td>0.80 ***</td>
</tr>
<tr>
<td></td>
<td>H (m)</td>
<td>0.55 *</td>
<td>0.81 ***</td>
</tr>
<tr>
<td>2</td>
<td>DBH (cm)</td>
<td>0.18 ns</td>
<td>0.60 *</td>
</tr>
<tr>
<td></td>
<td>BA (m\textsuperscript{2} ha\textsuperscript{-1})</td>
<td>0.19 ns</td>
<td>0.58 *</td>
</tr>
<tr>
<td></td>
<td>H (m)</td>
<td>0.39 ns</td>
<td>0.69 **</td>
</tr>
<tr>
<td>3</td>
<td>DBH (cm)</td>
<td>0.53 *</td>
<td>0.67 **</td>
</tr>
<tr>
<td></td>
<td>BA (m\textsuperscript{2} ha\textsuperscript{-1})</td>
<td>0.56 *</td>
<td>0.64 **</td>
</tr>
<tr>
<td></td>
<td>H (m)</td>
<td>0.46 ns</td>
<td>0.69 **</td>
</tr>
<tr>
<td>4</td>
<td>DBH (cm)</td>
<td>0.28 ns</td>
<td>0.77 ***</td>
</tr>
<tr>
<td></td>
<td>BA (m\textsuperscript{2} ha\textsuperscript{-1})</td>
<td>0.29 ns</td>
<td>0.74 ***</td>
</tr>
<tr>
<td></td>
<td>H (m)</td>
<td>0.34 ns</td>
<td>0.72 **</td>
</tr>
<tr>
<td>5</td>
<td>DBH (cm)</td>
<td>0.34 ns</td>
<td>0.77 ***</td>
</tr>
<tr>
<td></td>
<td>BA (m\textsuperscript{2} ha\textsuperscript{-1})</td>
<td>0.34 ns</td>
<td>0.75 ***</td>
</tr>
<tr>
<td></td>
<td>H (m)</td>
<td>0.40 ns</td>
<td>0.68 ***</td>
</tr>
</tbody>
</table>

\(^a\) Asterisks *, ** and *** indicate significance at p<0.05, 0.01 and 0.001 respectively, and ns indicates P > 0.05.
4.6 Discussion

4.6.1 Luxury weed control increased soil $\delta^{15}$N and decreased soil $\delta^{13}$C

Hypothesis 1 suggested that establishment silviculture (including weed control and fertilisation treatments) would influence C cycling (as indicated by soil $\delta^{13}$C) and nutrient transformation (particularly N) at plantation establishment. Routine weed control (RWC) resulted in increased residues returned to the soil from weed biomass compared to the luxury weed control (LWC), resulting in increased total and labile C and N pools (HWEOC and HWETN respectively). Increased labile C and N pools and weed roots in the surface layers provided increased substrates for N mineralisation under this treatment. Reduced weed biomass under LWC led to reduced labile C and N pools and increased nitrification although not significantly different from the RWC. Increased NO$_3$-N under LWC was related significantly to the soil and foliar $\delta^{15}$N. Soil $\delta^{15}$N was negatively correlated to labile C and N pools, and suggests that lower weed residues were associated with reduced C and N cycling to the labile pools.

Soil $\delta^{15}$N changes as a result of discrimination against $^{15}$N during microbial assimilation of organic N and fractionation during microbial assimilation (Hogberg 1997). In addition, where nitrification is the pathway taken during N transformation, discrimination against $^{15}$N can be large, resulting in residual N pools that are $^{15}$N enriched (Evans and Ehleringer 1993; Robinson 2001). Soil $\delta^{15}$N at this site, increased with depth (in the mineral soil layers), which is most likely associated with the accretion of enriched microbial cells and to the loss of $^{15}$N enriched dissolved organic N (DON) (Amundson et al. 2003). However, $\delta^{15}$N in the top 0 – 5 cm soil layer was depleted relative to the lower soils layers, which is typical due to the contribution of $\delta^{15}$N depleted leaf litters. Nitrogen transformations such as volatilisation and denitrification
result in greater fractionation against $^{15}\text{N}$ and may contribute to soil $\delta^{15}\text{N}$ enrichment, however the $^{15}\text{N}$ enrichment of soils from discrimination during N transformations is considered to be small in comparison to the potential for microbial enrichment of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Boddey et al. 2000; Horwarth et al. 2001). While soil $\delta^{15}\text{N}$ at this site was more enriched at 10–20 cm, which is consistent with the other research findings (Nadelhoffer et al. 1996; Kitayama and Iwamoto 2001), the magnitude of this enrichment varied, depending on the weed control treatment.

The presence of organic residues and soil disturbance are considered to be the primary causes of variations in N cycling (Aranibar et al. 2008). Organic residues within a soil can significantly impact on the fungal composition present in the soil (Hobbie et al. 1999; Henn and Chapela 2001). Both soil organic residues and microbial activity can have direct influences on the cycling of nutrients through the plant-soil interface (Silva et al. 2011). At this site, RWC treatments resulted in soils that were $\delta^{13}\text{C}$ enriched and $\delta^{15}\text{N}$ depleted. Soil $\delta^{13}\text{C}$ enrichment results from the discrimination against $\delta^{13}\text{C}$ during microbial decomposition and respiration or by the increased contribution of isotope enriched organic compounds including microbial cells (Ehleringer et al. 2002). Given that soil $\delta^{13}\text{C}$ varied as a result of different weed control treatments and that soil labile C and N pools (HWEOC and HWETN) increased at the 0–5 cm depth at both soil sampling positions (PR and IPR) in RWC compared to the LWC, it is possible that $\delta^{13}\text{C}$ variation was related to the increased weed residues and the associated microbial activity, under the RWC treatment. Labile C and N pools represent recently mineralized organic matter, fine roots and microbial products and are indicative of increased microbial activity in the soil (Sparling et al. 1998, Horwarth et al. 2001) and while increased microbial decomposition can increase nutrient cycling, increased organic residues can also increase C: N ratios and effectively reduce C and N turnover rates (Horwarth et al. 2001; Silva and Anand 2011).
This can influence turnover rates of C and N dynamics under these treatments. Increased microbial activity (as indicated by increased labile C and N pools) in the RWC treatments led to a greater potential for N mineralisation and immobilisation (as indicated by soil $\delta^{15}$N). Various authors have reported increased biomass and residues returned to the soil, in the upper soil horizons, can lead to increased microbial growth (Hogberg and Read 2006) and influence soil $\delta^{13}$C (Cheng et al. 2008; Jobbagy and Jackson 2000) and $\delta^{15}$N (Cheng et al. 2010). However, this does not explain why $\delta^{13}$C increased as a result of fertilisation in the planting row at the 0 - 5 cm depth, although there is another theory on soil $\delta^{13}$C enrichment in the upper soil layers that warrants discussion.

$^{13}$C enrichment can also occur due to the contribution of organic matter from either C$_3$ or C$_4$ vegetation (Balesdent et al. 1987; Kohn 2010; Silva and Anand 2011), and results in isotopic changes in the soil substrate. Ibell et al. (2010) using multidimensional scaling and Anosim global R testing (similarity testing) of weed compositions at this site, showed that the weed biomass under the luxury fertilisation and routine weed control treatments was greater in quantity in the LF+RWC and RF+RWC treatments compared to the RF+LWC and LF+LWC treatments. Weed composition also varied significantly ($p<0.05$) between the LF+RWC and both the RF+LWC and LF+LWC where the soil $\delta^{13}$C under the luxury fertilisation treatments may have represented a mix of C$_3$ and C$_4$ plant residues, leading to an intermediate soil $\delta^{13}$C representative of both plant types (Cadisch et al. 1997) in the upper soil layers. Butnor et al. (2003) found that fertilisation increased allocation of C to the above ground biomass in Pinus taeda which reduced belowground root respiration (and hence soil $\delta^{13}$C). This could also explain enriched $\delta^{13}$C in the soils under the fertilisation treatments because the effect was only seen in the planting rows, in the luxury fertilisation treatments despite similar weed biomass in the inter-planting rows.

These results support Hypothesis 1, which expect that establishment silviculture
including weed control and fertilisation treatments) would influence C cycling (as indicated by soil δ\(^{13}\)C) and nutrient transformations (particularly N) at plantation establishment, although further research would be required to confirm the relationships associating soil δ\(^{15}\)N and δ\(^{13}\)C to the variability in the soil organic matter, soil fungal communities and below-ground respiration rates.

4.6.2 Foliar δ\(^{15}\)N reflected soil δ\(^{15}\)N at various canopy sampling positions

Foliar δ\(^{15}\)N was significantly different as a result of canopy sampling position. The δ\(^{15}\)N in plants can vary with N source (Robinson 2001; Amundson et al. 2003), fractionation against \(^{15}\)N during N transfer (Evans 2001), variation in fractionation factors during assimilation of different N pools (NH\(_4^+\) or NO\(_3^-\)), or with N sourced from mycorrhizae (Emmerton et al. 2001; Hobbie and Colpaert 2003). Fractionation of \(^{15}\)N during assimilation changes with different inorganic N sources, because the enzymes required for N assimilation (glutamine synthetase or nitrate reductase) change with the inorganic N source. Nitrate reductase discriminates heavily against \(^{15}\)N during NO\(_3^-\) assimilation and causes the remaining and unassimilated NO\(_3^-\) within the plant to become enriched compared to the assimilated organic N (Evans 2001).

The accumulation of \(^{15}\)N in the soil N pools can also lead to increased intra-plant δ\(^{15}\)N variation over time as can the reallocation of N within the plant (Gebauer and Schulze 1991; Handley and Raven 1992). Foliage can also reflect the \(^{15}\)N of ectomycorrhizal fungi, because negative correlations have been observed between available N and the colonisation of mycorrhizal fungi (Hobbie et al. 1999; Evans 2001). When N is not limiting plants acquire N from the soil pools and δ\(^{15}\)N of foliage reflects the δ\(^{15}\)N of the soil N pools. However when N is limiting (or turnover rates are slow), fractionation during N transfer to the plant by mycorrhizal fungi results in lower δ\(^{15}\)N in the foliage relative to the fungi (Boddey et al. 2000). In addition, N limitation at a site
can be attributed to increased microbial immobilization of inorganic N which decreases the proportion of fungal-assimilated N transferred to the plant while further increasing microbial fractionation and reducing plant δ^{15}N (Hobbie and Colpaert 2003).

At an ecosystem level, foliage with higher δ^{15}N can be representative of ecosystems with high N losses (Lajtha and Michener 1994; Amundson et al. 2003) and higher relative rates of N cycling (Emmett et al. 1998; Templer et al. 2007), while decreased foliar δ^{15}N suggests a greater reliance on microbial N sources which are typically δ^{15}N depleted (Hobbie and Hobbie 2006, Cheng et al. 2010). Luxury weed control treatments therefore not only decreased the amount of organic residues (as indicated by lower δ^{13}C), contributing to C cycling but also reduced microbial activity (as indicated by lower labile C and N pools), nutrient immobilisation in weed biomass and labile N available in the long-term (as indicated by increased soil N transformations, soil δ^{15}N and foliar δ^{15}N). These results support Hypothesis 2, which expect the natural abundance of ^{15}N (δ^{15}N) may be an effective tool for quantifying the effects of establishment silviculture on soil N transformations and tree N uptake. However, Hypothesis 2 also expected that tree growth would reflect δ^{15}N and this will be explored in the next section.

4.6.3 Relationships among foliar N, δ^{15}N, WUE and tree growth

We explored the possibility (Hypothesis 3) that foliar δ^{15}N (as an indicator of silvicultural effects of N transformations in the soil and tree N uptake) was related to tree WUE (as indicated by foliar δ^{13}C) and tree growth. Foliar δ^{15}N was strongly and positively correlated to DBH, BA and H at age 8 years, for each canopy position for all treatments combined, indicating direct relationships among soil N transformations, foliar δ^{15}N and tree growth. The absence of weed competition in the luxury weed control treatment at establishment increased tree growth compared to routine weed control at 8 years old by 14% for DBH, 29% for BA and 8% for H. Weed biomass residues in the routine weed
control treatment may have facilitated the development of greater pools of organic and labile C and N, but the benefits to overall productivity under these treatments were compromised by the immobilization of available N and water into the weed biomass. This resulted in the reduced partitioning of water and nutrient resources into plantation growth at early establishment. Both foliar N and foliar $\delta^{15}\text{N}$ were positively correlated to foliar $\delta^{13}\text{C}$ at various canopy sampling positions.

Water and N are required for plant growth and various studies have identified water or mineral nutrition as the two greatest limitations to plantation productivity (Woods et al. 1992; Sword et al. 1998; Bergh et al. 1999; Xu et al. 2002). Tree water and N use can influence tree growth through their effects on C assimilation (Wright et al. 2003). Carbon assimilation may also be limited by the availability of water, nutrients or radiation (Sands and Mulligan 1990; Sword et al. 1998; Tang et al. 2004). Yet the terms of water use efficiency (WUE) (photosynthesis per unit of water used) and photosynthetic N use efficiency (PNUE) (photosynthesis per unit of nitrogen used) can help explain how these resources vary simultaneously. During photosynthesis a change in the efficiency of one variable may change the direction of another. Wright et al. (2003) outline how variations in either WUE or PNUE can be used to optimize C gain in any given situation. For example, plants in low rainfall areas had higher proportional increases in N allocation to the foliage (lower PNUE) for any level of photosynthesis compared to species from high rainfall areas, but had lower stomatal conductance for a given photosynthetic rate which led to increased transpirational water use (increased WUE). The results presented here indicate how increased soil N transformations, as a result of luxury weed control increased N cycling (as shown by increased soil and foliar $\delta^{15}\text{N}$). This resulted in a greater allocation of N to foliage and greater accumulated growth. The positive correlation of foliar $\delta^{15}\text{N}$ with foliar $\delta^{13}\text{C}$ at each canopy sampling positions and that of foliar N with
foliar $\delta^{13}C$ support the theory that increased N cycling led to increased WUE (through either increased photosynthesis or decreased stomatal conductance), where moisture stress may lead to stomatal closure, decreasing CO$_2$ supply and resulting in increased $\delta^{13}C$ in foliage (Farquhar et al. 1989).

Other studies have found foliar $\delta^{13}C$ positively correlated to foliar N concentrations in the upper crowns of forest plantations (Prasolova et al. 2001; Prasolova et al. 2003; Prasolova et al. 2005) and that relationships between foliar $\delta^{13}C$ and foliar N vary with canopy sampling position (Waring and Silvester 1994, Livingstone et al. 1998). Prasolova et al. (2005) found that the relationship between foliar N and foliar $\delta^{13}C$ in the F$_1$ pine hybrid changed with genetic material, season, environmental conditions and canopy sampling positions. They also found that the relationship between foliar N and $\delta^{13}C$, occurred in the upper outer canopy at a wet site while at the dry site the relationship occurred at each canopy sampling position. Increased availability of N and photosynthesis as shown by greater accumulated growth also increased WUE. This is shown by the positive correlation of foliar $\delta^{13}C$ with DBH and BA at various canopy positions. Choi et al. (2005) concluded that in 15 year-old Loblolly pine, larger trees had increased water demand which led to increased stomatal control of water loss and increased WUE. Tutua et al. (2008) found that negative correlations occurred between periodical increments in DBH and foliar $\delta^{13}C$ and $\delta^{18}O$ in a F$_1$ hybrid pine plantation and suggested that soil water availability (as indicated by $\delta^{18}O$) was responsible for the negative effects on tree growth increments at age 10 years, in the larger trees.

Although our results do indicate a change in foliar $\delta^{13}C$ with canopy sampling position, there was no significant response of foliar $\delta^{13}C$ to the weed control and fertilisation treatments. The F$_1$ pine hybrid under investigation in this research has been previously shown to exhibit clone variability in photosynthetic capacity, foliar N
concentrations and foliar δ¹³C (WUE) (Prasolova et al. 2003) and with the interaction between genetic and environmental conditions (Xu et al. 2000; Prasolova et al. 2003). The pooling of clones within each plot could explain why foliar δ¹³C showed no response to the treatments applied (McCarroll and Loader 2004). However, despite the absence of treatment effects on foliar N or foliar δ¹³C, the relationships among the foliar N, WUE and δ¹⁵N indicate that relationships may exist between the weed control treatments, N nutrition and tree WUE due to the simultaneous processes occurring among N nutrition, water and C gain that influence growth.

4.7 Conclusion

Weed control treatments affected weed residues returned to the soil and this influenced soil C and N cycling dynamics resulting in changes to soil δ¹³C, HWETN and HWEOC and soil δ¹⁵N. Luxury weed control treatments increased soil N transformations resulting in nitrification and increased leaching loss which led to increased δ¹⁵N in soils and foliage. This suggests that luxury weed control treatments represent a management system with faster N cycling available for plant growth. Soil δ¹³C was negatively correlated to with foliar δ¹⁵N while foliar δ¹⁵N was positively correlated to plant growth and tree WUE. Routine weed control on the other hand, led to increased weed residues, soil δ¹³C, HWETN and HWEOC and immobilisation of N by weeds and potentially microbial biomass, which would have reduced N turnover rates and is indicative of a management system with lower δ¹⁵N in soils and foliage. This study focused on the linkages identified as a result of weed control treatments among soil δ¹³C and δ¹⁵N, foliar δ¹⁵N, tree N nutrition, tree WUE and tree growth, and aimed to explain some of the processes behind these linkages. Soil δ¹⁵N, δ¹³C and foliar δ¹⁵N provide reasonable indices for these processes in both the soils and foliage.
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Statement of contribution to co-authored published paper

This paper includes a co-authored published paper. The bibliographic details of the published paper including all authors are:


My contribution to the published paper involved:

Acting as the principle and corresponding author, assisting with the establishment of the trial design, collection of the soil, weed and tree biomass and foliage samples, preparation of samples for soils and foliar nutrition (total N, P and K concentrations), C and N total stable isotope composition and inorganic C and N sample preparation, measurement of weed biomass, foliage and growth, water potential and photosynthesis data for statistical analysis, the comprehensive statistical analysis and preparation of data into tables, and providing written drafts outlining the direction, scope and structure of the analysed data.

(Signed)

Name of student:

(Coauthor signature)

Corresponding author of published paper: Name of corresponding author

(Signed)

Supervisor: (Name of Supervisor)
Chapter 5 Effects of weed control and fertilisation at early establishment on tree nitrogen and water use in an exotic F₁ hybrid pine of subtropical Australia

5.1 Abstract

We investigated the effects of weed control and fertilisation at early establishment on foliar stable carbon (δ¹³C) and nitrogen (N) isotope (δ¹⁵N) compositions, foliar N concentration, tree growth and biomass, relative weed cover and other physiological traits in a 2-year old F₁ hybrid (Pinus elliottii var. elliottii (Engelm) x Pinus caribaea var. hondurensis (Barr. ex Golf.))(PEExPCH) plantation grown on a Yellow Earth in southeast Queensland of subtropical Australia.

Treatments included routine weed control, luxury weed control, intermediate weed control, mechanical weed control, nil weed control, and routine and luxury fertilisation in a randomised complete block design. Initial soil nutrition and soil fertility variables included hot water extractable organic carbon (C) (HWEOC) and total nitrogen (N)(HWETN), total C and N, C:N ratio, labile N pools (nitrate (NO₃⁻) and ammonium (NH₄⁺)), extractable potassium (K⁺)), soil δ¹⁵N and δ¹³C. Relative weed cover; foliar N concentrations, tree growth rate and physiological variables including photosynthesis, stomatal conductance, photosynthetic nitrogen use efficiency, foliar δ¹⁵N, foliar δ¹³C and xylem pressure potential (ΨₓPP) were also measured at early establishment.

Foliar N concentration at 1.25 years was significantly different among the weed control treatments and was negatively correlated to the relative weed cover at 1.1 years. Foliar N concentration was also positively correlated to foliar δ¹⁵N and foliar δ¹³C, tree height, height growth rates and tree biomass. Foliar δ¹⁵N was negatively correlated to
the relative weed cover at 0.8 and 1.1 years. Increasing foliar N concentration, C_i and g_s were related to photosynthesis, while more negative Ψ_XPP was related to greater WUE_i and decreasing C_i in the mornings.

These results indicate how increasing N resources and weed competition have implications for tree N and water use at establishment in F1 hybrid plantations of southeast Queensland, Australia. These results suggest the desirability of weed control, in the inter-planting row, in the first year to maximise site N and water resources available for seedling growth. It also showed the need to avoid over-fertilisation, which interfered with the balance between available N and water on these soils.

5.2 Introduction

The supply of nutrients and water at early plantation establishment can be a major factor limiting tree growth in forest plantations in Southeast Queensland, Australia (Xu et al. 1995 a, b, c; Huang et al. 2008 a, b). Competition for these resources may result in adjustments to tree physiological processes; yet, information on how silviculture can increase tree growth and the efficiency of water and N use for commercial plantations in the subtropics is largely lacking. Investigation of the relationship between physiological processes and tree growth could also explain how growth is limited by resource availability. For example, limited water availability has been shown to decrease plantation productivity by reducing stem volume, above-ground biomass, below-ground root development (Ludovici and Morris 1996), canopy development, height, basal area and current annual stem increment (Albaugh et al. 2004). Nutrient supply is well known to limit root (Ludovici and Morris, 1996), and crown development, as well as current annual stem increment. When applied in combination, the supply of nutrients (fertilisation) and water (irrigation) interact to increase growth in Pinus taeda L. (Albaugh et al. 2004), projected leaf area and growth in Pinus radiata D. Don
plantations (McMurtrie et al. 1990) and annual stem volume yield in *Picea abies* L. (Bergh et al. 1999).

While numerous studies have identified the benefits of silvicultural management of water and nutrient supply for forest plantation productivity, research on the relative importance of different physiological mechanisms are less common. Also, nutrients, carbon and water influence assimilation and tree growth by altering different aspects of physiological processes. For example, N deficiencies in *Pinus pinaster* (Aiton) decreased water use efficiency (WUE), where the decrease in N was related with a reduction in carbon assimilation by enhanced stomatal conductance (Guehl 1995). Similarly, instantaneous WUE, photosynthetic N use efficiency (PNUE) (the ratio of photosynthesis to leaf N concentration) and water potential readings, in *Ulmus americana* L., were linked together as indicators of water and N use (Reich et al. 1989). In this study, Reich et al. (1989) found that stomatal limitations facilitated by high water stress contributed more to the decline in total net photosynthesis, than did biochemical limitations such as those that occurred at low N and water concentrations. Tang et al. (2004) found that while nutrient amendments stimulated foliage production in mature *Pinus taeda*, the effects were limited at low water availability.

Plant water status, as measured by xylem pressure potentials (Ψ_XPP), provides an indication of availability of water in the xylem. A decline in plant water status (or plant water stress) is important because it controls the supply of compounds required for growth processes, cell turgor, cell division, cell enlargement and stomatal opening (Kramer and Boyer 1995). The determination of pressure volume curves can allow the for a species can allow us to better understand the relationship between relative water content, turgor loss and osmotic potentials of the plant material (Schulte and Henry 1992).
The natural abundances of stable isotopes, another measure of growth process, reflect isotopic fractionation during different stages of C and N assimilation, decomposition and loss (Farquhar et al. 1989; Robinson 2001). For example, Choi et al. (2005), found that foliar δ\(^{13}\)C (time integrated WUE) and δ\(^{15}\)N (N cycling) in plants and soils reflected changes in C and N cycling processes in *Pinus taeda* under different irrigation and fertilisation regimes.

This current study investigated physiological parameters and stable isotope composition of the soil and foliage during early plantation establishment to quantify tree WUE (as reflected by foliar δ\(^{13}\)C) and N use (using foliar N concentration, δ\(^{15}\)N and PNUE). These measurements were used to relate growth and physiological responses to weed control and fertilisation in the 2-year-old F\(_1\) hybrid pine, a widely planted species in plantations of subtropical Australia. We hypothesized that weed control and fertilisation treatments, influenced (1) foliar N concentration and tree growth (in the first 2 years of plantation establishment), by altering the availability of nutrients (particularly N), tree WUE and water status (Ψ\(_{xPP}\)). (2) The natural abundance of \(^{15}\)N (δ\(^{15}\)N) may be an effective tool for quantifying the effects of establishment silviculture on N competition, uptake and tree growth during establishment.

5.3 Materials and methods

5.3.1 Field site and experimental design

The experimental site was located in Beerburrum State Forest in Southeast Queensland (27°2’55S, 153°1’18”E). The geology of the site is comprised of the Marburg formation from the Jurassic era. The site has a predominantly north-west aspect with an altitude between 12-14 m above sea level with >1% to <3% slope classes. The pre-cleared vegetation at this site was Scribbly gum (*Eucalyptus signata* F. Muell); bloodwood
(Corymbia gummifera (Gaertn.) K.D. Hill & L.A.S. Johnson), occasional ironbark (E. drepanophylla F. Muell. (ex Benth); tea-tree; acacia and casuarina mixed forest with a grassy understorey of grass-trees (Xanthorrhoea spp. Sol. (ex Sm.)) and bladey grass (Imperata cylindrica (L.) P. Beauv). The site is currently a second rotation pine plantation. The first rotation was planted in 1977 with Pinus caribaea Morelet and Pinus elliottii Englem. and the site is considered to be of medium site quality. First rotation fertilisation included 60 kg ha$^{-1}$ superphosphate applied aerially. The site was clear felled in 2004-05 and replanted in 2006.

The soil type for this experimental site was described as Yellow Earths (Stace et al. 1968). This soil type occupies the mid-slopes and is characterized by sandy clay loam texture (Table 5.1). The primary weed spectrum on the site prior to site preparation in 2006 included bladey grass (Imperata cylindrica), paspalum (Paspalum dilatatum Poir.), ink weed (Phytolacca octandra L.), sow thistle (Sonchus oleraceus L.), scotch thistle (Cirsium vulgare Savi. Ten) and bracken fern (Pteridium spp. G. Forst). Annual precipitation in the region is approximately 1409 mm, distributed in the summer months (Figure 5.1). Mean annual minimum and maximum temperatures are 14.8°C and 26.4°C respectively and the relative humidity ranges from 67% (at 9 pm) to 56% (at 3 pm) (DPIF 2006).
Figure 5.1 Mean monthly rainfall and mean minimum and maximum temperatures for Beerburrum Forestry Station near the experimental site.

5.3.2 Site preparation and planting

Prior to the site preparation watercourse exclusion zones were mapped. The site was chopper rolled in late 2005 using a drum roller behind a dozer, and aerial sprayed in March 2006, with a combination of Round-up Bio-active® [Nufarm](Glyphosate) (7.5 mL L$^{-1}$) and Glymate®[Generex](2,4-D amine)(2 mL L$^{-1}$). The site was then cultivated using strip ploughing in April - May 2005. Tubestock (2.5 x 2.5 x 7.5 cm containers) of F$\text{1}$ hybrid clone 3640 (PEE x PCH) were planted onto the site in June 2006 at 2.4 x 5 m spacing, which provided a density of 833 trees ha$^{-1}$. Eighteen experimental plots were established on the site shortly after planting and the gross plot area consisted of 96 trees (6 rows x 16 trees).

5.3.3 Weed control and fertilisation treatments

The eighteen plots established comprised 3 replicates of 6 treatments. The fertilisation treatments included: (1) routine fertilisation and routine weed control [RF+RWC] and
(2) luxury fertilisation and routine weed control [LF+RWC]. Routine fertilizer treatments were applied between July and August 2006 in the first year of planting. The routine fertilisation treatment included a basal application of trifos® (special blend) [Incitec] at 50 kg ha\(^{-1}\) P over 833 trees (324 grams per tree). The luxury fertilizer applications initially included 25 kg ha\(^{-1}\) of N and 50 kg ha\(^{-1}\) P applied as mono-ammonium phosphate (GF MAP ®) [Growforce](276 grams per tree); plus 50 kg ha\(^{-1}\) P as trifos (special blend) (324 grams per tree) and 75 kg ha\(^{-1}\) of N as urea [Incitec Pivot] (196 grams per tree). The urea was applied as a split application of 98 grams of fertilizer per tree in a semi-circle, with the first application to one side of the tree in March 2007 and second to the other side of the tree in August 2007.

The weed control treatments included: (1) routine weed control and routine fertilisation (RF+RWC); (2) routine fertilisation and luxury weed control [RF+LWC]; (3) routine fertilisation and mechanical weed control [RF+MWC]; (4) routine fertilisation and intermediate weed control [RF+IWC]; and (5) routine fertilisation and nil weed control [RF+NWC]. All weed control treatments included a post-plant application of Simazine® [Nufarm](simazine) (5.5 mL L\(^{-1}\)) over the trees in the planting rows. Weed control treatments varied with the frequency of application and method of control in the band and inter-planting row. Planting row, band sprays of Roundup® (4 mL L\(^{-1}\)) and Pulse® [Nufarm](polyether modified polysiloxane)(2 mL L\(^{-1}\)) were applied to each treatment in September 2006 (3 months), December 2006 (6 months) and March 2007 (9 months), excluding the nil weed control treatment [RF+NWC] which had nothing but the post-plant Simazine band tending. All treatments (except for the RF+NWC) were later brush cut (using an industrial grade whipper snipper with blade attachment) in the inter-planting row at 9 and 21 months for woody weed control. The RF+LWC treatment varied from the other treatments with an extra band and inter-
planting row herbicide spray at 14 months. The RF+LWC and RF+IWC (intermediate weed control) treatments, both had an extra inter-planting row herbicide spray at 18 months of age. The RF+MWC was brush cut in the inter-planting row at 14 months without any further herbicide application.

5.3.4 Sampling and chemical analyses

5.3.4.1 Soil characterisation and chemical analyses

To characterise soil chemical and physical properties, soil samples were collected from five random locations for each of the three plots representing the routine weed control and routine fertilisation treatments (RF+RWC) on June 19th-21st 2006 which was after planting but prior to fertilisation. The samples were collected from three depths (0–5, 5–10 and 10–20 cm) in both the planting row (PR) and in the inter-planting row (IPR). Position was separated to represent both the cultivated planting row and non-cultivated inter-planting row. The five samples from each plot were bulked together for each depth and each sampling position, and a single composite soil sample was prepared for each soil depth and position for each of the three sampled plots. Soil samples were refrigerated after sampling and maintained at ~4°C until processing. Soil parameters measured included texture, ammonium (NH₄⁺-N), nitrate (NO₃⁻-N), potentially mineralizable N (PMN), gravimetric soil moisture content (MC), hot water extractable organic C (HWEOC), hot water extractable total N (HWETN), total C, total N, stable C isotope composition (δ¹³C), stable N isotope composition (δ¹⁵N), total P and extractable K. The methods used to process each sample are as described previously in Ibell et al. (2010) or as described in Chapter 3 section 3.3.4 of this thesis. Table 5.1 and Table 5.2 outline the results of the soil physical and chemical properties analysis respectively.
**Table 5.1:** Particle size analysis and pH (means, S.E.) in the top 20 cm soil profile of a Yellow Earth soil type from the cultivated planting row of the experimental site in an 18 month-old plantation of the F₁ hybrid between Slash pine and Caribbean pine in southeast Queensland, Australia. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>pH (0.01 M CaCl₂)</th>
<th>Sand (%)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 5</td>
<td>3.8 (0.2)</td>
<td>82.4 (3.3)</td>
<td>6.9 (1.9)</td>
<td>10.7 (1.4)</td>
</tr>
<tr>
<td>5 - 10</td>
<td>4.0 (0.2)</td>
<td>81.8 (2.3)</td>
<td>7.1 (1.5)</td>
<td>11.2 (0.8)</td>
</tr>
<tr>
<td>10 - 20</td>
<td>4.0 (0.2)</td>
<td>80.7 (2.7)</td>
<td>7.7 (1.2)</td>
<td>11.7 (1.7)</td>
</tr>
</tbody>
</table>
Table 5.2: Total carbon and nitrogen, carbon (C) isotope composition ($\delta^{13}$C) and nitrogen (N) isotope composition ($\delta^{15}$N), C: N ratio, hot water extractable total C (HWETC) and N (HWETN), ammonium N ($\text{NH}_4^+$-N), exchangeable K at two sampling positions (planting row (PR) and inter-planting row (IPR), at three planting depths (0-5, 5-10 and 10--20 cm) on a Yellow Earth soil type, under different management practices at early establishment of an exotic pine plantation. Values are means and S.E. (n=3).
Means followed by different letters indicate significant differences between the main effects of soil sampling position or soil sampling depth and the interactions of soil sampling depth and soil sampling position (p<0.05).

<table>
<thead>
<tr>
<th>Sampling position</th>
<th>Sampling depth (cm)</th>
<th>C (g kg(^{-1}))</th>
<th>N (g kg(^{-1}))</th>
<th>(\delta^{13}C) (%)</th>
<th>(\delta^{15}N) (%)</th>
<th>C:N ratio</th>
<th>HWOEC (mg kg(^{-1}))</th>
<th>HWETN (mg kg(^{-1}))</th>
<th>(NH_4^+) (mg kg(^{-1}))</th>
<th>K (ext) (meq 100g(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Position x depth</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PR</td>
<td>0 – 5</td>
<td>1.86 b</td>
<td>0.056 a</td>
<td>-26.7 b</td>
<td>2.57 bc</td>
<td>33.3 b</td>
<td>317 b</td>
<td>17.2 a</td>
<td>5.8 a</td>
<td>0.081 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.17)</td>
<td>(0.006)</td>
<td>(0.17)</td>
<td>(0.30)</td>
<td>(0.98)</td>
<td>(22.5)</td>
<td>(2.49)</td>
<td>(0.57)</td>
<td>(0.007)</td>
</tr>
<tr>
<td></td>
<td>5 – 10</td>
<td>1.52 bcd</td>
<td>0.045 a</td>
<td>-26.9 b</td>
<td>2.26 cd</td>
<td>33.5 b</td>
<td>278 bc</td>
<td>13.0 a</td>
<td>5.9 a</td>
<td>0.066 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.19)</td>
<td>(0.005)</td>
<td>(0.32)</td>
<td>(0.26)</td>
<td>(0.38)</td>
<td>(9.09)</td>
<td>(1.27)</td>
<td>(0.44)</td>
<td>(0.018)</td>
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<tr>
<td></td>
<td>10 – 20</td>
<td>1.28 cd</td>
<td>0.038 a</td>
<td>-26.8 b</td>
<td>3.07 ab</td>
<td>33.3 b</td>
<td>251 bc</td>
<td>11.3 a</td>
<td>4.4 a</td>
<td>0.061 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.25)</td>
<td>(0.006)</td>
<td>(0.22)</td>
<td>(0.43)</td>
<td>(1.87)</td>
<td>(21.8)</td>
<td>(0.98)</td>
<td>(0.78)</td>
<td>(0.015)</td>
</tr>
<tr>
<td>0 – 5</td>
<td>2.86 a</td>
<td>0.076 a</td>
<td>-27.4 c</td>
<td>0.95 e</td>
<td>37.4 a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 – 10</td>
<td></td>
<td>(2.17)</td>
<td>(0.019)</td>
<td>(0.15)</td>
<td>(0.33)</td>
<td>(1.94)</td>
<td>(59.3)</td>
<td>(1.73)</td>
<td>(0.41)</td>
<td>(0.004)</td>
</tr>
<tr>
<td>10 – 20</td>
<td>1.73 bc</td>
<td>0.055 a</td>
<td>-26.7 b</td>
<td>1.76 d</td>
<td>31.4 bc</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.09)</td>
<td>(0.003)</td>
<td>(0.10)</td>
<td>(0.48)</td>
<td>(2.21)</td>
<td>(21.4)</td>
<td>(2.09)</td>
<td>(0.29)</td>
<td>(0.012)</td>
</tr>
<tr>
<td>IPR</td>
<td>5 – 10</td>
<td>1.14 d</td>
<td>0.040 a</td>
<td>-26.2 a</td>
<td>3.55 a</td>
<td>29.0 c</td>
<td>202 c</td>
<td>11.3 a</td>
<td>3.2 a</td>
<td>0.054 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.03)</td>
<td>(0.003)</td>
<td>(0.03)</td>
<td>(0.17)</td>
<td>(1.35)</td>
<td>(23.6)</td>
<td>(1.58)</td>
<td>(0.78)</td>
<td>(0.005)</td>
</tr>
<tr>
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<td>2.36 a</td>
<td>0.066 a</td>
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<td>1.76 b</td>
<td>35.34 a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 – 10</td>
<td></td>
<td>(0.26)</td>
<td>(0.005)</td>
<td>(0.20)</td>
<td>(0.41)</td>
<td>(1.35)</td>
<td>(60.3)</td>
<td>(2.3)</td>
<td>(0.40)</td>
<td>(0.007)</td>
</tr>
<tr>
<td>10 – 20</td>
<td>1.62 b</td>
<td>0.050 b</td>
<td>-26.8 b</td>
<td>2.01 b</td>
<td>32.43 b</td>
<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>(0.11)</td>
<td>(0.004)</td>
<td>(0.15)</td>
<td>(0.27)</td>
<td>(1.10)</td>
<td>(11.8)</td>
<td>(1.3)</td>
<td>(0.40)</td>
<td>(0.011)</td>
</tr>
<tr>
<td>0 – 5</td>
<td>1.21 c</td>
<td>0.039 c</td>
<td>-26.5 a</td>
<td>3.31 a</td>
<td>31.15 b</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 – 10</td>
<td></td>
<td>(1.12)</td>
<td>(0.003)</td>
<td>(0.18)</td>
<td>(0.23)</td>
<td>(1.41)</td>
<td>(18.1)</td>
<td>(0.8)</td>
<td>(0.47)</td>
<td>(0.007)</td>
</tr>
<tr>
<td>10 – 20</td>
<td>1.55 b</td>
<td>0.046 a</td>
<td>-26.8 a</td>
<td>2.64 a</td>
<td>33.34 a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PR</td>
<td></td>
<td>(0.13)</td>
<td>(0.004)</td>
<td>(1.37)</td>
<td>(0.21)</td>
<td>(0.62)</td>
<td>(13.4)</td>
<td>(1.22)</td>
<td>(0.39)</td>
<td>(0.008)</td>
</tr>
<tr>
<td>IPR</td>
<td>1.91 a</td>
<td>0.057 b</td>
<td>-26.8 a</td>
<td>2.08 b</td>
<td>32.61 a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.26)</td>
<td>(0.006)</td>
<td>(0.19)</td>
<td>(0.42)</td>
<td>(1.56)</td>
<td>(55.9)</td>
<td>(2.32)</td>
<td>(0.29)</td>
<td>(0.009)</td>
</tr>
</tbody>
</table>
5.3.4.2 Relative weed cover analysis

The weed plots were digitally photographed over an 18-month period, on the following dates: 1 - April 2007 (0.8 year), 2 - July 2007 (1.1 years) and 3 - January 2008 (1.6 years). Each weed plot was labelled on small wooden stakes at opposite corners of the quadrat and location was recorded using a Garmin global positioning system 76, for future identification and mapping. Relative weed cover for each plot was determined using the digital photographs for each 1 m$^2$ quadrat for each measurement date. 1.5 meter stakes (marked with 10 cm increments) were used in each photograph as reference scales. Digital photographs were analysed using the dot matrix method of Kershaw (1973).

5.3.4.3 Foliar sampling and nutrient analysis

Foliar nutrient concentrations and stable isotope samples were taken from all the plots in August 2007 at 1.25 years. Nutrient samples were also taken in February 2008, at age 1.75 years, at the time of photosynthesis determination. In both cases, the foliage was selected from a northern aspect in the uppermost recently expanded needles. All foliar samples were oven dried at 40 °C and ground in a mechanized puck and ball grinder. Total C, total N, δ$^{13}$C and δ$^{15}$N were determined using the Dumas micro-combustion technique on a GVI Isoprime Mass Spectrometer (Manchester, UK) with a Eurovector 3000 elemental analyser (Milan, Italy), where δ$^{13}$C was calculated as follows.

$$
\delta^{13}C(\%o) = \left( \frac{R_{sample}}{R_{std}} - 1 \right) \times 1000
$$

(1)

where $R_{sample}$ is $\delta^{13}/^{12}$C ratio of a sample and $R_{std}$ the $\delta^{13}/^{12}$C ratio of the international Pee Dee Belemnite (PBD) standard. The standard deviation of the $\delta^{13}$C standard (n = 9)
was 0.14‰. All analyses were carried out at Griffith University, Brisbane, Queensland, Australia.

5.3.4.4 Tree growth

Tree growth measurements included tree height (H) at 0.3 (not presented), 0.92 and 1.7 years, diameter at ground level (DGL) at 0.92 and 1.7 years and diameter at breast height (DBH) at 1.7 years. Periodic annual growth increment (PAI) was determined for H and DGL using the equation outlined below for periods between 0.3 and 0.92, 0.92 and 1.7 years for H and between 0.92 and 1.7 years for DGL using the method of Philip (1994).

\[
PAI = \frac{(Growth \ parameter \ at \ Age2 - growth \ parameter \ at \ Age1)}{(Age2 - Age1)}
\]  \hspace{1cm} (2)

Where growth parameters are DGL and H and the ages were 0.3, 0.92 or 1.7 years respectively.

5.3.4.5 Above-ground biomass

Biomass was estimated using two trees from each of the three replicates. Trees were cut at the soil level with a chainsaw in August 2007 and transported to Beerwah Tree Seed Centre for preparation, measurement and drying. After total wet weight determination, needles on branches and stems were removed and weighed. Trees were then individually wrapped in hessian and dried in a kiln at 40°C until a constant dry weight was attained. Samples were then reweighed and total dry weights of stems, needles and branches were determined. Branch number was then assessed and wood discs removed for basic density analysis in the laboratory.

5.3.4.6 Branch number and basic density

Once dried, stems were taken back to the laboratory for branch number assessment and basic density sample preparation. Branches were counted prior to the basic density
sample preparation, where each woody branch union on the stem was counted. Stem samples were then cut into ~1 cm discs at 0.5 m intervals, up to 2 m using a drop-saw. Discs were then stored in air-tight conditions until processing. At processing each disc was dressed and the bark removed. For basic density only RF+RWC, LF+RWC, RF+LWC, RF+MWC and RF+NWC treatments were prepared. Basic density samples were prepared with resin unextracted. The samples were boiled in water (24 hr), then stored in water under vaccum, weighed and the sample volume determined by water displacement. Sample preparation and measurement were made at the Wood Quality Laboratory, Agri-ScienceQueensland (Department of Agriculture, Forestry and Fisheries). Unextracted basic density was calculated according to the AS/ NZS 1080.3:2000 Timber Density (Standards Australia 2000).

5.3.5 Physiological measurements

5.3.5.1 Photosynthesis

Photosynthesis was measured, over a one week period, in February 2008 (1.75 years), using a Li-Cor 6400 Portable Photosynthesis System (Licor Inc., Lincoln, Nebr.), equipped with a 2 x 3 cuvette and LED red-blue light source. The light-source was set to 1500 μmol m$^{-2}$ s$^{-1}$ photosynthetic active radiation (PAR), CO$_2$ was set at 360 μmol mol$^{-1}$ and flow rates were kept between 400 and 500 kPa. Intrinsic water use efficiency (WUE$_i$) was determined from the ratio of photosynthesis ($A_n$) to stomatal conductance ($g_s$). Temperature inside the cuvette was kept relative to the ambient air temperature. Diurnal estimates of photosynthesis ($A_n$), were made on the same branches at between 10 - 12 pm and 1 - 3 pm, on four trees within one replicate of each treatment.

The four trees used for photosynthesis determination were pre-selected, following the previous growth assessment, and were chosen as being close to the mean height and diameter at ground level for each treatment. Nine fully expanded, recently matured
needles on the north-facing side of the tree were placed across the cuvette to form a continuous mat and kept horizontally and in full sunlight during measurements (Thompson and Wheeler 1992). Measurements were taken after two minutes, allowing time for measurement to stabilize in the cuvette. Following the afternoon \( A_n \) measurements the area of needle present in the cuvette was marked, removed and kept refrigerated prior to transportation to laboratory for leaf specific area determination (Johnson, 1984). Assimilation rates and stomatal conductance were expressed on a per unit basis for leaf specific area in the cuvette using the method of Johnston (1984). This method uses volumetric displacement and the cumulative length of the needles in the cuvette.

5.3.5.2 Xylem pressure potential (\( \Psi_{XPP} \))

In February 2008 xylem pressure potential (\( \Psi_{XPP} \)) measurements (as a measure of plant water status) were made on an excised mature shoot with needles intact, from a northern aspect in the mid-upper canopy. The shoot was of current growth foliage, 2-4 mm diameter, and was from the same tree used for photosynthesis. \( \Psi_{XPP} \) was measured within two minutes of excision, using a Model 600 pressure chamber (PMS Instruments, Albany).

5.4 Statistical analyses

Genstat (14) (VSN International 2008) was used to analyse the data. Two-way ANOVA was used to analyse the soil characterisation data using soil sampling depth and position as factors. ANOVA was used to analyse evenly replicated data including relative weed cover, tree growth and PAI variables at different measurement times while residual maximum likelihood REML was used to analyse foliar N concentrations at 1.25 years and unextracted bulk density at 1.7 years. REML was used due to the incomplete (or unbalanced) replication of treatments within each block. Correlation
coefficients were used to calculate the relationships among foliar nutrient concentrations at age 1.25 years, tree growth variables, relative weed cover (for each measurement time), biomass and growth and physiological measurements. Unextracted basic density was analysed using a two-way ANOVA with position and treatment as factors. Fishers LSD was used for the treatment mean comparisons. Correlation analysis was used to investigate relationships between bulk density and tree growth variables.

Where the effects of weed control and fertilisation treatments have been investigated for causal relationships, regression analysis has been used. In other cases were relationships have been identified but cannot be assumed to be causal, correlation analysis has been used. A series of regression models was used to investigate the influence of weed control and fertilisation on gas exchange parameters, foliar N concentration and tree water status. Gas exchange parameters included stomatal conductance ($g_s$), photosynthesis ($A_n$), transpiration ($E$), intrinsic water use efficiency (WUEi)($A/g_s$) and internal CO$_2$ concentration ($C_i$). Water potential was also used as an indicator of plant water status. Each physiological relationship was investigated for changes with time of day (morning and afternoon). Three models were developed based on subsets of the data and included: (1) all measures (morning and afternoon in both the upper canopy); (2) morning measures at the upper canopy positions and, (3) afternoon measures at the upper canopy positions. The most parsimonious regression model is presented as selected from a parallel, separate and common line. In addition, physiology data representing the upper canopy sampling position was also used to investigate significant relationships between gas exchange parameters, foliar N concentrations, photosynthetic nitrogen use efficiency (PNUE), foliar $\delta^{13}$C and $\delta^{15}$N and water potential. This dataset was modelled using only time of day (morning and afternoon separately as well as combined). Based on the identification of significant
relationships, a multiple regression was performed to see if a more complex model was more appropriate to explain the observed significant relationships. Finally correlations were used to compare growth data and physiology data to identify relationships.

5.5 Results

5.5.1 Soil characterisation

There was a significant interaction between sampling position and depth on soil total C ($p = 0.008$); soil δ$^{13}$C ($p < 0.001$); soil δ$^{15}$N ($p = 0.007$); C:N ratio ($p = 0.002$); HWEOC ($p = 0.001$) and HWETN ($p = 0.05$) (Table 5.2). Sampling position had a significant effect on total N ($p = 0.015$) and NH$_4^+$-N ($p = 0.022$), while soil sampling depth had a significant effect on total N ($p < 0.001$); NH$_4^+$-N ($p = 0.044$); total P ($p = 0.002$), and extractable K ($p = 0.015$) (Table 5.2).

5.5.2 Relative weed cover

Relative weed cover (%) was less as a result of the luxury weed control treatments when compared to all the other treatments at 0.8 (April 2007) and 1.1 years (July 2007) ($p = 0.018$) but only significantly different at 1.1 years (Table 5.3). By 1.6 years (January 2008) there was no significant difference between treatments for relative weed cover.
Table 5.3: Periodic relative weed cover (%) in the inter-row area for different fertilisation and weed control treatments for a F₁ hybrid, subtropical plantation on a Yellow Earth. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Relative weed cover (%)</th>
<th>0.8 year (April 2007)</th>
<th>1.1 years (July 2007)</th>
<th>1.6 years (Jan 2008)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF + RWC</td>
<td>68.7 (8.1) a</td>
<td>58.8 (11.6) a</td>
<td>76.6 (7.7) a</td>
<td></td>
</tr>
<tr>
<td>LF + RWC</td>
<td>65.9 (3.0) a</td>
<td>60.8 (7.5) a</td>
<td>75.6 (3.3) a</td>
<td></td>
</tr>
<tr>
<td>RF + LWC</td>
<td>46.0 (3.2) a</td>
<td>21.2 (4.6) b</td>
<td>54.9 (4.0) a</td>
<td></td>
</tr>
<tr>
<td>RF + MWC</td>
<td>58.5 (2.0) a</td>
<td>54.4 (7.2) a</td>
<td>75.2 (5.9) a</td>
<td></td>
</tr>
<tr>
<td>RF + IWC</td>
<td>56.3 (5.2) a</td>
<td>52.0 (4.0) a</td>
<td>57.9 (3.3) a</td>
<td></td>
</tr>
<tr>
<td>RF + NWC</td>
<td>61.1 (2.8) a</td>
<td>58.8 (5.0) a</td>
<td>69.0 (6.7) a</td>
<td></td>
</tr>
</tbody>
</table>

a Means followed by the same letter are not significantly different from each other at $p >0.05$.

5.5.3 Foliar N concentration and $\delta^{15}N$

Foliar N concentrations were significantly different at 1.25 years as a result of the weed control and fertilisation treatments, however when treatments were analysed together, foliar N concentrations were not significantly different between the luxury fertilisation plus routine weed control (LF+RWC), RF+LWC and routine fertilizer and intermediate weed control (RF+IWC) treatments (Table 5.4). When treatments were separated RF+LWC and RF+MWC were not significantly different from each other but RF+LWC was significantly different from all other weed control treatments. Routine and luxury fertilisation treatments were not significantly different despite an observable increased in foliar N concentration in the LF>RWC treatment.
While foliar $\delta^{15}N$ and $\delta^{13}C$ were not significantly different as a result of the treatments, there was a non-significant increase in $\delta^{15}N$ in the RF+LWC treatment (0.99 ‰) compared to the other treatments which ranged between -0.07 ‰ $\delta^{15}N$ for RF+MWC and -0.86 ‰ $\delta^{15}N$ for the RF+NWC. Foliar $\delta^{15}N$ in the luxury fertilisation treatments was enriched (-0.19 ‰) when compared to the routine fertilizer treatments (-0.42 ‰).

Table 5.4: Foliage N concentration, C isotope composition ($\delta^{13}C$) and N isotope composition ($\delta^{15}N$) for different weed control and fertilisation treatments at age 1.25 years, in a F$_1$ hybrid, subtropical pine plantation on a Yellow Earth. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Foliage $\delta^{13}C$ (%)</th>
<th>N (%)</th>
<th>$\delta^{15}N$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fertilisation</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RF + RWC</td>
<td>-31.5 (0.2) a</td>
<td>1.36 (0.05) a</td>
<td>-0.42 (0.28) a</td>
</tr>
<tr>
<td>LF + RWC</td>
<td>-31.2 (0.3) a</td>
<td>1.88 (0.12) a</td>
<td>-0.19 (0.08) a</td>
</tr>
<tr>
<td><strong>Weed control</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RF + RWC</td>
<td>-31.5 (0.2) a$^a$</td>
<td>1.36 (0.05) bc</td>
<td>-0.42 (0.28) a</td>
</tr>
<tr>
<td>RF + LWC</td>
<td>-31.3 (0.1) a</td>
<td>1.66 (0.04) a</td>
<td>0.99 (0.52) a</td>
</tr>
<tr>
<td>RF + MWC</td>
<td>-31.3 (0.1) a</td>
<td>1.48 (0.06) ab</td>
<td>-0.07 (0.97) a</td>
</tr>
<tr>
<td>RF + IWC</td>
<td>-31.6 (0.1) a</td>
<td>1.26 (0.05) c</td>
<td>-0.27 (0.48) a</td>
</tr>
<tr>
<td>RF + NWC</td>
<td>-31.2 (0.2) a</td>
<td>1.38 (0.14) bc</td>
<td>-0.86 (0.42) a</td>
</tr>
</tbody>
</table>

$^a$ Means followed by the same letter are not significantly different from each other ($p > 0.05$) within the weed control and fertilisation treatments.
5.5.4 Tree growth

Height (H) at age 0.92 year (H 0.92), and periodical annual increment for height at age 0.92 year (H PAI 0.3-0.92) were both significantly different as a result of the treatments, where height growth (H 0.92 and H PAI 0.3-0.92) for LF+RWC was greater than those of the RF+LWC treatment, but where RF+LWC was not always different from the other treatments. Height growth for H 1.7 and H PAI 0.92 - 1.7, were also significantly different as a result of the treatments where LF+RWC and RF+LWC were significantly different from the other treatments. Diameters at ground level at different measurement times (DGL 0.92, DGL 1.7 and DGL PAI 0.92 -1.7) were significantly different as a result of the treatments where LF+RWC, was significantly different from all of the other treatments. Diameter at breast height at 1.7 years (DBH 1.7) was also significantly different as a result of the treatments, where LF+RWC was greater than RF+LWC, but the latter was not significantly different from the routine fertilisation plus mechanical weed control treatment (RF+MWC) (Table 5.5).

5.5.5 Above-ground biomass

LF+RWC resulted in significantly more total above-ground biomass (needles, branches and stem) (p < 0.001), compared to those of RF+LWC and RF+RWC treatments (Table 6.6). LF+RWC and RF+LWC were significantly different from all the other treatments for needle and branch biomass, while LF+RWC resulted in the greatest accumulation of stem biomass, followed by RF+LWC and RF+RWC treatments.

Branch numbers were not significantly different between treatments despite a doubling of branches in the luxury, routine and mechanical weed control treatments when compared to the luxury fertilisation treatments. A comparison of allocation patterns for foliage and branches and stem to total biomass between weed control and fertilisation treatments showed no significant variation between treatments.
Table 5.5: Mean tree height (H), diameter at ground level (DGL), diameter at breast height (DBH) at ages 0.92 and 1.7 years, and periodical growth increments for height (H PAI) at 0.3-0.92, 0.92-1.7 years and DGL PAI 0.92 -1.7 years, under different weed control and fertilisation treatments in a F1 hybrid, subtropical pine plantation on a Yellow Earth. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>H 0.92 (m)</th>
<th>H 1.7 (m)</th>
<th>DGL 0.92 (cm)</th>
<th>DGL 1.7 (cm)</th>
<th>DBH 1.7 (cm)</th>
<th>H PAI 0.3 - 0.92 (m yr⁻¹)</th>
<th>H PAI 0.92 - 1.7 (m yr⁻¹)</th>
<th>DGL PAI 0.92 - 1.7 (cm yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF + RWC</td>
<td>0.65 (0.01) c</td>
<td>1.72 (0.04) cd</td>
<td>2.03 (0.04) c</td>
<td>4.35 (0.14) c</td>
<td>1.86 (0.06) cd</td>
<td>0.47 (0.02) d</td>
<td>1.38 (0.36) cd</td>
<td>3.02 (0.13) c</td>
</tr>
<tr>
<td>LF + RWC</td>
<td>0.90 (0.02) a</td>
<td>2.47 (0.05) a</td>
<td>2.83 (0.06) a</td>
<td>6.44 (0.28) a</td>
<td>2.96 (0.17) a</td>
<td>0.75 (0.01) a</td>
<td>2.01 (0.07) a</td>
<td>4.62 (0.32) a</td>
</tr>
<tr>
<td>RF + LWC</td>
<td>0.78 (0.01) b</td>
<td>2.17 (0.07) b</td>
<td>2.50 (0.07) b</td>
<td>5.55 (0.31) b</td>
<td>2.43 (0.13) b</td>
<td>0.64 (0.03) b</td>
<td>1.77 (0.07) b</td>
<td>3.88 (0.33) b</td>
</tr>
<tr>
<td>RF + MWC</td>
<td>0.73 (0.07) bc</td>
<td>1.90 (0.19) c</td>
<td>2.20 (0.13) c</td>
<td>4.62 (0.37) c</td>
<td>2.05 (0.32) bc</td>
<td>0.57 (0.08) bc</td>
<td>1.48 (0.14) c</td>
<td>3.11 (0.27) c</td>
</tr>
<tr>
<td>RF + IWC</td>
<td>0.66 (0.02) c</td>
<td>1.68 (0.02) cd</td>
<td>2.07 (0.04) c</td>
<td>4.48 (0.11) c</td>
<td>1.86 (0.04) cd</td>
<td>0.49 (0.004) cd</td>
<td>1.32 (0.03) cd</td>
<td>3.12 (0.19) c</td>
</tr>
<tr>
<td>RF + NWC</td>
<td>0.55 (0.04) d</td>
<td>1.48 (0.10) d</td>
<td>1.50 (0.11) d</td>
<td>3.45 (0.26) d</td>
<td>1.47 (0.11) d</td>
<td>0.35 (0.03) e</td>
<td>1.19 (0.08) d</td>
<td>2.51 (0.17) d</td>
</tr>
</tbody>
</table>

a Means followed by the same letter are not significantly different from each other (p > 0.05).
**Table 5.6**: Total above-ground biomass (kg), needle and branches weight, stem weight, branch number, the ratio between foliage and stem and total biomass and unextracted bulk density for different weed control and fertilisation treatments at age 1.75 years in a F$_1$ hybrid, subtropical pine plantation on a Yellow Earth soil type. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total biomass (dry wt)(kg)</th>
<th>Needle and branch (dry wt) (kg)</th>
<th>Stem (dry wt) (kg)</th>
<th>Branch number</th>
<th>Ratio foliage to total biomass (%)</th>
<th>Ratio stem to total biomass (%)</th>
<th>Unextracted bulk density (kg m$^{-3}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF + RWC</td>
<td>0.67 (0.14) c$^a$</td>
<td>0.30 (0.09) b</td>
<td>0.37 (0.06) c</td>
<td>19 (2.1) a</td>
<td>43.5 (2.9) a</td>
<td>56.5 (2.9) a</td>
<td>369.2 (11.06) b</td>
</tr>
<tr>
<td>LF + RWC</td>
<td>1.61 (0.15) a</td>
<td>0.74 (0.13) a</td>
<td>0.87 (0.03) a</td>
<td>11 (0.6) a</td>
<td>44.1 (4.3) a</td>
<td>55.9 (4.3) a</td>
<td>348.2 (5.55) a</td>
</tr>
<tr>
<td>RF + LWC</td>
<td>1.03 (0.11) b</td>
<td>0.57 (0.09) a</td>
<td>0.53 (0.09) b</td>
<td>21 (4.1) a</td>
<td>49.2 (4.3) a</td>
<td>50.8 (4.3) a</td>
<td>363.9 (11.17) ab</td>
</tr>
<tr>
<td>RF + MWC</td>
<td>0.60 (0.11) cd</td>
<td>0.30 (0.04) b</td>
<td>0.30 (0.06) cd</td>
<td>21 (1.3) a</td>
<td>50.0 (2.5) a</td>
<td>50.1 (2.5) a</td>
<td>Not measured</td>
</tr>
<tr>
<td>RF + IWC</td>
<td>0.40 (0.07) cd</td>
<td>0.18 (0.04) b</td>
<td>0.23 (0.03) cd</td>
<td>14 (1.5) a</td>
<td>41.2 (3.7) a</td>
<td>58.8 (3.7) a</td>
<td>Not measured</td>
</tr>
<tr>
<td>RF + NWC</td>
<td>0.30 (0.08) d</td>
<td>0.12 (0.03) b</td>
<td>0.19 (0.05) d</td>
<td>13 (3.0) a</td>
<td>36.1 (2.9) a</td>
<td>63.9 (2.9) a</td>
<td>378.7 (6.39) b</td>
</tr>
</tbody>
</table>

$^a$ Means followed by the same letter are not significantly different from each other ($p > 0.05$).
5.5.6 Relationships among relative weed cover, foliar $\delta^{15}$N and tree growth

When the weed control treatments were analysed separately, foliar N concentrations at 1.25 years were positively correlated to foliar $\delta^{15}$N (Figure 5.2a). Significant correlations were observed between relative weed cover and foliar $\delta^{15}$N at age 0.8 year ($r = -0.65, p = 0.012, n = 14$) and age 1.1 years ($r = -0.71, p = 0.004, n = 14$) respectively, and for foliar N concentration and relative weed cover at 1.1 years ($r = -0.64, p = 0.012, n = 14$) (Figures 5.3a and b). Foliar $\delta^{15}$N was significantly and positively correlated to height measures (H 0.92, H 1.7, H PAI 0.3 - 0.92 and H PAI 0.92 - 1.7), diameter at ground level (DGL 0.92) and diameter at breast height (DBH 1.7) at 1.25 years (Table 5.7), and positively correlated to total biomass, needle and branch biomass and stem biomass.

Relative weed cover at 0.8 year (measurement 1) was negatively correlated to height growth rate (H PAI 0.92 - 1.7) (Table 5.7) while relative weed cover at 1.1 years (measurement 2) was negatively correlated to height and height growth rate (H 1.7, H PAI 0.3 - 0.92, H PAI 0.92 - 1.7), and diameter at ground level at 1.7 years. Relative weed cover at 0.8 year was also negatively correlated to needle and branch weight. Relative weed cover at 1.1 years was negatively correlated to needle and branch weight, total above-ground biomass and stem weight (Table 5.7).

(a)
Figure 5.2: Relationship between (a) foliar N concentration and foliar $\delta^{15}$N; (b) foliar $\delta^{15}$N and relative weed cover measured at (i) 0.8 year (symbols in black) and (ii) 1.1 years (symbols in Grey) and (c) foliar N concentration and foliar $\delta^{13}$C at 1.25 years as a result of different weed control and fertilisation treatments in an F$_1$ hybrid pine plantation grown on a Yellow Earth soil type.
5.5.7 Foliar N concentration, tree WUE (foliar $\delta^{13}$C) and tree growth

When all treatments were analysed together, foliar N concentration was positively correlated to foliar $\delta^{13}$C (Figure 5.2c). When only the weed control treatments were analysed, foliar N concentrations were positively correlated to the total above-ground biomass ($r = 0.60$, $p = 0.02$, $n = 14$) and needle and branch biomass ($r = 0.64$, $p = 0.01$, $n = 14$) and stem biomass ($r = 0.53$, $p = 0.05$, $n = 14$). Foliar N concentrations at age 1.25 years were also significantly and positively correlated to $H_{0.92}$, $H_{1.7}$, $H_{PAI \ 0.3} - 0.92$ and $H_{PAI \ 0.92} - 1.7$ at age 1.25 years (Table 5.7). As expected, there were strong positive and highly significant correlations between tree growth and biomass parameters for both the weed control and fertilisation treatments (Table 5.7). When only the fertilisation treatments were analysed, foliar N concentration at age 1.25 years was significantly and positively correlated to all tree growth measures (Table 5.7)

Table 5.7: Correlation coefficients for growth parameters, relative weed cover (RWC)(0.8 and 1.1 years), foliar nitrogen (N) concentration, foliar N isotope composition ($\delta^{15}$N) (‰) at age 1.25 years and biomass parameters at age 1.7 years, as a result of weed control ($n=14$) and fertilisation ($n=6$) treatments in an F$\text{I}$ hybrid pine plantation grown on a Yellow Earth soil type.
<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>RWC (%) at 0.8 year</th>
<th>RWC (%) at 1.1 years</th>
<th>Foliar N (%)</th>
<th>Foliar δ^{15}N (%)</th>
<th>Total above-ground biomass</th>
<th>Needle and branch biomass</th>
<th>Stem biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>H 0.92</td>
<td>-</td>
<td>-</td>
<td>-0.60*</td>
<td>0.53*</td>
<td>0.84*</td>
<td>0.64*</td>
<td>-</td>
</tr>
<tr>
<td>H 1.7</td>
<td>-0.58*</td>
<td>-</td>
<td>-0.68**</td>
<td>-0.66**</td>
<td>0.91**</td>
<td>0.76**</td>
<td>-</td>
</tr>
<tr>
<td>H PAI 0.3 - 0.92</td>
<td>-0.63*</td>
<td>-</td>
<td>-0.71**</td>
<td>-0.56*</td>
<td>0.85*</td>
<td>0.81***</td>
<td>-</td>
</tr>
<tr>
<td>H PAI 0.92 - 1.7</td>
<td>-0.59*</td>
<td>-</td>
<td>-0.70**</td>
<td>-0.69**</td>
<td>0.94**</td>
<td>0.79***</td>
<td>-</td>
</tr>
<tr>
<td>DGL 0.92</td>
<td>-</td>
<td>-</td>
<td>-0.57*</td>
<td>-</td>
<td>0.91**</td>
<td>0.61**</td>
<td>-</td>
</tr>
<tr>
<td>DGL 1.7</td>
<td>-</td>
<td>-</td>
<td>-0.58*</td>
<td>-</td>
<td>0.90*</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DGL PAI 0.92 - 1.7</td>
<td>-</td>
<td>-</td>
<td>-0.54*</td>
<td>-</td>
<td>0.87*</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>DBH 1.7</td>
<td>-0.51*</td>
<td>-</td>
<td>-0.63*</td>
<td>-</td>
<td>0.94**</td>
<td>0.69**</td>
<td>-</td>
</tr>
<tr>
<td>Foliar N (%)</td>
<td>-</td>
<td>-0.64*</td>
<td>-</td>
<td>-</td>
<td>0.66**</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Foliar δ^{15}N (%)</td>
<td>-0.65*</td>
<td>-0.71**</td>
<td>-</td>
<td>0.66**</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Foliar δ^{13}C (%)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total above-ground biomass</td>
<td>-</td>
<td>-0.66**</td>
<td>0.60*</td>
<td>0.89*</td>
<td>0.63*</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Needle and branch biomass</td>
<td>-</td>
<td>-0.72**</td>
<td>0.64*</td>
<td>0.80*</td>
<td>0.71**</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Stem biomass</td>
<td>-</td>
<td>-0.57*</td>
<td>0.53*</td>
<td>0.92**</td>
<td>0.53*</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Branch number</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*Asterisks *, ** and *** indicate significant at $p < 0.05, 0.01$ and $0.001$ respectively, and - is not significant ($p > 0.05$).
5.5.8 Basic wood density and growth

There were significant main effects for treatment ($p = 0.03$) and sampling position ($p < 0.001$). Basic density (without resin extracted during processing) was the greatest in the RF+NWC (378.7 kg m$^{-3}$) and the RF+RWC treatments (369.2 kg m$^{-3}$), which were significantly different from all the other treatments. Basic density was the least in the LF+RWC treatment (348.2 kg m$^{-3}$) followed by the RF+LWC treatment (361.5 kg m$^{-3}$), which were not significantly different from each other (Table 6). Wood density was always greater at the base of the stem compared to the top of the stem (387.0 kg m$^{-3}$ - sampling position 1 (P1) (base of stem); 376.3 kg m$^{-3}$ (P2), 349.5 kg m$^{-3}$ (P3) and 344.8 kg m$^{-3}$ (P4) (top of stem)). A comparison of growth variables to mean bulk density found significant negative correlations to height at 0.92 ($r = -0.61$, $p=0.04$, $n=11$) and 1.7 years ($r =-0.60$, $p=0.04$, $n=11$) and height growth rate at 0.92 ($r =-0.65$, $p=0.03$, $n=11$) and 1.7 years ($r =-0.61$, $p=0.04$, $n=11$).

5.5.9 Gas exchange

5.5.9.1. Treatment influences on physiological measurements

When stomatal conductance ($g_s$) was regressed on transpiration ($E$) for the treatments the most variation was explained by the morning and afternoon measurements combined ($R^2 = 0.92$, $p < 0.001$, $n = 39$) (Figure 5.3 a). In this relationship the luxury fertilisation (LF+RWC) was significantly different from the routine (RF+RWC) and nil weed control (RF+NWC) treatments, but not from the luxury weed control (RF+LWC) or mechanical weed control treatments (RF+MWC) (Figure 5.3a).

The combined morning and afternoon measurements best explained the variation in the relationships between $g_s$ and photosynthesis ($A_n$), and $E$ and $A_n$. The relationships between $g_s$ and $A_n$ ($R^2 = 0.71$, $p < 0.001$, $n = 39$), and between $E$ and $A_n$ ($R^2 = 0.70$, $p < 0.001$),
0.001, n = 39) indicated that the luxury fertilisation (LF+RWC) and the luxury weed control treatment (RF+LWC) were both significantly different from the nil weed control (RF+NWC), while the mechanical and routine weed control treatments were not significantly different from nil weed control treatment. However for the relationships between $E$ and $A_n$ the RF+RWC was not significantly different from the LF+RWC or the RF+LWC treatments. The most parsimonious for all three above-mentioned models was represented by the treatments having a response with the same slope (parallel regression model).

When WUE$_i$ was regressed against internal CO$_2$ concentrations ($C_i$)($R^2 = 0.98$, $p < 0.001$, $n = 39$), it was the RF+RWC and LF+RWC treatments that had greatest response for $C_i$ for any level of WUE$_i$ (Figure 5.3d). The most parsimonious model was represented by the treatments having an independent slope (independent regression model).

(a)
(b)

\[ R^2 = 0.71, \ p < 0.001, \ n = 39 \]

(c)

\[ R^2 = 0.70, \ p < 0.001, \ n = 39 \]
Figure 5.3: Relationships between transpiration (E (mmol m\(^{-2}\) s\(^{-1}\))) and stomatal conductance (g\(_s\) (μmol m\(^{-2}\) s\(^{-1}\))) (a); stomatal conductance (g\(_s\) (μmol m\(^{-2}\) s\(^{-1}\))) and photosynthesis (A\(_n\) (μmol m\(^{-2}\) s\(^{-1}\))) (b); transpiration (E (mmol m\(^{-2}\) s\(^{-1}\))) and photosynthesis (A\(_n\) (μmol m\(^{-2}\) s\(^{-1}\))) (c), and intrinsic WUE (WUE\(_i\) (μmol m\(^{-2}\) s\(^{-1}\))) and internal CO\(_2\) concentrations transpiration (Ci (μmol μmol m\(^{-2}\) s\(^{-1}\))) for the combined morning and afternoon measurements, at upper canopy sampling positions as a result of different weed control and fertilisation treatments in an F\(_1\) hybrid pine plantation grown on a Yellow Earth soil type.

5.5.9.2 Relationships among foliar N concentration, δ\(^{13}\)C and δ\(^{15}\)N, growth and physiological measurements

When the relationship between a subset of physiological measurements (including foliar δ\(^{13}\)C), N nutrition (foliar N concentration and δ\(^{15}\)N) and water potential data from the upper-canopy sampling position were investigated combining the morning and afternoon measures, there were significant relationships between water potential and C\(_i\) (R\(^2\) = 0.63, p = 0.012, n = 39) or WUE\(_i\) (R\(^2\) = 0.64, p = 0.010, n = 39). The most
parsimonious model was the parallel regression model where the routine and nil weed control treatments had the lowest intercept and the greatest slope.

There were also significant relationships between WUEi and both foliar N concentration ($R^2 = 0.345$, $p = 0.002$, $n = 39$) and foliar $\delta^{13}$C ($R^2 = 0.62$, $p < 0.001$, $n = 39$) and between foliar $\delta^{15}$N and transpiration ($R^2 = 0.31$, $p = 0.003$, $n = 39$) or WUEi ($R^2 = 0.40$, $p < 0.001$, $n = 39$).

When relationships among physiological measurements investigated using a multiple regression, for the combined morning and afternoon data, photosynthesis was explained by stomatal conductance and $C_i$ ($R^2 = 0.94$, $p < 0.001$, $n = 39$).

Correlations comparing growth data and morning physiology measurement identified negative relationships between DGL PAI at 1.7 years and stomatal conductance ($r = -0.54$, $p = 0.03$, $n = 15$) and transpiration ($r = -0.58$, $p = 0.02$, $n = 15$), and between transpiration and both height ($r = -0.51$, $p = 0.05$, $n = 15$) and height PAI at 1.7 years ($r = -0.55$, $p = 0.03$, $n = 15$).

Correlations of growth data to afternoon physiology measurement identified positive relationships between DGL at 0.92 years and $C_i$ ($r = 0.61$, $p = 0.01$, $n = 15$) and negative relationship between DGL 0.92 years and both WUEi ($r = -0.70$, $p = 0.003$, $n = 15$) and xylem potential ($r = -0.52$, $p = 0.04$, $n = 15$) as well as a positive relationship between DBH at 1.7 years and both $C_i$ ($r = -0.59$, $p = 0.01$, $n = 15$) and negative relationships between DBH at 1.7 years WUEi ($r = -0.63$, $p = 0.01$, $n = 15$), and WUEi and both height at 0.92 years ($r = -0.50$, $p = 0.05$, $n = 15$) and height at 1.7 years ($r = -0.50$, $p = 0.05$, $n = 15$).
5.6 Discussion

5.6.1. Establishment silviculture enhances N transformations in the soil

Increased weed control frequency at 1.1 years reduced weed competition (as indicated by decreased relative weed cover) and increased available N resources, which was confirmed by increased tree growth, biomass and foliar N concentrations in these treatments (Hypothesis 1). Competition for N resources during the establishment phase was reflected by the negative correlation observed between relative weed cover and N availability. The relationship among foliar N, foliar $\delta^{15}$N and relative weed cover highlight the indirect relationship amongst weed competition, soil N transformations and tree growth. Although foliar $\delta^{15}$N in the luxury weed control treatments was not significantly different between the treatments, weed control increased foliar N concentration and led to a non-significant increase in foliar $\delta^{15}$N. In addition, foliar N concentrations at 1.25 years were positively correlated to foliar $\delta^{15}$N.

A reduction in weed residues returned to the soil decreases the potential for immobilization by weed biomass and micro-organisms. Decreased immobilization of N can lead to increased losses of N by nitrification, volatilisation, and denitrification (Koba et al. 2003; Pu et al. 2001; Pu et al. 2002). When N transformations result in nitrification in soils, there is strong fractionation against $^{15}$N and mineral N pools can become $^{15}$N enriched (Hogberg 1997; Adams and Grierson 2001). A decrease in weed residues, such as under the luxury weed control, can lead to a decreased capacity of the soils to replenish N pools in the long-term and reduced potential for the immobilization of products occurring from N transformations. This can result in elevated soil NO$_3$-N and enriched soil $\delta^{15}$N (Matsushima and Chang 2007; Ibell et al. 2010). Furthermore, soil $^{15}$N enrichment can lead to increased foliar $\delta^{15}$N as shown in F$_1$ hybrid trees under luxury weed control treatments at another experimental site in Southeast Queensland, Australia (Ibell et al. 2013). We hypothesized (Hypothesis 2) that natural abundance of
$^{15}$N (as indicated by foliar $\delta^{15}$N) may be an effective tool for quantifying the impact of silvicultural treatments on plant N uptake and tree growth, but this was not validated at this site, despite being confirmed at an older 8 year-old plantation of the same species (Ibell et al. 2010, 2013). This could be due to a number of reasons.

Firstly, while foliar N concentrations were positively correlated to tree height and biomass as a result of both weed control and fertilisation, there was no relationship between foliar N concentrations and foliar $\delta^{15}$N in the fertilisation treatments. Robinson (2001) summarizes the precautions required when using $\delta^{15}$N as a tracer, one of which is to only compare plants grown on common N sources. Luxury fertilisation included applied urea which is prepared by the conversion of atmospheric N to ammonium, and hence $\delta^{15}$N in urea fertilizer reflects $\delta^{15}$N of the atmosphere (0‰) (Shearer et al. 1974; Macko and Ostrom 1994). The application of urea in the luxury fertilisation treatments may therefore dilute $\delta^{15}$N in the soils, which would, in part, explain why the relationship between foliar N concentrations and foliar $\delta^{15}$N was not stronger in the fertilisation treatment.

Secondly, when the soil characterisation results were analysed (with samples taken prior to treatment application) there was some indication that cultivation, during site preparation, increased N mineralisation in the planting rows. Site preparation in the planting row led to decreased total C, HWEOC, HWETN pools and an increase in soil $\delta^{15}$N, soil $\delta^{13}$C and NH$_4^+$-N with most soil sampling depths when compared to the inter-planting row. This indicates that cultivation at site preparation increased the decomposition of organic C and N pools in the planting rows and the associated products of N mineralisation, leading to increased soil $\delta^{15}$N. This carry-over effect of soil cultivation at site establishment also helps to explain why, despite elevated foliar $\delta^{15}$N in the luxury weed control treatments, $\delta^{15}$N was not significantly different between weed control treatments at this site. While other studies suggest that foliar $\delta^{15}$N is a
reasonable indicator of soil N transformations resulting from weed control (Ibell et al. 2010; Matsushima et al. 2012), tree growth and foliar N concentrations in some circumstances (Falxa-Raymond et al. 2012, Matsushima et al. 2012), disturbances such as site cultivation, or the use of industrial-N fertilizers, appear to limit its effectiveness.

5.6.2 Weed control and fertilisation influence tree physiology

Hypothesis 1 also predicated that silvicultural treatments could influence WUE and water relations ($\Psi_{XPP}$) in the 2-year-old F$_1$ hybrid pine plantation. While weed control, fertilisation and site preparation all contributed to increased availability of N resources, foliar N concentrations showed a positive correlation with WUE (foliar $\delta^{13}$C) at 1.25 years. This relationship suggests that increasing availability of N resources led to increased tree WUE. Various authors have also reported positive correlations between foliar N concentrations and foliar $\delta^{13}$C (Livingstone et al. 1999; Prasolova et al. 2000; Prasolova et al. 2003; Xu et al. 2000, Cabrera-Bosquet et al. 2007, Matsushima et al. 2012) although this relationship can vary depending on canopy sampling position (Prasolova and Xu 2003; Prasolova et al. 2003; Ibell et al. 2012), and site water availability (Hogberg et al. 1995; Prasolova et al. 2000; Prasolova et al. 2003).

Any increase in N will have a down-stream effect on photosynthesis, WUE and many other physiological parameters because these processes occur simultaneously (Wright et al. 2003). Increased N may increase water use (demand) or water loss (supply), per unit of assimilated N (Warren and Adams 2006). Increased N may lower stomatal conductance due to faster use of water supply, increasing WUE (Farquhar et al. 1998; Livingstone et al. 1999; Cabrera-Bosquet et al. 2007). Mitchell and Hinckley (1993) found that variations in foliar N influenced WUE indirectly through photosynthesis-induced increases in CO$_2$ demand, rather than directly through CO$_2$ supply.
Warren and Adams (2006) and Livingstone et al. (1999) related WUE changes with foliar N concentration using PNUE measurements, where both foliar N concentration and photosynthesis interacted to alter stomatal conductance. PNUE is a major determinant of plant productivity (Garnier et al. 1995) and has been attributed to a number of biochemical and morphological responses (Evans 1989; Lambers and Poorter 1992). Hence, variations in N, PNUE and WUE may influence tree growth differently at one site, when compared to another site depending on the most limiting resource (Wright et al. 2003). The regression analysis indicated that weed control and fertilisation influenced the fundamental relationships between photosynthesis, transpiration, stomatal conductance, C_i and WUE_i. In addition, there were significant relationships between WUE_i and both foliar N concentration and foliar δ^{13}C, and between foliar δ^{15}N and transpiration or WUE_i. These relationships indicate indirect relationships exist between foliar N concentration, photosynthesis, WUE and soil N cycling (as indicated by foliar δ^{15}N), resulting from the integration between the effects of weed competition (N immobilization) and site preparation (N cycling) on these soils. Other factors can also influence WUE (foliar δ^{13}C and C isotope discrimination) through an effect on gas exchange and photosynthesis (Bowling et al. 2002). These include, but are not limited to, vapour pressure deficit (VPDl) and its effect on stomatal regulation of gas exchange (Whitehead et al. 1983) and water stress particularly in conifers (Farquhar et al. 1989; Warren et al. 2001).

Regression analysis also confirmed significant relationships between water potential and C_i or WUE_i where the luxury fertilisation and weed control treatments had the greatest intercept for WUE_i and the smallest intercept for C_i for any level of Ψ_{XPP} (although the luxury weed control treatment was not significantly different from the mechanical weed control treatment). Increased water demand and more negative Ψ_{XPP} in the luxury fertilisation and weed control trees could be explained by the increase in
foliar N concentration, stem, needle and branch biomass and a potential lag between water loss by transpiration and water availability from the soil (Kramer and Boyer 1995). When $\Psi_{XPP}$ decline under water stress, trees adjust water use by two methods: (1) dehydration avoidance (e.g., lowering of stomatal conductance) and (2) dehydration tolerance (osmoregulation) (Blake and Tschaplnski 1992).

The luxury fertilisation treatment had increased N resources, accelerated growth and increased the partitioning of C to the stem diameter and above-ground biomass compared to the other treatments. As a result, increased stem growth led to lower stem-wood basic density at 2 years in the luxury fertilisation treatment when compared to the routine fertilisation treatment. The change in basic density was correlated to increasing tree height and height growth rates. Any alteration in xylem anatomy that results from changes to the wood density can influence water stress and hence, drought tolerance (Chan 2007; Cochard et al. 2004). This is because wood density is inversely related to tree growth rates and stem water storage capacity (Enquist et al. 1999). As a result, high wood densities can prevent a decline (more negative) in xylem pressures and xylem cavitation under water stress (Hacke et al. 2001; Cochard et al. 2004).

While Pinus species are particularly vulnerable to cavitation during water-stress (Martínez-Vilalta et al. 2004; Domec and Gartner 2003), mean $\Psi_{XPP}$ levels in the present study (-0.1 to -0.4 MPa) were far higher (less negative) than those associated with non-stomatal limitations to photosynthesis in other species of pine (-1.4 Mpa)(Green and Mitchell 1992, Blake and Li 2003). Despite the lack of evidence that water stress levels (as measured by $\Psi_{XPP}$) had reached the levels to influence either biochemical or the cavitation threshold, other physiological changes (tree growth and the relationships between foliar N, foliar $\delta^{13}$C and foliar $\delta^{15}$N and physiological relationships) suggest that weed control and fertilisation may play a critical role in tree
WUE, N availability, water status and pine tree growth during the early establishment period.

5.7 Conclusions

Silvicultural practices such as luxury weed control and fertilisation treatments have the potential to increase the availability of N and water resources for pine plantations. On Yellow Earth soils, trees responded similarly to luxury weed control and fertilisation where both treatments increased foliar N concentrations, tree growth and biomass. Foliar N concentrations and foliar δ¹⁵N were negatively correlated to relative weed cover, and were positively correlated to each other in the weed control treatments. However, the addition of urea fertilizer, and the time since cultivation, in the weed control treatments, reduced the effectiveness of foliar δ¹⁵N as an indicator of increased N transformations in the soil suggesting that foliar δ¹⁵N may be of reduced effectiveness as an index in N transformations in plantations less than 2 years of age.

Finally, the results indicate how silviculture can have implications for drought performance where the competition for water and N resources may decrease growth due to influences to tree physiological processes such as photosynthesis. In summary, these results indicate links among relative weed cover, foliar N concentrations, tree WUE, water relations, stem bulk density and tree growth. These results suggest the desirability of weed control, in the inter-planting row, in the first year to maximise site N and water resources available for seedling growth. It also showed the need to avoid over-fertilisation, which interfered with the balance between available N and water on these soils.

5.8 References


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Chapter 6 Effects of weed control and fertilisation on tree physiological processes, foliar δ^{13}C and δ^{15}N and growth at early establishment in an exotic F_{1} hybrid pine plantation grown on a Grey Podzolic soil type, of subtropical Australia

6.1 Abstract

This study investigated how nitrogen (N) nutrition and key physiological processes varied under changed water and nitrogen competition resulting from different weed control and fertilisation treatments in a 2-year old F_{1} hybrid (Pinus elliottii Engelm var. elliottii x P. caribaea var. hondurensis Barr. ex Golf.) plantation on a grey podzolic soil type, in southeast Queensland.

The study integrated a range of measures including growth variables (including diameter at ground level (DGL), diameter at breast height (DBH) and height (H)), foliar variables (including foliar N concentration, foliar δ^{13}C and δ^{15}N) and physiological variables (including photosynthesis (A_{n}), stomatal conductance (g_{s}), transpiration (E), intrinsic water use efficiency (WUE_{i}) (A/g_{s}) and xylem pressure potential ($\Psi_{XPP}$)) to better understand the mechanisms influencing growth under different weed control and fertilisation treatments. Five levels of weed control were applied: standard (routine); luxury; intermediate; mechanical and nil weed control, all with routine fertilisation plus an additional treatment, routine and luxury fertilisation. Relative weed cover was assessed at 0.8, 1.1 and 1.6 years after plantation establishment to monitor the effectiveness of weed control treatments. Soil investigation included soil ammonium (\text{NH}_{4}^{+}-N), nitrate (\text{NO}_{3}^{-}-N), potentially mineralizable N (PMN), gravimetric soil moisture content (MC), hot water extractable organic carbon (HWETC), hot water
extractable total N (HWETN), total C, total N, stable C isotope composition (δ^{13}C),
stable N isotope composition (δ^{15}N), total P and extractable K.

There were significant relationships between foliar N concentrations and relative
weed cover, and between tree growth and foliar N concentration or foliar δ^{15}N, but
initial site preparation practices also increased soil N transformations in the planting
rows reducing the observable effects of weed control on foliar δ^{15}N. A positive
relationship between foliar N concentration and foliar δ^{13}C or photosynthesis indicated
that increased N availability to trees positively influenced non-stomatal limitations to
photosynthesis. However, trees with increased foliar N concentrations and
photosynthesis were negatively related to xylem pressure potential in the afternoons
which enhanced stomatal limitations to photosynthesis and WUE.<

Luxury and intermediate weed control and luxury fertilisation positively
influenced growth at early establishment by reducing the competition for water and N
resources. This influenced fundamental key physiological processes such as the
relationships between foliar N concentration, A, E, g_s and Ψ_XPP. Results also
confirmed that time from cultivation is an important factor influencing the effectiveness
of using foliar δ^{15}N as an indicator of soil N transformations.

6.2 Introduction

Pine plantations in subtropical southeast Queensland, Australia, are typically planted on
sandy coastal sites, characterized by dry winters, wet summers and low nitrogen (N)
and phosphorus (P) availability (Xu et al. 1995 a, b, c; 2000). While water availability
and nutrition are often reported as the key factors limiting tree growth of pine
plantations (Boomsa and Hunter 1990), site conditions may be of overriding importance
at some sites where poor drainage and water-logging can limit tree growth, particularly
in tropical and subtropical regions of Australia (Xu et al. 2000). Thus site preparation
techniques may differ (such as strip plough, spot cultivation or high mounding),
depending on the site and soil characteristics. This paper differs from a previously published paper on a Yellow Earth site which was strip cultivated but had similar treatments applied (Ibell et al. 2013), whereas this site represents a soil type which was high-mounded due to a lower water table.

Silvicultural practices aim to increase the availability of resources by reducing the competition for nutrients (Smethurst and Nambiar 1989; Will et al. 2006; Huang et al. 2008a) and water (Sands and Nambiar 1984; Ewers et al. 1999; Huang et al. 2008b, c). Weed control and fertilisation may also increase the efficiency of water and nutrient use (Robinson et al. 2001; Huang et al. 2008a, b, c), tree survival (Amishev and Fox 2006) and growth (Colbert et al. 1990; Will et al. 2002; Samuelson et al. 2004; Tutua et al. 2008). However, little is known on the effects of silvicultural practices such as weed control and fertilisation on the integrated responses of soil N transformations and tree physiology (water potential, photosynthesis, stomatal conductance, transpiration and tree water use efficiency) in subtropical pine plantations of southeast Queensland.

Water stress can limit growth by reducing turgor, cell enlargement, stomatal activity, other metabolic processes (Kramer and Boyer 1995) as well as nitrogen (N) availability in soils. On the other hand, weed control has been shown to reduce water stress in Pinus radiata D. Don plantations (Sands and Nambiar, 1984) and increase net photosynthesis (A_n), nutrient and water use efficiency in Pinus banksiana (Lamb) (Robinson et al. 2001). Fertilisation in combination with weed control can increase tree volume, height, basal area, leaf area and foliar N concentrations in Pinus taeda L. plantations (Jokela et al. 2004). Despite this, the benefits of silvicultural treatments may not occur where there are other physiological constraints, e.g. water deficit, low light interception or physiological age (Binkley et al. 1995; Mencuccini and Grace 1996). For example, fertilisation that aims to improve plantation productivity (Munger et al. 2003) could also increase the vulnerability of trees to drought, if it lowers their
tolerance to dehydration (DeLucia and Schlesinger 1991). As a result, short-term increases in plantation productivity at early establishment may have some negative impacts on longer-term productivity.

While the complete removal of competing vegetation can improve forest plantation productivity, it can also reduce soil fertility over the long-term (Busse et al. 1996; Ibell et al. 2010). This is because weed control can influence C and N pools, reduce weed biomass for immobilisation and exposes the remaining pools to N mineralization and N losses by volatilization and leaching (Vitousek and Matson, 1985). However more research is needed to understand the interactions between water and N availability in response to weed control and fertilisation and the effects on physiological processes that control tree growth. This research aims to investigate the relationships between weed control and fertilisation and how they influence N, water availability and the key physiological processes that influence tree growth.

Studies that integrate physiological responses, resource use and tree growth may help explain the processes limiting tree growth. Environmental limitations influence tree growth by altering C, N and key growth processes. Since little is known about the integration of these relationships a study was conducted to determine how N and C isotope compositions (δ\(^{15}\)N and δ\(^{13}\)C), foliar N concentrations and water relations respond to silvicultural treatments under specific site conditions during the early establishment.

The objective of this study was to determine how weed control and fertilisation influence soil N transformations and physiological processes in a high-mounded, 2-year-old F1 hybrid pine plantation of subtropical Australia. We hypothesized that (1) soil N transformations (as shown by foliar N concentrations and foliar δ\(^{15}\)N) would be influenced by weed control and fertilisation treatments in the first 2 years of plantation establishment, and that (2) weed control and N fertilisation influence tree growth by
altering water relations ($\Psi_{XPP}$) and tree physiological parameters under the experimental conditions on a Grey Podzolic soil type in a 2-year-old, F$_1$ hybrid pine plantation of subtropical Australia.

6.3 Materials and methods

6.3.1 Site characteristics

The experimental site is located in Beerburrum State Forest in Southeast Queensland (27°2′55″S, 153°1′18″E), Australia. The site has a predominant north-west aspect and is on a Marburg geological formation from the Jurassic era. The altitude is 12-14 m above sea level with >1% to <3% slope classes. The original vegetation was a scribbly gum (*Eucalyptus signata*) (F. Muell), bloodwood (*Corymbia gummifera*) [(Gaertn) K.D. Hill & L.A.S. Johnson], occasional ironbark (*E. drepanphylla*) (F. Muell. ex Benth), *Melaleuca spp.* (tea-tree), *Acacia spp.*, *Casuarina spp.* (casuarina) mixed forest with a grassy understorey of grass trees (*Xanthorrhoea spp.* (Sol. ex Sm.)) and bladey grass (*Imperata cylindrica* ((L.) P. Beauv)). The first rotation at this site was planted in 1977 and was clear felled in 2004-05. Second rotation was planted in 2006 with *Pinus caribaea* and *Pinus elliottii*. Original fertilisation for the first rotation was with 60 kg P ha$^{-1}$ as superphosphate that was applied aerially at this site.

The site chosen in this investigation comprised a soil located on the lower slopes, and was a typical sandy clay loam. The primary weed spectrum on the site prior to the site preparation in 2006 included bladey grass (*Imperata cylindrica*), paspalum (*Paspalum dilatatum* (Poir.)), ink weed (*Phytolacca octandra* (L.)), sow thistle (*Sonchus oleraceus* (L.)), scotch thistle (*Cirsium vulgare* (Savi. Ten)) and bracken fern (*Pteridium spp.* (G. Forst)). Other species associated with this site included *Melaleuca leucadendron*, *Lomatia spp.*, *Tristania laurina* (Brush box), sundews and giant mosses. The annual precipitation in the region is approximately
1409 mm, which is distributed predominantly in the summer months (see Figure 5.1). Mean annual minimum and maximum temperatures were 14.8°C and 26.4°C respectively while the relative humidity ranges from 67% (at 9 pm) to 56% (at 3 pm).

6.3.2 Site preparation and planting

Containerised (12.5 x 5 cm) seedlings of the F₁ hybrid *Pinus elliotti var. elliotti* x *Pinus caribea var hondurensis*, clone 3640, were planted onto the site in June 2006 with 2.4 m between the trees and 5 m between the rows, at an approximate density of 833 trees ha⁻¹. The experimental area was prepared by high mounding in the planting rows. In 2006, shortly after planting, the experimental site was established with plots containing approximately 16 trees x 6 rows. Eighteen plots in total were marked out, which included 3 replicates for each of the 6 treatments described below. Watercourse exclusion zones were mapped out prior to the site preparation.

6.3.3 Weed control and fertilisation treatments

The treatments included a non-factorial mix of weed control and fertilisation treatments. Six treatments were investigated and included: (1) routine fertilisation and routine weed control [RF+RWC]; (2) luxury fertilisation and routine weed control [LF+RWC]; (3) routine fertilisation and luxury weed control [RF+LWC]; (4) routine fertilisation and mechanical weed control [RF+MWC]; (5) routine fertilisation and intermediate weed control [RF+IWC]; and (6) routine fertilisation and nil weed control [RF+NWC]. The fertilisation treatments are defined as routine and luxury fertilisation which are applied with the two routine weed control treatments. Routine fertiliser treatments were applied between July and August 2006 in the first year of planting. The routine fertilisation treatment included a basal application of trifos® (special blend) [Incitec] at 50 kg P ha⁻¹ (324 g tree⁻¹). The luxury fertiliser applications initially included 25 kg ha⁻¹ of N and 50 kg ha⁻¹ P applied as mono-ammonium phosphate (GF MAP ®) [Growforce](276 g
per tree); plus 50 kg ha\(^{-1}\) P as trifos (special blend) (324 grams per tree) and 75 kg ha\(^{-1}\) of N as urea [Incitec ] (196 grams per tree). The urea was applied as a split application of 98 grams of fertilizer per tree in a semi-circle, with the first application to one side of the tree in March 2007 and a second application to the other side of the tree in August 2007.

The weed control treatments were defined as the weed control treatments used with the routine fertilizer treatments (RF+RWC, RF+LWC, RF+MWC, RF+IWC and RF+NWC). All weed control treatments included a post-plant application of Simazine® [Nufarm] (simazine) (5.5 mL L\(^{-1}\)) over the trees in the planting rows. Weed control treatments varied with the frequency of application and method of control in the band and inter-planting rows. For the planting rows, band sprays of Roundup® (4 mL L\(^{-1}\)) and Pulse® [Nufarm] (polyether modified polysiloxane) (2 mL L\(^{-1}\)) were applied to each treatment in September 2006 (3 months), December 2006 (6 months) and March 2007 (9 months), excluding the nil weed control treatment [RF+NWC] which had nothing but the post-plant Simazine band tending. All treatments (except for the RF+NWC) were later brush cut (using an industrial grade trimmer with blade attachment), in the inter-planting row at 9 and 21 months for woody weed control. The RF+LWC treatment varied from the other treatments with an extra band and inter-planting row herbicide spray at 14 months. The RF+LWC and RF+IWC treatments, both had an extra inter-planting row herbicide spray at 18 months. The RF+MWC was brush cut in the inter-planting row at 14 months without any further herbicide application.
6.3.4 Sampling and chemical analyses

6.3.4.1 Relative weed cover analyses

Three 1 x 1 m quadrats were established to assess relative weed cover in the inter-row of each plot. Each weed plot was permanently marked and labelled with small wooden stakes at opposite corners of the quadrat and each position recorded with a Garmin 76 GPS for future identification and mapping. Photographs were taken at three sampling times over an 18-month period at time 1 - April 2007 (0.8 year), time 2 - July 2007 (1.1 years) and time 3 - January 2008 (1.6 years). Each weed plot photograph was taken from a standing position over the top using a digital camera and included two 1.5 meter stakes on two sides of the plot with 10 cm increments marked to delineate the scale of the plot. Digital photographs were later analysed using the dot matrix method (Kershaw 1973) to determine the relative weed cover for each plot, on each sampling measure date.

6.3.4.2 Soil characterisation and chemical analyses

Soil samples were collected in June 2006 in both the planting row (PR) and in the inter-planting row (IPR) to three depths (0-5, 5-10 and 10-20 cm). Five samples for each depth in each plot were bulked together to give one composite soil sample for each soil depth in the planting row and inter-planting row, in the three routine weed control treatment plots. Soil samples were refrigerated after sampling and maintained at ~4°C until processing. Soil variables measured included ammonium (NH$_4^+$-N), nitrate (NO$_3^-$-N), potentially mineralizable N (PMN), gravimetric soil moisture content (MC), hot water extractable organic carbon (HWETC), hot water extractable total N (HWETN), total C, total N, stable C isotope composition ($\delta^{13}$C), stable N isotope composition ($\delta^{15}$N), total P and extractable K. The methods used to process and analyse these samples are described previously by Ibell et al. (2010) and outlined in Chapter 3,
section, 3.3.4 of this thesis. Tables 6.1 and 6.2 outline the means of the soil physical and chemical properties respectively.

**Table 6.1:** Particle size analysis and pH in the top 20 cm soil profile of a Grey Podzolic soil, taken from the cultivated planting row of the experimental site in an 18 month-old plantation of the F₁ hybrid between Slash pine and Caribbean pine in southeast Queensland, Australia. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>pH (0.01 M CaCl₂)</th>
<th>Sand (%)</th>
<th>Silt (%)</th>
<th>Clay (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 5</td>
<td>3.1 (0.2)</td>
<td>84.1 (2.6)</td>
<td>7.4 (2.6)</td>
<td>8.5 (1.0)</td>
</tr>
<tr>
<td>5 - 10</td>
<td>3.4 (0.3)</td>
<td>86.4 (1.9)</td>
<td>5.4 (2.2)</td>
<td>8.1 (1.4)</td>
</tr>
<tr>
<td>10 - 20</td>
<td>3.6 (0.3)</td>
<td>85.0 (1.2)</td>
<td>6.6 (0.8)</td>
<td>8.4 (1.8)</td>
</tr>
</tbody>
</table>
Table 6.2: Total carbon (C) and nitrogen (N), C isotope composition ($\delta^{13}C$) and N isotope composition ($\delta^{15}N$), C: N ratio, hot water extractable total C (HWETC) and N (HWETN), nitrate N (NO$_3^-$-N), ammonium (NH$_4^+$-N), potentially mineralizable N (PMN), exchangeable potassium (K), total P and gravitational moisture content in the 0-20 cm soil profile prior to post-planting weed control and fertilisation treatment application in an F$_1$ hybrid, exotic pine plantation, on a Grey Podzolic soil type. Sampling positions are from the planting row (PR) or the inter-planting row (IPR). Values are means (n=3).

<table>
<thead>
<tr>
<th>Sampling position</th>
<th>Sampling depth (cm)</th>
<th>Total N (%)</th>
<th>Soil $\delta^{15}N$ (‰)</th>
<th>NH$_4^+$-N (mg kg$^{-1}$)</th>
<th>NO$_3^-$-N (mg kg$^{-1}$)</th>
<th>PMN (mg kg$^{-1}$)</th>
<th>HWETN (mg kg$^{-1}$)</th>
<th>Total C (%)</th>
<th>Soil $\delta^{13}C$ (‰)</th>
<th>C:N ratio</th>
<th>HWETC (mg kg$^{-1}$)</th>
<th>K (ext) (cmol kg$^{-1}$)</th>
<th>P (mg kg$^{-1}$)</th>
<th>MC (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth x position</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PR</td>
<td>0 - 5</td>
<td>0.075 b</td>
<td>2.03 a</td>
<td>3.0 a</td>
<td>1.05 a</td>
<td>26.6 a</td>
<td>23.4 bcd</td>
<td>2.24 b</td>
<td>-26.9 ab</td>
<td>29.4 b</td>
<td>476 bc</td>
<td>0.061 ab</td>
<td>41.3 a</td>
<td>15.3 d</td>
</tr>
<tr>
<td></td>
<td>5 - 10</td>
<td>0.081 b</td>
<td>1.97 a</td>
<td>3.5 a</td>
<td>1.07 a</td>
<td>8.7 a</td>
<td>21.2 cd</td>
<td>2.46 b</td>
<td>-27.1 ab</td>
<td>30.2 b</td>
<td>403 cd</td>
<td>0.062 ab</td>
<td>32.2 a</td>
<td>16.3 d</td>
</tr>
<tr>
<td></td>
<td>10 - 20</td>
<td>0.082 b</td>
<td>1.28 a</td>
<td>2.7 a</td>
<td>0.72 a</td>
<td>11.1 a</td>
<td>23.8 bc</td>
<td>2.69 b</td>
<td>-27.3 b</td>
<td>32.9 a</td>
<td>508 bc</td>
<td>0.072 a</td>
<td>50.8 a</td>
<td>18.4 c</td>
</tr>
<tr>
<td>IPR</td>
<td>0 - 5</td>
<td>0.127 a</td>
<td>1.30 a</td>
<td>4.4 a</td>
<td>0.67 a</td>
<td>19.7 a</td>
<td>41.2 a</td>
<td>4.38 a</td>
<td>-27.4 b</td>
<td>34.4 a</td>
<td>989 a</td>
<td>0.072 a</td>
<td>56.6 a</td>
<td>28.6 a</td>
</tr>
<tr>
<td></td>
<td>5 - 10</td>
<td>0.082 b</td>
<td>1.34 a</td>
<td>3.6 a</td>
<td>0.69 a</td>
<td>13.7 a</td>
<td>26.9 b</td>
<td>2.48 b</td>
<td>-27.0 ab</td>
<td>30.0 b</td>
<td>550 b</td>
<td>0.055 b</td>
<td>39.6 a</td>
<td>22.6 b</td>
</tr>
<tr>
<td></td>
<td>10 - 20</td>
<td>0.061 c</td>
<td>2.15 a</td>
<td>3.5 a</td>
<td>0.30 a</td>
<td>9.7 a</td>
<td>19.6 d</td>
<td>1.66 c</td>
<td>-26.4 a</td>
<td>26.9 c</td>
<td>351 d</td>
<td>0.040 c</td>
<td>59.5 a</td>
<td>19.8 c</td>
</tr>
<tr>
<td>Depth</td>
<td>0 - 5</td>
<td>0.101 a</td>
<td>1.66 a</td>
<td>3.7 a</td>
<td>0.86 a</td>
<td>23.1 a</td>
<td>32.3 a</td>
<td>3.31 a</td>
<td>-27.2 a</td>
<td>31.9 a</td>
<td>733 a</td>
<td>0.067 a</td>
<td>48.9 a</td>
<td>21.9 a</td>
</tr>
<tr>
<td></td>
<td>5 - 10</td>
<td>0.082 b</td>
<td>1.65 a</td>
<td>3.6 a</td>
<td>0.88 a</td>
<td>11.2 a</td>
<td>24.0 b</td>
<td>2.41 b</td>
<td>-27.0 a</td>
<td>30.1 b</td>
<td>476 b</td>
<td>0.058 a</td>
<td>35.9 a</td>
<td>19.5 b</td>
</tr>
<tr>
<td></td>
<td>10 - 20</td>
<td>0.072 b</td>
<td>1.72 a</td>
<td>3.1 a</td>
<td>0.51 b</td>
<td>10.4 a</td>
<td>21.7 b</td>
<td>2.18 b</td>
<td>-26.8 a</td>
<td>29.8 b</td>
<td>429 b</td>
<td>0.056 a</td>
<td>55.1 a</td>
<td>19.1 b</td>
</tr>
<tr>
<td>Position</td>
<td>PR</td>
<td>0.080 a</td>
<td>1.76 a</td>
<td>3.1 b</td>
<td>0.94 a</td>
<td>15.5 a</td>
<td>22.8 b</td>
<td>2.46 b</td>
<td>-27.1 a</td>
<td>30.8 a</td>
<td>462 b</td>
<td>0.065 a</td>
<td>41.4 a</td>
<td>16.7 b</td>
</tr>
<tr>
<td></td>
<td>Mean 1</td>
<td>Mean 2</td>
<td>Mean 3</td>
<td>Mean 4</td>
<td>Mean 5</td>
<td>Mean 6</td>
<td>Mean 7</td>
<td>Mean 8</td>
<td>Mean 9</td>
<td>Mean 10</td>
<td>Mean 11</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IPR</td>
<td>0.072</td>
<td>b</td>
<td>1.60 a</td>
<td>3.9 a</td>
<td>0.55 b</td>
<td>14.3 a</td>
<td>29.2 a</td>
<td>2.84 a</td>
<td>-26.9 a</td>
<td>30.4 a</td>
<td>630 a</td>
<td>2.84 a</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Means followed by different letters indicate significant differences between the main effects of soil sampling position or soil sampling depth and the interactions of soil sampling depth and soil sampling position (\( P < 0.05 \)).*
6.3.4.3 Foliar sampling and analysis

Foliar nutrient and stable isotope samples were taken from all the plots at 1.25 years. Foliage was selected from a northern aspect in the upper-most recently matured foliage. Foliar samples were then oven dried at 40°C and ground using a puck and ball grinder. Total C, total N, δ^{13}C and δ^{15}N were determined on a GVI Isoprime Mass Spectrometer (Manchester, UK) with a Eurovector elemental analyser (Milan, Italy), where δ^{13}C was calculated as outlined in Equation 1.

$$
\delta^{13}C(\%) = \left( \frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \right) \times 1000
$$

(1)

where \(R_{\text{sample}}\) is δ^{13}/^{12}C ratio of the sample and \(R_{\text{std}}\) is the ^{13}C/^{12}C ratio of the international, Pee Dee Belemnite (PBD) standard. The standard deviation of the δ^{13}C standard samples (n = 9) was 0.14 %. All analyses were carried out at Griffith University, Brisbane, Queensland, Australia.

Needle samples used for photosynthesis measurement at 1.75 years were also kept for analysis of total C, N, δ^{13}C and δ^{15}N. Due to the intensive nature of the physiological measurements and site conditions only one replicate was sampled for physiological measurements, leaf specific area calculation and the related foliar N concentrations at 1.75 years.

6.3.4.4 Tree growth

Growth measurements included tree height (H) at 0.3, 0.92 and 1.7 years, diameter at ground level (DGL) at 0.9 and 1.7 years and diameter at breast height (DBH) at 1.7 years. Periodic annual increments (PAI) were calculated as the H and DGL values at the 1st measure subtracted from the same parameter value at the 2nd measure divided by age 1 subtracted from the age 2. Periodic annual increment for height was assessed between 0.3
and 0.92, 0.92 and 1.7 years and for DGL between 0.92 and 1.7 years, using Equation 2 outlined below as in Philip (1994).

\[
PAI = \frac{\text{Growth parameter at Age2} - \text{growth parameter at Age1}}{(\text{Age2} - \text{Age1})}
\]

(2)

Where growth parameters are DGL and H and age is 0.3, 0.92 or 1.7 years.

6.3.5 Physiological measurements

6.3.5.1 Photosynthesis

A photosynthesis survey was conducted over one week in early February of 2008 (1.75 years) using a Li-Cor 6400 gas analysis system (Licor 6400, Lincoln, Nebr.). Measurements were taken between 10 am and 12 pm and again between 1 and 3 pm for each tree to account for diurnal variation. Four individual trees from one replicate of the treatments were used as the experimental units for the photosynthesis and water potential surveys. Nine fully expanded, recently matured needles on the north-facing side of the tree were placed into a red-blue (LED) light source 2 x 3 cm Li-Cor chamber. Measures for photosynthesis were taken two minutes after clamping on the cuvette onto the needles, allowing each sample to stabilize. In the afternoon, after the photosynthesis measurements had been taken on each set of leaves, the edges of the chamber were marked onto the needles. Needles were then removed for specific leaf area calculation determination. Specific leaf area was calculated with the method of Johnson (1984) using volumetric displacement, the cumulative length and the number of needles. Photosynthetically active radiation (PAR) was set at 1500 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), \( \text{CO}_2 \) at 360 \( \mu \text{mol.mol}^{-1} \) and flow rates were kept between 400 and 500 kPa. Intrinsic water use efficiency (WUE\(_i\)) was determined from the ratio of net photosynthesis (\( A_n \)) to stomatal conductance (\( g_s \)) and photosynthetic N use efficiency (PNUE) was determined as the ratio of net photosynthesis to foliar N concentration.
6.3.5.2 Xylem pressure potential

Xylem pressure potential ($\Psi_{\text{XPP}}$) readings were made with a Scholander pressure chamber (PMS Instruments, Corvallis, Oregon), using an excised, north-facing mature shoot (maximum diameter of approximately 2-4 mm), removed from the upper canopy. $\Psi_{\text{XPP}}$ was measured diurnally (between 10 am and 12 pm and between 2 pm and 5 pm) where a shoot was excised immediately after the photosynthesis measurements were taken within a few minutes of removing at a temporary measuring station central to the plots.

6.4 Statistical analyses

GenStat 14$^{\text{th}}$ Edition (VSN International, 2011) was used to analyse the data. Analysis of variance (ANOVA) was used to analyse equally replicated data including soil characterisation, relative weed cover, foliar N concentrations at 1.25 years, tree growth and PAI parameters at different measurement times. Fishers protected 95% LSD was used for mean comparisons. Correlation coefficients were used to investigate the relationships between foliar N concentration at 1.25 years and tree growth parameters or relative weed cover for all measure times or biomass.

Where the effects of weed control and fertilisation treatments have been investigated for causal relationships, regression analysis has been used. In other cases were relationships have been identified but cannot be assumed to be causal, correlation analysis has been used. A series of regression models was used to investigate the influence of weed control and fertilisation on gas exchange parameters, foliar N concentration and tree water status. Gas exchange parameters included stomatal conductance ($g_s$), photosynthesis ($A_n$), transpiration (E), intrinsic water use efficiency ($\text{WUE}_i=A/g_s$) and internal CO$_2$ concentration ($C_i$). Water potential was also used as an indicator of plant water status. Each physiological relationship investigated the effects time of day (morning and afternoon) and canopy sampling position (upper or lower canopy). Five models were developed based on subsets of the data and included: (1) all
measures (morning and afternoon in both the upper and lower canopy); (2) morning measures in both canopy positions; (3) afternoon measures in both canopy positions; (4) upper canopy position at both morning and afternoon measures, and (5) lower canopy at both morning and afternoon measures. The most parsimonious regression model is presented as selected from a parallel, separate and common line. In addition, a subset of the physiology data representing the upper canopy sampling position was then used to investigate significant relationships between gas exchange parameters, foliar N concentrations, photosynthetic nitrogen use efficiency (PNUE), foliar δ\textsuperscript{13}C and δ\textsuperscript{15}N and water potential. This dataset was modelled using only time of day (morning and afternoon separately as well as combined). Based on the identification of significant relationships, a multiple regression was performed to see if a more complex model was appropriate to explain the observed significant relationships. Finally correlations were used to compare growth data and physiology data to identify relationships.

6.5 Results

6.5.1 Soil properties

The results from the ANOVA showed that there were significant interactions between sampling position (planting row (PR) and inter-planting row (IPR)) and depth (0-5, 5-10 and 10-20 cm) for soil total C, total N, δ\textsuperscript{13}C, C:N ratio, moisture content, hot water extractable organic C (HWEOC), hot water extractable total N (HWETN) and extractable potassium (K). Results indicate a decrease in soil total C, total N, δ\textsuperscript{13}C, HWETC, HWETN and moisture content with soil sampling depth in the IPR but not in the PR due to mixing of soil with cultivation and mounding. There was also a significant difference for the main effects of sampling position for NO\textsubscript{3}\textsuperscript{-}-N and NH\textsubscript{4}\textsuperscript{+}-N where nitrate was greater and ammonium was lower in the PR. A significant main effect of soil sampling depth for NO\textsubscript{3}\textsuperscript{-}-N was also observed where nitrate N concentrations were greater in the
top 0 – 10 cm (Table 6.2). There was no significant variation in either soil sampling depth or position for soil $\delta^{15}$N, total P or PMN.

### 6.5.2 Relative weed cover

The relative weed cover was significantly different at 0.8 and 1.1 years after planting. At 0.8 and 1.1 years relative weed cover was the lowest in the routine fertiliser plus luxury weed control (RF+LWC) followed by the routine fertiliser plus intermediate weed control (RF+IWC). By 1.6 years there was no significant difference in relative weed cover among the treatments (Table 6.3).

#### Table 6.3 Relative weed cover in the inter-planting row area for different fertilisation and weed control treatments in a F$_1$ hybrid pine plantation grown on a Grey Podzolic soil type. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatments</th>
<th>0.8 year (April 2007)</th>
<th>1.1 years (July 2007)</th>
<th>1.6 years (January 2008)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF + RWC</td>
<td>55.6 (2.35) b</td>
<td>48.3 (6.23) b</td>
<td>57.2 (4.33) a</td>
</tr>
<tr>
<td>LF + RWC</td>
<td>62.1 (3.75) b</td>
<td>51.2 (9.17) b</td>
<td>62.4 (4.75) a</td>
</tr>
<tr>
<td>RF + LWC</td>
<td>27.0 (5.70) d</td>
<td>11.1 (4.20) c</td>
<td>60.4 (5.12) a</td>
</tr>
<tr>
<td>RF + MWC</td>
<td>62.1 (1.66) b</td>
<td>53.4 (3.26) b</td>
<td>78.2 (0.95) a</td>
</tr>
<tr>
<td>RF + IWC</td>
<td>41.3 (2.70) c</td>
<td>41.3 (4.55) b</td>
<td>66.0 (7.67) a</td>
</tr>
<tr>
<td>RF + NWC</td>
<td>77.9 (1.84) a</td>
<td>69.9 (4.33) a</td>
<td>79.3 (8.46) a</td>
</tr>
</tbody>
</table>

* Means followed by the same letter are not significantly different from each other at $P > 0.05$.

### 6.5.3 Foliar N concentration, $\delta^{15}$N and $\delta^{13}$C

Neither foliar $\delta^{15}$N nor foliar $\delta^{13}$C was significantly different among the treatments.

The luxury fertilisation plus routine weed control had a significantly higher foliar N
concentration than the routine fertilisation combined with routine weed control, mechanical weed control and nil weed control, whereas the nil weed control (RF+NWC) and mechanical weed control (RF+MWC) had the lowest foliar N concentrations of all treatments (Table 6.4).

**Table 6.4:** Foliar N concentration (%), C isotope composition ($\delta^{13}C$)(‰) and N isotope composition ($\delta^{15}N$) (‰) for different weed control and fertilisation treatments at age 1.25 years in a F$_1$ hybrid pine plantation grown on a Grey Podzolic soil type. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Foliar $\delta^{13}C$ (‰)</th>
<th>Foliar N concentration</th>
<th>Foliar $\delta^{15}N$ (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RF + RWC</td>
<td>-31.6 (0.07) a</td>
<td>1.43 (0.13) b</td>
<td>-0.60 (0.45) a</td>
</tr>
<tr>
<td>LF + RWC</td>
<td>-31.3 (0.08) a</td>
<td>1.92 (0.13) a</td>
<td>-0.40 (0.14) a</td>
</tr>
<tr>
<td>RF + LWC</td>
<td>-31.7 (0.09) a</td>
<td>1.53 (0.08) ab</td>
<td>0.03 (0.32) a</td>
</tr>
<tr>
<td>RF + MWC</td>
<td>-31.6 (0.06) a</td>
<td>1.28 (0.03) b</td>
<td>-0.26 (0.68) a</td>
</tr>
<tr>
<td>RF + IWC</td>
<td>-31.6 (0.18) a</td>
<td>1.53 (0.23) ab</td>
<td>-0.21 (0.65) a</td>
</tr>
<tr>
<td>RF + NWC</td>
<td>-31.7 (0.09) a</td>
<td>1.24 (0.08) b</td>
<td>-0.36 (0.52) a</td>
</tr>
</tbody>
</table>

* Means followed by the same letter are not significantly different from each other ($P > 0.05$).

**6.5.4 Tree growth**

The luxury fertilisation treatment significantly increased tree growth as compared to all the routine fertilisation treatments. Within the five weed control treatments there were no significant differences for height at 0.92 and 1.7 years, diameter at breast height (DBH) at 1.7 years or for the periodic annual increment (PAI) for height (PAI) between 0.3 and 0.92 years. There was a significant difference in diameter at ground level (DGL) at 0.92 years, DGL at 1.7 years, height PAI at 0.92 - 1.7 years and for DGL PAI 0.92 - 1.7 among the treatments. Luxury weed control (RF+LWC) was not significantly different from the routine (RF+RWC), mechanical (RF+MWC) or intermediate weed
control (RF+IWC) for DGL at 0.92 and 1.7 years or height PAI at 0.92 - 1.7 years, yet for DGL PAI at 0.92 -1.7 years luxury (RF+LWC), routine (RF+RWC) and intermediate (RF+IWC) treatments were significantly different when compared to mechanical (RF+MWC) and nil (RF+NWC) (Table 6.5).

6.5.5 Relationships among relative weed cover, foliar N concentration, biomass and growth

The luxury fertilisation treatment significantly increased tree growth as compared to all the routine fertilisation treatments. Within the five weed control treatments there were no significant differences for height at 0.92 and 1.7 years, diameter at breast height (DBH) at 1.7 years or for the periodic annual increment (PAI) for height (PAI) between 0.3 and 0.92 years. There was a significant difference in diameter at ground level (DGL) at 0.92 and 1.7 years, height PAI at 0.92 - 1.7 years and for DGL PAI 0.92 -1.7 among the treatments. Luxury weed control (RF+LWC) was not significantly different from the routine (RF+RWC), mechanical (RF+MWC) or intermediate weed control (RF+IWC) for DGL at 0.92 years, DGL at 1.7 years or height PAI at 0.92 - 1.7 years, yet for DGL PAI at 0.92 -1.7 years, the luxury (RF+LWC), routine (RF+RWC) and intermediate (RF+IWC) treatments were significantly different compared to mechanical (RF+MWC) and nil (RF+NWC) (Table 6.5).

6.5.5.1 Relationships among relative weed cover, foliar N concentration, and tree growth

There was a significant negative correlation between foliar N concentration and relative weed cover at 0.8 year ($r = -0.57$, $p = 0.02$, $n = 15$) and 1.1 years ($r = -0.50$, $p = 0.05$, $n = 15$) (Figure 6.1) when the five weed control treatments were compared. When only the fertilisation treatments were considered (RF+RWC and LF+RWC), there were no significant correlations between relative weed cover and foliar N concentration.
Figure 6.1: Relationship between foliar N concentration and relative weed cover measured at 0.8 years (black symbols) and 1.1 years (Grey symbols) in an F₁ hybrid pine plantation grown on a Grey Podzolic soil type.
Table 6.5: Tree height (H), diameter at ground level (DGL) and diameter at breast height (DBH) at ages 0.3, 0.92 and 1.7 years and periodical growth increments (PAI) for height (H) at 0.3-0.92, 0.92-1.7 and DGL at 0.92 -1.7 years among the different weed control and fertilisation treatments in a F1 hybrid pine plantation grown on a Grey Podzolic soil type. Values are means and S.E. (n=3).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Means</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>H 0.92 (m)</td>
<td>H 1.7 (m)</td>
<td>DGL 0.92 (cm)</td>
<td>DGL 1.7 (cm)</td>
<td>DBH 1.7 (cm)</td>
<td>H PAI 0.3 - 0.92 (m⁻¹ yr⁻¹)</td>
<td>H PAI 0.92 - 1.7 (m⁻¹ yr⁻¹)</td>
</tr>
<tr>
<td>RF + RWC</td>
<td>0.69 (0.01) b</td>
<td>1.84 (0.07) b</td>
<td>2.24 (0.07) bc</td>
<td>4.86 (0.11) b</td>
<td>2.24 (0.11) b</td>
<td>0.54 (0.03) b</td>
<td>1.47 (0.07) b</td>
</tr>
<tr>
<td>LF + RWC</td>
<td>0.96 (0.04) a</td>
<td>2.41 (0.07) a</td>
<td>2.99 (0.10) a</td>
<td>6.20 (0.03) a</td>
<td>3.34 (0.11) a</td>
<td>0.80 (0.02) a</td>
<td>1.86 (0.06) a</td>
</tr>
<tr>
<td>RF + LWC</td>
<td>0.71 (0.04) b</td>
<td>1.89 (0.05) b</td>
<td>2.27 (0.09) bc</td>
<td>5.00 (0.17) b</td>
<td>2.21 (0.14) b</td>
<td>0.58 (0.04) b</td>
<td>1.52 (0.04) b</td>
</tr>
<tr>
<td>RF + MWC</td>
<td>0.78 (0.03) b</td>
<td>1.84 (0.08) b</td>
<td>2.43 (0.07) b</td>
<td>4.78 (0.22) b</td>
<td>2.14 (0.17) b</td>
<td>0.63 (0.03) b</td>
<td>1.38 (0.08) bc</td>
</tr>
<tr>
<td>RF + IWC</td>
<td>0.71 (0.06) b</td>
<td>1.87 (0.12) b</td>
<td>2.26 (0.18) bc</td>
<td>4.86 (0.31) b</td>
<td>2.16 (0.17) b</td>
<td>0.56 (0.07) b</td>
<td>1.49 (0.08) b</td>
</tr>
<tr>
<td>RF + NWC</td>
<td>0.72 (0.07) b</td>
<td>1.69 (0.12) b</td>
<td>1.95 (0.14) c</td>
<td>4.19 (0.30) c</td>
<td>1.86 (0.18) b</td>
<td>0.55 (0.08) b</td>
<td>1.22 (0.06) c</td>
</tr>
</tbody>
</table>

a Means followed by the same letter are not significantly different from each other at $P > 0.05$. 

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6.5.5.2 Foliar N concentration, δ^{13}C and δ^{15}N

When foliar δ^{13}C and foliar N concentration were correlated for all treatments combined, there was a significant positive correlation ($r = 0.62$, $p = 0.004$, $n = 18$) (Figure 6.2). When foliar δ^{13}C and foliar N concentration were compared for the fertilisation treatments, there was a significant positive correlation ($r = 0.93$, $p = 0.005$, $n = 6$), when only the weed control treatments were examined, there was a significant positive relationship between foliar δ^{13}C and δ^{15}N ($r = 0.49$, $p = 0.05$, $n = 15$); when only the weed control treatments were examined there was also a significant positive relationship between foliar δ^{13}C and δ^{15}N ($r = 0.49$, $p = 0.05$, $n = 15$).
Figure 6.2: Relationships between foliar N concentration (%) and foliar $\delta^{13}$C (‰) at 1.25 years as a result of different weed control and fertilisation treatments in an F$_1$ hybrid pine plantation grown on a Grey Podzolic soil type.

6.5.5.3 Tree growth relationships with foliar $\delta^{15}$N

For the weed control treatments there were significant positive correlations between foliar $\delta^{15}$N at 1.25 years and DBH at 1.7 years ($r = 0.67$, $p = 0.005$, $n = 15$), diameter at ground level (DGL) at 1.7 years ($r = 0.52$, $p = 0.04$, $n = 15$), height (H) PAI between 0.3 and 0.92 years ($r = 0.58$, $p = 0.02$, $n = 15$) and between 0.92 and 1.7 years ($r = 0.59$, $p = 0.02$, $n = 15$), H at 1.7 years ($r = 0.66$, $p = 0.006$, $n = 15$) and stem biomass ($r = 0.53$, $p = 0.03$, $n = 15$). There were significant negative correlations between relative weed cover at 0.8 years and DGL 1.7 years ($r = -0.55$, $p = 0.03$, $n = 15$), or DGL PAI 0.92 - 1.7 years ($r = -0.53$, $p = 0.04$, $n = 15$), or H PAI 0.92 - 1.7 years ($r = -0.71$, $p = 0.002$, $n = 15$), and between relative weed cover at 1.1 years and DGL 1.7 years ($r = -0.63$, $p = 0.01$, $n = 15$), or DGL PAI 0.92 - 1.7 ($r = -0.65$, $p = 0.007$, $n = 15$), or H PAI 0.92 - 1.7 ($r = -0.62$, $p = 0.01$, $n = 15$), or needle and branch biomass ($r = -0.53$, $p = 0.04$, $n = 15$); and between relative weed cover at 1.6 years and DGL PAI 0.92 - 1.7 ($r = -0.56$, $p = 0.02$, $n = 15$), DGL and H 1.7 years ($r = -0.57$, $p = 0.02$, $n = 15$ and -0.53, $p = 0.03$, $n = 15$ respectively), and H PAI 0.92 - 1.7 ($r = -0.69$, $p = 0.004$, $n = 15$).

When data for the two fertilisation treatments were used, foliar N concentration was positively correlated with DGL PAI 0.92 - 1.7 years ($r = 0.84$, $p = 0.03$, $n = 6$), and DGL 1.7 years ($r = 0.84$, $p = 0.03$, $n = 6$), and foliar $\delta^{13}$C was significantly correlated with both DGL and DBH at 1.7 years ($r = 0.79$, $p = 0.05$, $n = 6$ and 0.8, $p = 0.05$, $n = 6$, respectively). When all six treatments were combined there were significant positive correlations for both foliar N concentration and foliar $\delta^{13}$C to all growth variables.
(where for all values $r > 0.53$, $p < 0.05$, $n = 18$), and significant negative correlations for relative weed cover at when correlated to H PAI (at 0.92-1.7 years) ($r = -0.52$, $p = 0.02$, $n = 18$), DGL at 1.7 years ($r = -0.47$, $p = 0.04$, $n = 18$) and DGL PAI (at 0.92-1.7 years) ($r = -0.55$, $p = 0.01$, $n = 18$).

### 6.5.6 Treatment influences on physiological measurements

When stomatal conductance ($g_s$) was regressed on transpiration ($E$) for the five weed control treatments more variation is explained in the afternoons with both canopy sampling positions combined ($R^2 = 0.91$, $p < 0.001$, $n = 23$) compared to the data collected in the morning. The most parsimonious model was represented by the treatments having a response with the same slope (parallel regression model). The intermediate weed control (RF+IWC) had a significantly lower $E$ response (lower intercept) than all the other treatments except for the routine (RF+RWC) weed control (Figure 6.3a). When the relationships between $g_s$ and photosynthesis ($A_n$), and between $E$ and $A_n$ were investigated, afternoon measurements (combined for the both canopy sampling positions) best explained the variation in the data. The most parsimonious model was represented by the treatments having a response with the same slope (parallel regression model). The relationships between $g_s$ and $A_n$ ($R^2 = 0.73$, $p < 0.001$, $n = 23$), and between $E$ and $A_n$ ($R^2 = 0.76$, $p < 0.001$, $n = 23$) showed results where regression models for the luxury fertilisation (LF+RWC) and nil weed control (RF+NWC) did not differ significantly, nor did the luxury weed control (RF+LWC) and routine weed control (RF+RWC) treatments differ significantly. However, the regression model for the intermediate weed control (RF+IWC) differed significantly from all the other treatments except the luxury weed control. For both these relationships, RF+NWC had the smallest intercept and intermediate and luxury weed control had the greatest intercept suggesting that intermediate and luxury weed control had a higher response in $A_n$ for a given level of $g_s$ or $E$, and that nil weed control and
luxury fertilisation had a lower response of $A_n$ for a given level of $g_s$ or $E$ (Figure 6.3b and c respectively).

(a)

(b)

(c)
Figure 6.3: Relationships between transpiration \((E \text{ (mmol m}^{-2}\text{ s}^{-1}))\) and stomatal conductance \((g_s \text{ (μmol m}^{-2}\text{ s}^{-1}))\) (a); stomatal conductance \((g_s \text{ (μmol m}^{-2}\text{ s}^{-1}))\) and photosynthesis \((A_n \text{ (μmol m}^{-2}\text{ s}^{-1}))\) (b); and transpiration \((E \text{ (mmol m}^{-2}\text{ s}^{-1}))\) and photosynthesis \((A_n \text{ (μmol m}^{-2}\text{ s}^{-1}))\) (c); in the afternoons, at upper and lower canopy sampling positions as a result of different weed control and fertilisation treatments in an \(F_1\) hybrid pine plantation grown on a Grey Podzolic soil type.

When photosynthesis was regressed against internal CO\(_2\) concentrations \((C_i)\)(\(R^2 = 0.40, p < 0.001, n = 37\)), it was the luxury weed control that had the greatest response of photosynthesis at any level of internal CO\(_2\) concentration. The most parsimonious model was represented by the treatments having a response with the same slope (parallel regression model). There was also a strong, negative relationship between \(C_i\) and WUE\(_i\) but this relationship was not influenced by the treatments and hence the common line model was selected (\(R^2 = 0.86, p < 0.001, n = 37\)) (Figure 6.4). For these two \(C_i\) regressions, it was the measures taken from upper canopy sampling position for both morning and afternoons, that best explained the variation in the data.
Figure 6.4: Relationships between internal CO₂ concentration (Cᵢ) and intrinsic water use efficiency (WUEᵢ (μmol m⁻² s⁻¹)) at the upper canopy sampling positions in both the mornings and afternoons as a result of different weed control and fertilisation treatments in an F₁ hybrid pine plantation grown on a Grey Podzolic soil type.

6.5.6.2. Relationships among foliar N concentration, δ¹³C and δ¹⁵N, growth and physiological measurements

When the relationship between a subset of physiological measurements (including foliar δ¹³C), N nutrition (foliar N concentration and δ¹⁵N) and water potential data from the upper-canopy sampling position were investigated combining the morning and afternoon measures, there was a significant negative relationship between water potential and photosynthesis (R² = 0.44, p < 0.001, n = 37)(Figure 6.5). The most parsimonious model was the parallel regression model where the luxury weed control treatment had the greatest intercept and was significantly different from all the other
treatments, indicating a higher response of photosynthesis with any given level of water potential.

![Graph showing relationships between water potential (MPa) and photosynthesis (A_n (μmol m^{-2} s^{-1})).](image)

**Figure 6.5:** Relationships between water potential (MPa) and photosynthesis (A_n (μmol m^{-2} s^{-1})) combined for morning and afternoon at the upper-canopy sampling position, as a result of different weed control and fertilisation treatments in an F_{1} hybrid pine plantation grown on a Grey Podzolic soil type.

When relationships among foliar N concentration, δ^{13}C, δ^{15}N and gas exchange measurements were examined for the morning, there was a significant negative relationship between foliar N concentration and stomatal conductance (R^{2} = 0.59, p = 0.005, n = 17), where the luxury weed control and luxury fertilisation treatments had significantly higher N for each level of stomatal conductance from all the other treatments except nil weed control. For foliar δ^{13}C there was a significant negative relationship to transpiration rate in the morning (R^{2} = 0.56, p = 0.007, n = 17), where the luxury weed control had significantly higher transpiration at any level of foliar δ^{13}C when compared to the luxury fertilisation and intermediate weed control, but not when
compared to the routine and nil weed control treatments. For each of the relationships in the morning, the parallel regression model was most parsimonious. There was also a significant relationship between foliar N concentration and intrinsic water use efficiency (WUE$_i$). However, there was no difference between the relationships for each treatment ($R^2 = 0.43, p= 0.002, n = 17$) and hence a common line model was fitted.

There was a significant negative relationship between foliar $\delta^{13}$C and PNUE ($R^2 = 0.66, p = 0.002, n = 17$), which was best explained by the morning measurements. The treatment effect on the relationship between foliar $\delta^{13}$C and PNUE indicated that the luxury fertilisation treatment was not significantly different from the nil weed control treatment but these were significantly different from the routine and luxury weed control treatments.

Trees with greater PNUE had higher transpiration rates ($R^2=0.70, p<0.001, n=17$) and lower foliar $\delta^{13}$C ($R^2=0.66, p=0.002, n=17$). In these relationships, the luxury fertilisation and luxury weed control treatments had the highest transpiration rates across the range of PNUE while the intermediate, luxury and routine weed controls had greater foliar $\delta^{13}$C across the range of PNUE.

When relationships among foliar N concentration, $\delta^{13}$C and $\delta^{15}$N, water potential and gas exchange data were examined in the afternoon, there were significant negative relationships between foliar N concentration and water potential ($R^2 = 0.29, p < 0.014, n = 17$) (Figure 6.6a) and between water potential and foliar $\delta^{13}$C ($R^2 = 0.38, p = 0.005, n = 17$) (Figure 6.6b); and significant positive relationships between foliar $\delta^{13}$C and photosynthesis ($R^2 = 0.48, p = 0.001 n = 17$) (Figure 6.6c) and between foliar N concentration and photosynthesis ($R^2=0.40, p = 0.003, n=17$) (Figure 6.6d). However, the relationship for each treatment, were not significantly different and hence these relationships were best represented by a common line.

(a)
(b) $R^2 = 0.29$, $p < 0.014$, $n = 17$

(c) $R^2 = 0.38$, $p < 0.005$, $n = 17$
Figure 6.6: Relationships between foliar N concentration (%) and water potential (MPa) (a); water potential and foliar δ^{13}C (b); foliar δ^{13}C and photosynthesis ($A_n$ (μmol m$^{-2}$ s$^{-1}$)) (c); and foliar N concentration and photosynthesis ($A_n$ (μmol m$^{-2}$ s$^{-1}$)) (d) in the afternoons in the upper-canopy sampling position from a F$_1$ hybrid pine plantations grown on a Grey Podzolic soil type.

When relationships among foliar N concentration, foliar δ^{13}C and δ^{15}N, physiological measurements (including water potential) were examined using multiple regressions, for
the combined morning and afternoon data, PNUE ($R^2 = 0.46$, $p < 0.001$, $n = 34$), photosynthesis ($R^2 = 0.82$, $p < 0.001$, $n = 34$) and transpiration ($R^2 = 0.75$, $p < 0.001$, $n = 34$) were explained by stomatal conductance and internal CO$_2$ concentration. When the morning and afternoon data were run independently, stomatal conductance and internal CO$_2$ concentration explained the variation for photosynthesis ($R^2 = 0.88$, $p < 0.001$, $n = 34$) in the morning, while in the afternoons water potential, stomatal conductance and internal CO$_2$ concentration explained the variation in both photosynthesis ($R^2 = 0.81$, $p < 0.001$, $n = 34$) and foliar $\delta^{13}$C ($R^2 = 0.56$, $p = 0.003$, $n = 34$).

Correlations comparing growth data and morning physiology measurement identified negative relationships between $C_i$ and DGL $0.92$ ($r = -0.62$, $p = 0.01$, $n = 14$), DGL at 1.7 years ($r = -0.73$, $p = 0.002$, $n = 14$), DGL PAI at 1.7 years ($r = -0.58$, $p = 0.02$, $n = 14$), DBH at 1.7 years ($r = -0.72$, $p = 0.003$, $n = 14$) and height ($r = -0.75$, $p = 0.002$, $n = 14$) and height PAI at 1.7 years ($r = -0.68$, $p = 0.006$, $n = 14$). There were also significant positive relationships between WUE$_i$ and DGL at 1.7 years ($r = 0.64$, $p = 0.01$, $n = 14$), DGL PAI at 1.7 years ($r = 0.60$, $p = 0.02$, $n = 14$), DBH at 1.7 years ($r = 0.62$, $p = 0.017$, $n = 14$) and height at 1.7 years ($r = 0.58$, $p = 0.02$, $n = 14$). Correlations of growth data and to afternoon physiology measurement identified positive relationships between DGL PAI at 1.7 years and both $C_i$ ($r = 0.69$, $p = 0.01$, $n = 14$) and transpiration ($r = 0.68$, $p = 0.01$, $n = 14$).

6.6 Discussion

6.6.1 Cultivation and fertilisation increase N resources

We hypothesized that (1) soil N transformations (as shown by foliar N concentration and foliar $\delta^{15}$N) would be influenced by weed control and fertilisation treatments in the first 2 years of plantation establishment. There were non-significant increases in foliar
\( \delta^{15}\text{N} \) as a result of luxury weed control treatments at this site, which suggests that cultivation of the top soil and mounding in the planting rows compounded any influence on soil N transformations at early establishment. Despite this foliar \( \delta^{15}\text{N} \) was significantly and positively correlated to tree growth at early establishment, suggesting that foliar \( \delta^{15}\text{N} \) levels reflect N transformations in the soil.

Weed control increased foliar \( \delta^{15}\text{N} \) at an 8 year old F\textsubscript{1} hybrid plantation site in southeast Queensland in a previous study (Ibell \textit{et al.} 2010), while an increase in weed competition reduced foliar \( \delta^{15}\text{N} \) in white spruce \textit{[Picea glauca (Monech) Voss]} (Matsushima and Chang 2007) and \textit{Pinus spp.} F\textsubscript{1} hybrid foliage (Ibell \textit{et al.} 2013a). The increase in foliar \( \delta^{15}\text{N} \) is due to a preferential fractionation against \( ^{15}\text{N} \) during higher rates of nitrification and nitrate leaching which leave the remaining N pools \( ^{15}\text{N} \) enriched (Hogberg 1997; Adams and Grierson 2001). In addition, over the long-term, the absence of weed residues to the soil can influence labile C and N pools, microbial activity and immobilisation of mineralised N on-site (Silva and Anand 2011).

Elevated soil NO\textsubscript{3}^-\text{-N} (through increased N mineralisation and nitrification) has been shown to enrich soil \( \delta^{15}\text{N} \) under different weed control and fertilisation treatments (Matsushima \textit{et al.} 2012, Ibell \textit{et al.} 2010). Reduced immobilisation of the products resulting from N mineralisation can lead to potentially greater losses of N through volatilisation, denitrification and leaching of NO\textsubscript{3}^-, particularly on wet soils (Pu \textit{et al.} 2001; Pu \textit{et al.} 2002; Koba \textit{et al.} 2003).

Cultivation and high mounding in the planting rows on the Grey Podzolic soils, were shown to increase soil N transformations (as evidenced by increased mineral N and labile soil components, including non-significant increases in soil \( \delta^{15}\text{N} \)) which may have compounded any influence of N transformations resulting from weed control or fertilisation treatments. This suggests that the elapsed time after cultivation and high mounding at early establishment reduces the effectiveness of using foliar \( \delta^{15}\text{N} \) as a
measure of weed control induced soil N transformations. Despite the reduced effectiveness of using foliar $\delta^{15}N$ for understanding soil N processes at early establishment due to compounding effects of site preparation, there were negative correlations between relative weed cover and foliar N concentration, between relative weed cover and stem growth and positive relationships among foliar N concentration, tree growth and foliar $\delta^{15}N$. This indicates that relationships may be present among weed competition, N availability and tree growth resulting from different weed control and fertilisation practices.

6.6.2 Stomatal limitations of tree growth

We also hypothesized that weed control and N fertilisation influence tree growth by altering tree physiological parameters, including water relations ($\Psi_{XPP}$) at early establishment. When xylem potentials were compared with other key physiological measures (combined for the morning and afternoons), there was a negative relationship between $\Psi_{XPP}$ and both photosynthesis and foliar $\delta^{13}C$. Photosynthesis increased across the range of xylem potentials, under the luxury weed control. Water balance can influence a great many tree growth processes in the establishment phase. Loss of cell turgor will limit cell expansion and subsequent growth. The availability of key resources, particularly water, can have implications for subsequent tree growth (Schultze et al. 1987). Livingstone et al. (1998) reported that maximisation of N resources in Pinus radiata D. Don trees increased water used per unit of C fixed, resulting in a trade-off between WUE and nitrogen use. Hence, even with the addition of increased N resources, the benefits of increased C uptake can decline with low water availability (Tang et al. 2004). The morning measures of gas exchange showed a decrease in stomatal conductance with increasing N resources. Water deficits can lead to stomatal limitations of internal CO$_2$, reducing C gain and reducing growth (Niinemets and Tenhunen 1997, Wright et al. 2003).
Water deficit reduces stomatal conductance in the mornings where water uptake by the roots can lag behind water loss through transpiration (Ehleringer et al. 1993). The negative relationships between transpiration and foliar δ¹³C, between foliar N concentrations and stomatal conductance, and between foliar δ¹³C or transpiration and PNUE in the mornings, suggest that trees with increased foliar N concentrations had reduced rates of stomatal conductance which were associated with reduced transpiration and increased foliar δ¹³C (transpirational efficiency). Yet, while internal CO₂ concentration (Cᵢ) was strongly and negatively related to WUEᵢ (intrinsic water-use efficiency)(Aᵦᵢ/gₛ) it was not influenced by the treatments. Although treatments were represented by a common line, afternoon xylem potentials were influenced by foliar N concentration and was negatively related to foliar δ¹³C (transpirational efficiency) suggesting that N nutrition is affecting carbon uptake, water loss and hydraulic conductivity.

While water deficit influences both transpiration and stomatal conductance, stomatal regulation minimises water loss in transpiration. Stomatal regulation also limits water loss more than CO₂ uptake (Ehleringer et al. 1993). Hence, photosynthesis can continue with stomatal regulation, up to the point where non-stomatal limitations (mesophyll capacity) influence photosynthesis. The mesophyll capacity largely regulates the ability of ribulose biphosphate (RuP₂) carboxylase-oxygenase (RUBISCO) and the regeneration potential of photosynthetic electron transport (von Caemmerer and Farquhar 1981) to function in photosynthesis. Although nutrition and light regime alter the rate of C uptake (Elheringer et al. 1993), this presupposes the availability of water for the different biochemical processes involved including photosynthesis and tree physiological processes.
6.6.3 Biochemical or non-stomatal limitations of tree growth

Competition can also cause biochemical (non-stomatal) limitations of photosynthesis (Huang et al. 2008b, c; Matsushima et al. 2012). Although there were no main effects on foliar $\delta^{13}C$ (across all treatments), foliar N concentration and foliar $\delta^{13}C$ were positively correlated at 1.25 years. Increases in foliar $\delta^{13}C$ can indicate either increased photosynthesis (carboxylation rate) or transpiration efficiency resulting from stomatal regulation, as described above (Ehleringer et al. 1993). The previous section showed that there was some influence on foliar $\delta^{13}C$ in the mornings which varied with the treatments. However, the significant positive correlations between both foliar N concentration or foliar $\delta^{13}C$ and all the measured growth parameters, in the combined treatments (fertilisation and weed control treatments analysed together), suggest that an increase in N resources enhanced tree growth as a result of higher carboxylation rates, as suggested by Matsushima et al. (2012) and Huang et al. (2008b and c). Other studies have shown the relationship between foliar N concentration and photosynthesis processes (Field and Mooney 1986; Evans 1989). For example, because leaf N is a component of RUBISCO and chlorophyll, leaf N is important in carboxylation and RUBISCO regeneration during assimilation (Wullschleger 1993). In addition, an increase in carbohydrate production, induced by higher rates of photosynthesis can also increase RUBISCO production and electron transport (Niinemets and Tenhunen 1997). Therefore, foliar N concentrations may limit biochemical reactions involved in photosynthesis.

Further investigation of the relationships between $g_s$, $E$, $g_s$ and $A_n$, $A_n$ and $E$ indicated that the capacity for photosynthesis varied with weed control and fertilisation treatments. Internal $CO_2$ concentration influenced photosynthesis where the luxury weed control had the greatest photosynthesis rates across the range of $C_i$ values. A strong positive relationship between transpiration and stomatal conductance indicated
that increasing CO$_2$ diffusion into the leaf (through stomatal conductance) also led to increased water loss (through transpiration). At this site, intermediate weed control (RF+IWC) had the smallest rate of transpiration for any given level of stomatal conductance and was significantly different from all the other treatments. Significant, positive relationships between $g_s$ and $A_n$, and between $E$ and $A_n$ suggest that increasing stomatal conductance and transpiration led to increased photosynthesis, but where the intermediate weed control treatments had a significantly lower ratio of stomatal conductance and transpiration compared to the other treatments.

Trees receiving luxury fertilisation and intermediate weed control showed the greatest diameter growth on this site. Livingstone et al. (1998) found that internal CO$_2$ reflects increases in N through photosynthesis rate and therefore any increase in photosynthesis for a given increase in N, can be larger than the corresponding reduction in $g_s$ due to increased WUE (resulting from greater water loss).

This study shows how trees respond to silvicultural treatments, how growth was related to foliar N concentration, foliar δ$^{13}$C and a range of physiological processes. Changes in $C_i$ can be attributed to both stomatal and non-stomatal limitations to photosynthesis. Non-stomatal contributions to photosynthesis have been reported in water stressed loblolly pine (Barber 1986; Green and Mitchell 1992). Green and Mitchell (1992) concluded that stomatal limitations dominate in well-watered loblolly seedlings with access to high N resources when decreasing $\Psi_{XPP}$ can enhance stomatal control of $g_s$ in response to turgor loss and decreasing soil-water contents at the root surface (Katul et al. 1997). Rapid loss of water through epidermal transpiration (Franks et al. 1995), imposed by high vapour-pressure deficit can also facilitate increasing WUE through the associated reductions in $g_s$ (Wong et al. 1985). While photosynthesis and $g_s$ are highly related, there can be an increase in the capacity of photosynthesis and $g_s$ in the presence of water stress (Green and Mitchell 1992), or with increased N resources.
In this study, photosynthesis was positively correlated to foliar N concentration, stomatal conductance and transpiration yet negatively correlated to xylem potential in the afternoons. Foliar N concentration was negatively related to xylem potential, while PNUE was positively related to transpiration, and foliar $\delta^{13}$C was negatively related to both transpiration and PNUE. These relationships suggest the effects of weed control and fertilisation on foliar N concentration, photosynthesis and water use efficiency are highly integrated.

In summary, a decline in water and N availability, imposed by weed competition, may both reduce growth in the early establishment phase on these soils. While increasing N resources through luxury fertilisation may have increased carboxylation rate, transpiration efficiency, growth and WUE, this may have also led to greater demands for available resources required for growth (Schultze et al. 1987). In the nil-weed control, competition for N, water deficits and stomatal and non-stomatal limitation of gas exchange, however, in treatments that increased available N, growth limitation was more likely to have results from water deficits.

6.7 Conclusion

These results indicate that the stimulation of growth, resulting from weed control and fertilisation, was associated with an increase in photosynthesis, transpiration, stomatal conductance and carboxylation (foliar $\delta^{13}$C). However, in the presence of increasing water deficits, trees with greater foliar N concentrations exhibited greater stomatal control of water loss and an increase in WUE. Finally, despite increasing foliar N concentrations with different weed control and fertilisation treatments and positive relationships between tree growth and foliar N concentration or foliar $\delta^{15}$N (in the weed control treatments), the time from cultivation and high mounding at site preparation decreased the effectiveness of using foliar $\delta^{15}$N as a measure of soil N transformations.
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Chapter 7 General Discussion and Conclusions

This research investigated the effects of early establishment weed control and fertilisation on carbon (C) and nitrogen (N) cycling on C isotope compositions ($\delta^{13}C$) and nitrogen isotope composition ($\delta^{15}N$) in the soil and foliage and on tree growth and nutrition in three F$_1$ hybrid pine plantations (*Pinus elliottii* Engelm var. *elliottii* x *Pinus caribaea* Morelet var. *hondurensis* (Sènècl.) W.H.G. Barett & Golfari.) of southeast Queensland. Although various research exists that investigates the effects of weed control and fertilisation on pines grown in plantations (Neary *et al.* 1990; Woods *et al.* 1992; Mason and Milne 1999; Samuelson *et al.* 2004), this research provides new evidence of how $\delta^{13}C$ and $\delta^{15}N$ can be used to interpret soil C and N cycling, outlining some of the methodological limitations. It also identifies how foliar N nutrition and tree water use, tree growth and physiological variables including xylem water potential ($\Psi_{xpp}$), photosynthesis ($A_n$), stomatal conductance ($g_s$), transpiration (E) and internal CO$_2$ concentration ($C_i$) respond to early establishment weed control and fertilisation on two typical soil types in southeast Queensland, exotic pine plantations. The following sections outline the main findings of these investigations and highlight the mechanisms influencing the results.

7.1 Weed growth dynamics

Luxury weed control maintained to 3 years (0.3 t ha$^{-1}$) reduced weed biomass by 99% compared to the routine weed control treatment (8.38 t ha$^{-1}$), 8 years after planting. In comparison the luxury fertilisation treatment increased weed biomass by 23% (6.45 t ha$^{-1}$) compared to the luxury weed control treatment (Chapter 3). In addition, the luxury fertilisation treatment increased the proportion of C$_4$ grasses in the inter-planting rows. Plantations with contiguous areas of dense grasses in the understorey can contribute to
increased potential wildfire-risk, hence luxury weed control at early establishment was more effective at reducing this risk (0.06 t ha\(^{-1}\)), 8 years after establishment.

**7.2 Relative weed cover**

On the Yellow Earth soil type, relative weed cover was only significantly lower in the luxury weed control treatments at 1.1 years (Chapter 5). On the Grey Podzolic soil type luxury weed control treatments significantly reduced relative weed cover at 0.8 and 1.1 years while the intermediate weed control significantly reduced reduce relative weed cover at 1.1 years only (Chapter 6). By 1.6 years after planting, relative weed cover was not significantly different among the treatments on either soil type. These results suggest increasing weed control frequency (intermediate or luxury weed control treatments) on the Grey Podzolic soil type, can reduce competition at early establishment (<2 years). The differences between relative weed cover on the two soil types could reflect the landscape position where the Yellow Earth soil which was slightly higher in elevation, may have had reduced water availability for weed growth during the dry season (0.8 years after establishment).

**7.3 Soil C cycling and \(\delta^{13}\)C**

**7.3.1 Labile carbon pools and increased microbial activity**

Seven years after establishment, routine weed control with routine fertilisation led to increased labile C and N pools (hot water extractable organic C (HWEOC); hot water extractable total N (HWETN), potentially mineralisable N (PMN), total N and \(\delta^{13}\)C at the 0–5 cm soil sampling depth in the planting rows and at 0–5 and 5–10 cm soil sampling depth in the inter-planting rows.

Greater labile C and N pools (HWEOC and HWETN respectively) represent increased microbial activity in the soil (Sparling et al. 1998). The results presented here found that soil \(\delta^{13}\)C followed a similar trend as HWEOC in the 0-5 and 5-10 cm soil
sampling depths, and in the inter-planting row, as well as at the 0 - 5 cm depth in the planting row. These similarities represented increases in labile carbon and organic residues returned to the soil as a result of routine weed control treatments. This was supported by significant positive correlations of weed biomass (t ha$^{-1}$) to total N, HWEOC, HWETN, PMN and moisture content at the 0-5 cm depths, for pooled positions soil sampling positions.

On the other hand, luxury fertilisation also increased soil $\delta^{13}$C in the planting row, at 0–5cm soil sampling depths and this was likely due to the partial labelling by an increased contribution of the C$_4$ weed Imperata spp. (Chmura and Aharon 1995) mixing with other organic residues returned to the soil (Chapters 3 and 4). Increases in soil $\delta^{13}$C can also indicate a change in the contribution of C$_4$ plant residues returned to the soil (Oelbermann and Voroney 2007; Cheng et al. 2008), where the photosynthetic plant types present, whether C$_3$ or C$_4$ (O’Leary 1988), can influence the relative $\delta^{13}$C of plant organic materials returned to the soil (Balesdent et al. 1987; Kohn 2010; Silva et al. 2011).

Small changes in soil $\delta^{13}$C can also associated with changes in the soil microbial community composition such as where mycorrhizal fungi are $\delta^{13}$C depleted due the assimilation of carbohydrates sourced from trees, whereas soils with greater proportions of bacteria are $\delta^{13}$C enriched due to the bacteria’s ability to breakdown $\delta^{13}$C enriched lignins (Ehleringer et al. 2002). As this field of research is out of the scope of this thesis this is an area that will be identified as an ‘Area for further research’ in section 7.12.

7.4 N transformations and soil $\delta^{15}$N

Routine weed control decreased N transformations resulting in nitrification and soil $\delta^{15}$N. Increased weed biomass as a result of routine weed control treatments also led to increased soil N pools, including PMN and HWETN at 0 - 5 cm depths in the IPR, and
HWETN and total N at the 0 – 5 cm depths in the PR and increased soil moisture content at the 0-5 cm in the IPR and at the 5 -10 cm depth in the IPR and PR. Soil moisture is conducive to increased mineralisation of labile N pools. However, under these treatments, although N mineralisation may have been increased it was immobilised to a greater extent by weed biomass and microbial biomass, in competition to tree growth. With increased labile C and N pools there is a potential for increased N mineralisation and greater immobilisation of both NH$_4^+$ and NO$_3^-$, which effectively reduces nitrification rates and hence losses of NO$_3^-$ due to denitrification and leaching (Hogberg 1997), reducing the associated δ$^{15}$N of the residual soil N pools (Evans and Ehleringer 1994; Robinson 2001).

On the other hand, soil δ$^{15}$N was greater under the luxury weed control treatments 7 years after establishment. Soil δ$^{15}$N represents the rate and pathway that N transformations take in soils (Nadelhoffer and Fry 1994; Templer et al. 2007). Variations in soil δ$^{15}$N can also be attributed to varying quantities of decomposed litters and plant residues returned to the soil (Nadelhoffer and Fry 1988; Boddey et al. 2000). In addition, there was a non-significant trend for increased soil NO$_3^-$-N in the inter-planting rows under the luxury weed control treatments. Increased soil NO$_3^-$-N is indicative of increasing N transformations resulting from nitrification and denitrification in the soil (Chapter 3).

When mineralised N is not immobilised, such as under luxury weed control treatments, ammonification can lead to nitrification, where NH$_4^+$-N is converted to NO$_2^-$ and then NO$_3^-$. During nitrification there is stronger discrimination against the heavier $^{15}$N isotope than during ammonification (Evans 2001). Accordingly, NO$_3^-$ is $^{15}$N depleted, leaving the remaining soil N pools enriched in $^{15}$N (Shearer et al. 1974). However soils with higher rates of denitrification (such as waterlogged soils) can have increased losses of N$_2$O and N$_2$ resulting in further enrichment of $^{15}$N in NO$_3^-$-N.
All these processes occur simultaneously in the soils (Shearer et al. 1974) and hence soil heterogeneity can sometimes influence soil N dynamics confounding indicators of N cycling processes.

### 7.5 Relationship between soil $\delta^{13}$C and soil and foliar $\delta^{15}$N

There was also a strong negative relationship between soil $\delta^{13}$C (indicative of organic matter), at three different soil depths in the inter-planting row, and foliar $\delta^{15}$N at different canopy sampling positions (Chapter 4). It is suggested that this relationship indicates that soils with depleted $\delta^{13}$C (or reduced organic matter returned to the soils) had greater N transformations resulting from less immobilisation and greater nitrification, denitrification and potential leaching, leaving the resultant soil N pools available for plant growth enriched with $\delta^{15}$N.

The build-up of organic residues returned to the soils is an important source of N in ecosystems as they age (Boddey et al. 2000). However, an imbalance of the soil C:N ratio can result in decreasing N available for decomposition and hence, slower nutrient recycling (Silva and Anand 2011)(Chapter 3). Soils with low organic residues have high turnover rates of available C:N which allows the NH$_4^+$-N pools to build up and soils to become $\delta^{15}$N enriched. Therefore, ecosystems with increased N losses and increased relative rates of N cycling (Emmett et al. 1998; Templer et al. 2007) are representative of soils with foliage enriched in $^{15}$N (Austin and Vitousek 1998; Amundson et al. 2003). The strongest correlations occurred between the 0-5 cm soil sampling depth and the lower tree canopy sampling positions (P3, P4 and P5), when compared to foliage in the upper canopy which may suggest the importance of organic matter at this sampling depth to the N transformation pathways.

In addition, other authors have linked negative relationships between organic residues and foliar $\delta^{15}$N with the occurrence of mychorrhizal fungi. This results because increased organic matter and labile C and N pools are indicative of increased
microbial activity, which effectively reduce N transformations resulting in nitrification (Boddey et al. 2000, Hobbie et al. 2000). Because N is slow to cycle under these conditions, N is facilitated through microbial sources. Microbial sources transfer N depleted in δ¹⁵N, partly due to the fractionation that occurs during assimilation from fungi to plant and partly due to N sources in these soils already being low in δ¹⁵N (Peoples et al. 1991, Brodribb et al. 2005). Hence, the relationship between foliar δ¹⁵N and soil δ¹³C could be indicative of the changes in N transformation processes with organic matter and microbial community structure at different sampling depths, but this subject area was outside the scope of this thesis but is included in section 7.12 ‘Areas for further research’.

7.6 N cycling and foliar δ¹⁵N

Foliar δ¹⁵N increased as a result of luxury weed control treatments and with sampling position up the tree canopy, 7 years after establishment. While foliage was depleted in δ¹⁵N compared to the soils, soil δ¹⁵N increased with soil sampling depth (from 0 - 20 cm) and varied with treatments, while foliar N concentration and δ¹⁵N increased with tree height. Soil N is also recycled through leaf turnover which is depleted in δ¹⁵N compared to the soils, which explains the decreased concentration of δ¹⁵N in the upper soil layers. However, because soil δ¹⁵N at different depths would reflect both the mixing of leaf and soil organic N pools, then the change in foliar δ¹⁵N with tree height could be representative of the build up of soil δ¹⁵N in N pools over time. Therefore, these results suggest how the use of foliar δ¹⁵N as an indicator of soil N cycling and management practices needs to be clearly separated, spatially and temporally from other potential compounding influences (tree height vs soil depth relationships).
7.7 Compounding effects on N cycling

On the Yellow Earth site, foliar N concentration was significantly different as a result of weed control treatments, and was positively correlated to foliar $\delta^{15}$N at 1.25 years (Chapter 5). At the same site, foliar N concentration was negatively correlated to relative weed cover at 1.1 years, and positively correlated to tree height, height growth rates and tree biomass. Foliar $\delta^{15}$N was also negatively correlated to relative weed cover at 0.8 and 1.1 years (Chapter 5).

These relationships indicate that at early establishment, on the Yellow Earth soils, competition for available N occurred with increasing weed competition (as measured by relative weed cover) between 0.8 and 1.1 years, in the inter-planting row. The change in N availability resulting from the treatments influenced tree growth. However, soil samples taken before treatments indicated that pre-establishment cultivation and fertilisation facilitated mineralisation in the planting rows and upper soil layers which would have compounded the results for foliar $\delta^{15}$N at 1.25 years resulting from weed control treatments.

In addition, the use of industrial grade N fertilisers (which are typically depleted in $\delta^{15}$N (Macko and Ostrom 1994)) in the fertilisation treatments, increased foliar $\delta^{15}$N at 1.25 years. Robinson (2001) suggests that using different sources of N (such as industrial fertilisers or manures) can be a potential factor negating the use of $\delta^{15}$N in research to investigate N cycling processes.

On the Grey Podzolic site, there were positive relationships between tree growth and foliar N concentration or foliar $\delta^{15}$N (in the weed control treatments), although again the time from cultivation and high mounding at site preparation decreased the effectiveness of using foliar $\delta^{15}$N as a measure of silvicultural treatment effects on soil N transformations at early establishment.
### 7.8 Tree growth and resource use efficiency

On both the Yellow Earth and Grey Podzolic soil type, foliar δ¹⁵N at 1.25 years was positively correlated to tree growth, and biomass variables, while after 8 years from planting, luxury weed control also increased tree growth by 14% for diameter at breast height (DBH), 29% for basal area (BA) and 8% for tree height (H).

Various studies have attributed reduced plantation growth to either the lack of water or nutrients (Woods et al. 1992; Bergh et al. 1999; Xu et al. 1995). The reduction in growth in the routine weed control treatments suggests competition for either water or nutrients. At 8 years after planting important relationships were identified among foliar N concentration, foliar δ¹⁵N, tree growth and WUE (as indicated by foliar δ¹³C).

At 2 years after planting on both soil types, foliar N concentration was related to foliar δ¹³C. Other authors have found tree N concentration linked to WUE (Guehl et al. 1995; Prasolova et al. 2003; Cabrera-Bosquet et al. 2007). However, Xu et al. (2003) and Prasolova et al. (2003) found that the relationship between WUE and foliar N concentrations were dependent on clone and environmental conditions in the F₁ hybrid pines grown in southeast Queensland. Genetic variability of the F₁ hybrid clones, within each plot at the Toolara Experiment (Chapter 3 and 4), could be one reason why the results may not have shown significantly different foliar δ¹³C as a result of treatments.

It has been suggested that it is the change in stomatal demand for internal CO₂, rather than stomatal control that links N and WUE (Mitchell and Hinkley 1993). This investigation found positive correlations of foliar δ¹⁵N to WUE in the luxury weed control treatments, at all canopy sampling positions, as well as a correlation between WUE and DBH, BA and H variables at 8 years.

Increased foliar N availability may increase tree WUE due to increased water demand, this may also reduce tolerance to drought (DeLucia and Schlesinger 1991).
For example, Chan (2007) found increasing growth of stems in *Pinus radiata* D. Don plantations beyond natural limitations of a site can predispose trees to stem cavitation, which decreases the hydraulic conductance (resistance of water flow) of stems. This can lead to a temporary (Irvine *et al.* 1998) or permanent (Cochard *et al.* 2004) reduction in the efficiency of the water conducting tracheids which may also decrease drought tolerance despite increased WUE. *Pinus* species are low conductors of water compared to other species, and hydraulic conductance is strongly correlated to stomatal conductance, which suggests that the regulation of liquid and vapour conductance in pines occur predominantly at the leaf level (Brodribb *et al.* 2005).

At the 2-year-old site, unextracted basic density on the Yellow Earth site was lower as a result of luxury fertilisation on the Yellow Earth soils. This is important because luxury fertilisation could leave trees more susceptible to water stress limiting biochemical processes or stem cavitation injury due to increased water demand on sites experiencing a significant dry seasons (Green and Mitchell 1992, Chan 2007).

**7.9 Tree physiology**

Chapter 5 and 6 indicated that increased weed control and fertilisation treatments, influenced the relationships among photosynthesis and stomatal conductance, $C_i$ and transpiration and carboxylation (foliar $\delta^{13}C$) which could help explain why tree growth was greater as a result of some treatments (Campoe *et al.* 2012, Hogberg *et al.* 1995, Kaiser 1987). However, although weed control and fertilisation led to increased diurnal stomatal limitations to photosynthesis due to decreasing xylem potentials, this did not out-weight the beneficial effects of N on non-stomatal limitations (increasing capacity for stomatal conductance, transpiration and photosynthesis (Warren and Adams 2006, Livingstone *et al.* 1999, Green and Mitchell 1992).
Summary

By using weed control to reduce competition or fertilizers to increase nutrient availability in the first 2 years of a pine plantations growth, increased N availability can drive increased carbon gain through photosynthesis (reducing non-stomatal limitations to growth associated with N limitation). However, maximising tree growth and WUE may lead to lower xylem potentials which can increase stomatal limitations to growth (through water deficit) in the short-term, and non-stomatal limitations to growth in the long-term (hydrolysis or possibly stem cavitation) due to increased hydraulic capacity of the stems. However, by 8 years-of-age although, routine weed control treatments in the inter-rows may compromise growth rates and increase wildfire risks if not slashed, although they provide longer-term benefits to site fertility such as slower C and N cycling and increased site water availability.
7.11 Implications from this research

1. Luxury weed control can increase N cycling rates (as shown by increased soil and foliar $\delta^{15}$N), while routine weed control encourages slower N cycling, increased soil organic matter build-up (as indicated by soil foliar $\delta^{13}$C and weed biomass) and N immobilisation (as indicated by increased pools of labile C and N) (Chapter 3);

2. Increased availability of N resources through fertilisation or luxury weed control led to significant variations in foliar N concentrations (depending on soil type) and tree growth (regardless of soil types), which suggests that N deficiencies can limit potential tree growth (Chapter 4 and Chapter 6);

3. Cultivation at site preparation, urea fertilizer applications and soil sampling depth and position influence soil N transformations particularly at early establishment (<2 years) and hence the spatial and temporal factors are important factors to standardise when using the $\delta^{15}$N techniques in N cycling studies (Chapter 5);

4. Increasing N turnover rates can influence tree physiological processes (photosynthesis, stomatal conductance and transpiration) and tree water use efficiency (as indicated by foliar $\delta^{13}$C), yet increased WUE may not equate to improved drought tolerance as greater water resources may be needed to support increase in tree growth (Chapter 4 and Chapter 5).

5. Increased WUE at early establishment stage (2 years) can be triggered in trees by either stomatal or non-stomatal mechanisms depending on whether increased WUE is triggered by a reduction in stomatal conductance or transpiration through internal or external triggers, or by non-stomatal processes such as N availability (photosynthetic capacity) or water deficit (Chapters 5 and 6); and

6. Luxury applications of weed control and fertilisation practices that reduce competition for N can maximise tree growth due to increased capacity for
photosynthesis and stomatal conductance on a daily basis, however increased N resources without commensurate increases in water availability may reduce drought resistance beyond a tree's natural capacity and potentially influence tree wood quality.

7.12 Areas for further research

Further investigation of the following relationships is recommended as resulting from observations noted in this thesis:

1. Microbial community structure its influence on soil $\delta^{13}$C and $\delta^{15}$N and foliar $\delta^{15}$N resulting from different weed management practices.

2. Relationships between physiological processes (including foliar $\delta^{13}$C) and tree growth on the different varieties of pine grown in Southeast Queensland or other regions.

3. Relationships between xylem pressure potential and wood quality in Southeast Queensland pine plantations (based on other work in New Zealand)

4. Relationships between fertilizer applications and variation in weed biomass compositions, and its subsequent impact on soil $\delta^{13}$C and/or wildfire hazard potential.
**Figure 7.1**: The schematic representation of the effects of weed control on soils at 8 years on soil C and N properties. The size of the arrow indicates the relative proportion of active cycling.
Figure 7.2: Schematic representation of slow and fast N cycling and C cycling and the influence on soil and foliar $\delta^{13}$C and $\delta^{15}$N. The size of the arrow indicates the relative proportion of active cycling.
7.13 References


Appendix

Appendix 1: Table describing the plots and weed control and fertilisation treatments used at EXP GYM 350 at Toolara State Forest.

<table>
<thead>
<tr>
<th>Block</th>
<th>Plot</th>
<th>Treatment</th>
<th>Fertiliser</th>
<th>Weed control</th>
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## Appendix 2: Treatment details for Experiments 1 and 2 at EXP NC 677 and 678 at Cpt 205 Toorbul, Beerburrum State Forest.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Pre-plant weed control</th>
<th>Post-plant weed control</th>
<th>Fert. treatment</th>
<th>Post-plant treatments</th>
</tr>
</thead>
</table>
| 1         | Aerial spray x 1        | Routine                 | Routine [P only] | *Year 0 simazine band spray over top of trees after planting to 2 m band  
*Year 0 band spray at 6 months to 2m band  
*Year 0 band spray at 9 months to 2m band  
*Year 0 band spray at 12 months to 2m band  
Brush cut in inter-row @ 9 months  
Box spray in inter-row @ 18 months  
*Brush woody weeds in inter-row @ 18 months |
| 2         | Aerial spray x 1        | Routine                 | Luxury [N & P]   | *Year 0 simazine band spray over top of trees after planting to 2 m band  
*Year 0 band spray at 6 months to 2m band  
*Year 0 band spray at 9 months to 2m band  
*Year 0 band spray at 12 months to 2m band  
*Year 0 band spray at 18 months to 2m band  
Brush cut in inter-row @ 9 months  
Box spray in inter-row @ 18 months  
*Brush woody weeds in inter-row @ 18 months |
| 3         | Aerial spray x 1        | Total                   | Routine [P only] | *Year 0 simazine band spray over top of trees after planting to 2 m band  
*Year 0 band spray at 6 months to 2m band  
*Year 0 band spray at 9 months to 2m band  
*Year 0 band spray at 12 months to 2m band  
*Year 0 band spray at 18 months to 2m band  
Hand spray in the inter-row @ 6 months  
Hand spray in the inter-row @ 12 months  
Hand spray in the inter-row @ 18 months  
*Brush woody weeds in inter-row @ 18 months (removed slash as the two processes together seemed extreme) |
| 4         | Aerial spray x 1        | Mechanical- Inter-row   | Routine [P only] | *Year 0 simazine band spray over top of trees after planting to 2 m band  
*Year 0 band spray at 6 months to 2m band  
*Year 0 band spray at 9 months to 2m band  
*Year 0 band spray at 12 months to 2m band  
*Year 0 band spray at 18 months to 2m band  
Slash/ brush cut only in the inter-row @ 9 months  
Slash/ brush cut only in the inter-row @ 14 months  
Slash/ brush cut only in the inter-row @ 18 months  
*Brush woody weeds in inter-row @ 18 months |
| 5         | Aerial spray x 1        | Intermediate Inter-row  | Routine [P only] | *Year 0 simazine band spray over top of trees after planting to 2 m band  
*Year 0 band spray at 6 months to 2m band  
*Year 0 band spray at 9 months to 2m band  
*Year 0 band spray at 12 months to 2m band  
Hand spray in the inter-row @ 9 months  
Hand spray in the inter-row @ 14 months  
Hand spray in the inter-row @ 18 months  
*Brush woody in inter-row @ 18 months |
| 6         | Aerial spray x 1        | Nil                     | Routine [P only] | *Nil post-plant band tend  
Nil inter-row tend |
Appendix 3: Table describing the allocation of relative weed plot numbers (weed plots) to the respective experimental unit (plot number, block and treatment) for each soil type at EXP NC 677 and 678 at Beerburrum State Forest.

<table>
<thead>
<tr>
<th>Soil type</th>
<th>Block</th>
<th>Plot</th>
<th>Treatment</th>
<th>Weed plots</th>
<th>Soil type</th>
<th>Block</th>
<th>Plot</th>
<th>Treatment</th>
<th>Weed plots</th>
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