Influence of Irrigation and Fertilization on the Belowground Carbon Allocation in a Pine Plantation

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Influence of Irrigation and Fertilization on the Belowground Carbon Allocation in a Pine Plantation

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CERTIFICATE OF ORIGINALITY

I hereby declare that this submission is my own work and to the best of my knowledge it contains no material previously published or written by another person, nor material which to a substantial extent has been accepted for the award of any other degree or diploma at UNSW or any other educational institution, except where due acknowledgement is made in the thesis. Any contribution made to the research by others, with whom I have worked at UNSW or elsewhere, is explicitly acknowledged in the thesis.

I also declare that the intellectual content of this thesis is the product of my own work, except to the extent that assistance from others in the project design and conception or in style, presentation and linguistic expression is acknowledged.

SIGNED……

PREFACE

This research arose from a need to understand more about the function of forest systems. The research was funded by a grant obtained by Associate Professor R. E. McMurtrie (University of New South Wales) and Dr. R. J. Raison (CSIRO Division of Forestry and Forest Products) from the National Greenhouse Dedicated Grants Scheme (Australia) to model the impact of elevated carbon dioxide (CO_2) levels on forest productivity. Before models are fully developed basic quantitative information about forest systems is required. One of the areas where little information exists is in belowground systems of forests where difficulties in access and observability confer unique challenges.

The research reported in this work is my own work except where acknowledgment is provided in the text.

Part of this thesis has previously been published:
Chapter 5 was published as "Pongracic S, M.U.F. Kirschbaum, Raison, R.J. (1997) "Comparison of soda lime and infra-red gas analysis techniques for *in situ* measurement of forest soil respiration", Can.J.For.Res., 27 1980-1895.

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Finally, and most especially, to Tony Richards, thank you for giving me a reason to finish.

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ABSTRACT

The aboveground and belowground productivity of forest systems are interlinked through complex feedback loops involving tree, soil and environmental factors. With a predicted significant change in environmental conditions through the enhanced greenhouse effect, it is important to understand the response of forest systems to these new conditions. An increase in atmospheric CO_2 is predicted to increase photosynthesis, and therefore whole plant productivity at the individual tree level. However this increase in photosynthesis may result in greater requirements for nutrients, particularly nitrogen (N). In order to acquire any additional available N, trees may respond by increasing their proportional allocation of C belowground to the root system.

This study aimed to quantify the belowground C allocation in a mature forest system consisting of a single species on a single site, but with different levels of water and nutrient stress. The belowground carbon dynamics of a range of irrigated and fertilized *Pinus radiata* stands in Australia were investigated during 1992 and 1993. Belowground carbon allocation was estimated using the model proposed by Raich and Nadelhoffer (1989) where belowground C allocation is the difference between soil respiration and carbon input through litterfall, plus coarse root production and an adjustment for any change in soil and litter layer carbon pools. This model is best described by the equation:

$$\text{Belowground C} = C_{soilresp} - C_{litterfall} + C_{coarseroot} + \Delta C_{forest\ floor} + \Delta C_{soil}$$

Soil respiration, measured using a modified soda lime absorption method either every 2 weeks or every 4 weeks for 2 years, showed a range in daily soil C flux from 137 – 785 $mgCO_2.m^{-2}.h^{-1}$. Soil respiration showed seasonal trends with summer highs and winter lows. Limited fine root biomass data could not indicate a strong relationship between measured soil respiration and fine root (<2mm diameter) biomass. Fifty three percent of the variation in soil respiration measurements in irrigated treatments was explained by a linear relationship between soil respiration, and soil temperature at 0.10 m depth and litter moisture content. In non-irrigated treatments, 61% of the variation in soil

respiration measurements was explained by a linear relationship between soil temperature at 1 cm depth and soil moisture content. Inter-year variation was considerable with annual soil respiration approximately 20% lower in 1993 compared with 1992. Annual soil C flux was calculated by linear interpolation and ranged from 3.4 – 11.2 tC ha^{-1} across the treatments.

Soil C pools remained unchanged over 10 years between 1983 and 1993 for all combinations of irrigated and fertilized stands, despite significant aboveground productivity differences over the decade. Measurements of standing litter showed a change between 1991 and 1993 for only 2 out of the 10 treatments. These two treatments had belowground C allocation estimated both with and without an adjustment for a change in standing litter.

Annual litterfall C ranged almost four fold from 0.6 – 2.2 tC ha^{-1} between the treatments in 1992 and 1993, and fell within the ranges of measured litterfall over 10 years at the field site. Again inter-year variation was large, with the 1993 litterfall values being approximately 97% greater across all treatments compared with 1992 values.

Belowground carbon allocation was calculated using C fluxes measured at the field site, and ranged 3 fold from 4.4 – 12.9 tC ha^{-1} between the treatments during 1992 and 1993. In 1993 the belowground C allocation was approximately 30% lower across all treatments compared with 1992 calculations. This was due to an approximate 23% reduction in annual soil C flux, a 97% increase in litterfall C and an 18% reduction in coarse root production between 1992 and 1993.

The field site was N limited, and differences in belowground C allocation could be shown across irrigated treatments with different N limitations. As N availability increased belowground C allocation was decreased in the irrigated treatments. It was difficult to determine differences in belowground C allocation caused by water stress as the effects of water and N limitation were confounded. An increase in N availability generally indicated an increase in coarse root and litterfall C production, which were reflected in increased

aboveground productivity. In high N treatments the coarse root fraction of belowground C allocation comprised approximately 50% of the total belowground C allocation, whereas in the N stressed treatments coarse roots only comprised 20% of the total belowground allocation

The mechanistic model BIOMASS was used to estimate annual gross primary productivity (GPP) for the different treatments at the field site. BIOMASS estimated GPPs of between 30-38 tC ha^{-1} for the different treatments during 1992 and 1993. The measured belowground carbon allocation ranged from 16 – 40 % of simulated GPP, with the lower proportion allocated belowground in the irrigated and high fertility stands. Aboveground competition through the absence of thinning also appeared to reduce allocation belowground in non-irrigated stands.

A direct trade off between bole and belowground C could not be demonstrated, unless data were separated by year and by the presence or absence of irrigation. Where data were separated in this manner, only three data points defined the reasonably strong, negative relationship between bole and belowground C. The value of this relationship is highly questionable and should be interpreted with caution. Thus a decrease in belowground C allocation may not necessarily indicate a concomitant increase in bole C allocation.

Inter-year variation in a number of C pools and fluxes measured at the field site was at least as great as the variation between stands having different water and N limitation. Extrapolation of belowground productivity estimates from a single years data should be undertaken cautiously.

The work undertaken in this study indicated that for a given forest stand in a given soil type, an increase in N availability reduced the absolute and relative C allocated belowground. However this decrease in C belowground may not directly translate as an increase in stem growth or increased timber production.

Forest productivity in an enhanced greenhouse environment is likely to result in an increased allocation of C belowground due to increased N limitation, unless

adequate N is present to support a more active canopy. Further work is required to more fully understand the dynamics of the belowground system in a changing environment. However further research should focus on mature forest systems in order to isolate the impacts of natural ageing changes from perturbation effects on the forest system. This would be best undertaken in long term monitoring sites where a C history of the stand may be available.

CHAPTER 1. BELOWGROUND ALLOCATION OF CARBON IN FORESTS

1.1 Introduction

Belowground production in forests is the focus of this thesis, particularly in the context of climate change. This thesis will:

- examine the current state of knowledge of belowground systems in forests (Chapter 1);
- examine the current state of knowledge of the effects of elevated atmospheric carbon dioxide (CO_2) concentrations on forest systems (Chapter 2);
- describe and interpret work undertaken to quantify belowground carbon (C) allocation in a *Pinus radiata* (D. Don) plantation by:
    - describing and summarising previous work at the Biology of Forest Growth (BFG) experimental site near Canberra, Australia (Chapter 3);
    - testing assumptions that underlie a method for estimating belowground C allocation using soil respiration methodology (Chapter 4);
    - describing and testing soil respiration methodology as a tool for quantifying belowground carbon allocation using a model suggested by Raich and Nadelhoffer (1989) (Chapter 5);
    - describing and interpreting soil respiration data obtained over 2 years from the BFG experimental site (Chapter 6); and
    - examining the influence of combinations of irrigation and fertilization on belowground carbon allocation at the BFG experimental site (Chapter 7);
- place the belowground C allocation in context of whole stand productivity for the *Pinus radiata* (D. Don) plantation using a mechanistic model of forest productivity (BIOMASS - Chapter 8); and
- examine the implications of this work for forest productivity in an enhanced greenhouse environment (Chapter 9).

This chapter provides the framework for the experimental work reported in later chapters. It will examine:

- the function of trees;
- the importance of belowground processes in forest ecosystems; and
- the influence of abiotic factors on belowground carbon allocation.

1.2 Tree structure and function

Trees are highly developed autotrophic organisms with specialised "organs" undertaking specific tasks. In general:

- foliage photosynthesises and transpires;
- branches support foliage for light capture;
- stems provide a structural framework and conductance tissue for branches and foliage;
- coarse roots anchor and support the tree and aid in water capture; and
- fine roots acquire nutrients and water.

These functions are interdependent suggesting that a balance between these various tasks and organs must exist for optimal whole tree functioning. Details of whole tree physiology is not discussed in this section as Chapter 2 examines the effects of elevated atmospheric CO_2 on physiological processes and forest growth.

1.3 Carbon allocation

Forest productivity results from the conversion of CO_2 to carbohydrates in the canopy via the process of photosynthesis. Substrate concentration gradients and carbon (C) sink activity primarily drive the allocation of these carbohydrates to various functional organs in the tree (Landsberg, 1986; Gower *et al*, 1995). Allocation processes depend on the functional balance between the rate of acquisition of C by foliage and the rate of acquisition of nutrients and water by roots. Mechanical and structural hydraulic constraints also influence C allocation patterns. A C sink is defined as any plant tissue that cannot fully

supply its own C requirements and may include foliage (Luxmoore *et al*, 1995). Sinks competing for carbon are (modified from Gower *et al*, 1995):

1. all live tissue engaging in both growth and maintenance respiration;
2. foliage;
3. fine roots;
4. woody tissue (stem, branches, coarse roots);
5. storage tissues (which are important in seasonal growth activity and not merely dormant when active growth has been completed (Cannell and Dewar, 1994));
6. secondary defence compounds - whose sink strength is determined by factors in the external environment;
7. reproductive organs; and
8. leachates and exudates.

Carbon allocation is the outcome of many interacting processes (Cannell and Dewar, 1994). These processes involve many interdependent and complex feedback mechanisms, driven both by the external environment and internal physiology, and are still poorly understood. Genetic drivers of C allocation in trees have received little attention to date (Ledig, 1983) and are likely to be crucial.

1.4 Belowground allocation

Belowground allocation is driven by coarse and fine root sink strength. Coarse root sink strength may be directly related to coarse root biomass, which is highly correlated with bole size in *Pinus radiata* (Jackson and Chittenden, 1981; Beets and Whitehead, 1996). This correlation is quite logical considering that the purpose of both coarse roots and boles is largely structural. For fine roots the sink strength is likely to be a function of both fine root biomass (and respiration) and fine root turnover, and is further influenced by root exudation, mycorrhizal associations or nodulation. Unfortunately a strong correlation between fine root mass or turnover and an easily measurable aboveground parameter has not yet been developed.

Belowground allocation can comprise a significant proportion of net primary production (NPP – equivalent to gross production less the carbon used in respiration) and can comprise up to 60% of total NPP on a dry site (Comeau and Kimmins, 1989), although the actual biomass of fine roots may comprise only 5% of total tree biomass (Santantonio, 1989). The NPP allocated to roots contributes to root biomass increase, root biomass replacement (turnover) and any other belowground carbon sinks such as root respiration, mycorrhizal or nodulation activity. Changes in fine root standing crops can be rapid and are related to stand age and to soil conditions (Farrell and Leaf, 1974). Deans (1979) showed that fine root growth was correlated with soil temperature and moisture in a Sitka spruce stand on peaty soil. Nambiar *et al*, (1979) also showed low soil temperature adversely affected growth and elongation of new roots in 8-month-old *Pinus radiata*. However direct correlations between fine root biomass and soil moisture and/or temperature are generally poor (Santantonio, 1989). Further discussion of belowground C allocation in forest systems will be provided in Chapter 7.

The functions of fine roots include water and nutrient uptake, the rate of which affect whole tree productivity. Roots obtain water by:

- uptake of water percolating past existing roots during new rainfall events;
- mass diffusion of water in the soil to roots as roots dry out soil in their immediate vicinity; and
- axial growth of roots into moist soil (Luxmoore *et al*, 1995).

Nutrient uptake is more complicated than water uptake and often occurs against a concentration gradient. This means it is an active (carbon costly) process to capture some nutrients. Fungal and bacterial associations in mycorrhizae or nodulation can aid nutrient uptake, and these interactions are generally carbon expensive (Luxmoore *et al*, 1995).

Despite the fact that coniferous forests can undertake photosynthesis throughout the year, foliage and branch growth are generally determinate, with a growth flush usually occurring in spring although some forest types, in appropriate conditions, can exhibit more than one growth flush per year (Luxmoore *et al*, 1995). Stem and root growth are generally indeterminate

(Luxmoore *et al,* 1995). However belowground activity prior to the aboveground growth flush has been reported (Grier *et al*, 1981; Wardlaw, 1990). A reduction in root growth generally occurs during active periods of shoot growth sometimes resulting in a bi-modal peak in root activity (Cannell and Dewar, 1994; Luxmoore *et al*, 1995). This also indicates that root growth depends on the availability of current assimilates (Wardlaw, 1990; Luxmoore *et al*, 1995).

Research into the mechanisms controlling root system activity is much less advanced than the knowledge of constraints on photosynthesis (Cannell and Dewar, 1994). Few studies have quantified belowground allocation fully and often different definitions of fine and coarse roots have been used. Fine roots are generally defined by a diameter class (usually less than 1 - 2 mm diameter) but are more sensibly defined by physical status – as non-suberised, non-woody tissue. Although improvements in root measuring techniques have occurred, the study of roots is still time consuming and laborious (Landsberg, 1986, Boone *et al*, 1998, Kelting *et al*, 1998, Vogt *et al*, 1998).

Where total C budgets have been developed for forest stands there appears to be a trade off between fine root activity and stem carbon increment, with a strong negative correlation between partitioning to fine roots and partitioning to stems (Santantonio, 1989). The potential to manipulate the shift in carbon from a non-commercial sink in the root systems to the bole of a tree will increase the harvest index (stem production as a proportion of total production) and result in greater financial returns from commercial stands. Increasing financial returns in agricultural crops have generally resulted from increasing allocation to the harvestable organs, rather than from increases in productivity *per se* (Beadle and Long, 1985; Santantonio, 1989; Wardlaw, 1990).

1.4.1 Influence of forest type on belowground allocation

In evergreen forests there appears to be a greater allocation of photosynthate belowground compared with deciduous trees (Vogt *et al*, 1986a, Gower *et al*, 2001), but this may be because coniferous forests are more often found on nutrient poor sites (Gower *et al*, 1995). In addition, evergreen forests undertake

photosynthesis throughout the year, which may increase potential to maintain a higher root mass (Vogt *et al*, 1986a), and the lower quality coniferous litter that releases nutrients slowly during decomposition may also influence the maintenance of a higher fine root biomass (Gower *et al*, 1995).

When comparing 3-year old pine with hardwood or mixed stands, Fredericksen and Zedaker (1995) found the greatest root biomass in the pure pine stand, followed by pine-hardwood mixtures, and the least root biomass maintained in the pure hardwood stands. Because of these large species differences in belowground allocation (Steele *et al*, 1997), most research referred to in this thesis relates to coniferous forests, where the bulk of belowground research has occurred to date.

1.4.2 Influence of age/size on belowground allocation

Carbon allocation to roots increases in absolute terms with tree age until canopy closure is achieved (Ledig, 1983; Vogt *et al*, 1983; Santantonio, 1989; Kozlowski, 1992; Luxmoore *et al*, 1995; Beets and Whitehead, 1996). After canopy closure it is logical that total carbon partitioning to foliage decreases, partitioning to roots decreases and partitioning to stem increases (Beets and Pollock, 1987). This shift in allocation may occur because trees become more reliant on nutrient retranslocation, rather than soil uptake to meet nutrient demand after canopy closure (Luxmoore *et al*, 1995), although some recent studies have indicated a greater root allocation in older stands as nutrient limitation increases (Gower *et al*, 1996b)

Grier *et al* (1981) estimated that in a young fir stand approximately 55% of NPP was allocated belowground and this proportion increased to 69% in a mature stand. Similarly Gholz *et al* (1986) found a 6% increase in fine root biomass in an old compared to a young stand of slash pine, but a large (111%) increase in fine root turnover in older stands. However the error associated with fine root estimates may be well be greater than 6%, so these data need to be interpreted with caution. In temperate systems older stands have a thicker litter layer, which can lead to increased immobilisation of nutrients. This nutrient

immobilisation may require greater allocation of C to fine roots to compete for nutrients (Grier *et al*, 1981). Thus the effects of stand age and changed nutrient availability on belowground C allocation may be confounded.
Once stands reach a reproductive age, reproductive structures form a significant C sink. Increased growth is generally positively correlated with greater production of reproductive cones (Luxmoore *et al*, 1995). Ledig (1983) found that seven year old *Pinus radiata* trees allocated approximately 16% of existing dry weight to cone production and Linder and Rook (1984) estimated that 10-15% of existing dry weight was allocated to cone production in *Pinus sylvestris*. Work on *P. radiata* at the Biology of Field Growth (BFG) experiment indicated that that approximately 5% of total above growth was held in reproductive structures (Cremer, 1992). The carbon contained within the reproductive structures represents a small, but significant, potentially re-locatable quantity of carbon that could be redirected towards bole growth in commercial stands where reproduction is not a priority.

Fine roots can rapidly recolonise sites after perturbations. Raich (1980) estimated that root biomass was the same in a tropical forest site that had been clearfelled 12 months previously and an adjacent, intact forest. Nambiar (1983) suggested that a site was fully occupied by fine roots at age 2-3 in *P. radiata* stands on sandy soils. Similarly Escamilla *et al* (1991a) showed that 7- year old slash pine had a randomly distributed fine root mass independent of weed competition. This indicates that fine root biomass is likely to be maximised early in the life of a stand.

1.4.3 Influence of site fertility on belowground allocation

When a tree growth response is achieved after the application of fertilizer, this is partly due to an increase in photosynthesis from an increase in foliage area/biomass rather than simply an increase in photosynthetic efficiency (Mead *et al*, 1984; Linder and Rook, 1984; Luxmoore *et al*, 1995; Beets and Whitehead, 1996). Greater availability of nutrient alters the functional balance between roots and foliage. In highly fertile stands there is generally less C allocated belowground than on sites of low fertility (Landsberg, 1986; Vogt *et al*,

1983) and on high quality sites a smaller fine root live biomass is generally maintained (Deans, 1981; Vogt *et al*, 1983; Vogt *et al*, 1986a; Haynes and Gower, 1995).

According to Linder and Rook (1984) a 20-year old fertilized stand of *Pinus sylvestris* L. had approximately 40% of total GPP allocated belowground compared to 60–75 % of GPP allocated belowground in a non fertilized stand. However no difference in fine root production could be discerned between these fertilized and unfertilized stands (Linder and Troeng, 1981). Beets and Whitehead (1996) also reported this similarity in fine root production in fertilized and unfertilized stands of *P. radiata,* as did Adams *et al* (1989) for a *P. taeda* stand. This unaltered fine root production after fertilization suggests that the proportion of GPP allocated belowground decreases in fertilized stands.

The C and nitrogen (N) interactions in foliage have been extensively studied and the relationship of C acquisition to foliar N has been modelled relatively successfully by a variety of workers (e.g. McMurtrie and Landsberg, 1992). Much less is known about root N and C interactions. Root nutrient uptake is likely to be a function of soil nutrient availability and root distribution and activity rather than root mass (Cannell and Dewar, 1994). Concentrations of nitrogen (N) and phosphorus (P) are higher in roots than in shoots on severely nutrient deficient sites (Cannell and Dewar, 1994; Luxmoore *et al*, 1995). Cannell and Dewar (1994) contend that N taken up at a stressed site is shared more-or-less equally between roots and shoots, and that because shoots have a greater carbon allocation, foliar N concentration is lower than root N concentration. Cannell and Dewar (1994) also suggest that N used by roots is supplied via phloem after being moved aboveground to the foliage and then retranslocated to other N-limited organs, rather than directly used by the roots when N is acquired.

The increased aboveground productivity (growth) achieved after fertilization may be a result of both greater photosynthate being produced by foliage and a shift in C allocation from roots to the bole (Santantonio, 1989; Snowdon and Benson, 1992, 1986Beets and Whitehead, 1996).

1.4.4 Influence of water limitation on belowground allocation

One of the functions of forest root biomass is water acquisition. Therefore the water status of a site is likely to influence fine root biomass. When comparing fine root biomass in similar stands on a dry and wet site, Comeau and Kimmins (1989) found 13% more NPP was allocated belowground on the dry site, which also had the higher fine root biomass. Santantonio and Hermann (1985) also found a greater fine root biomass in Douglas fir on a low rainfall compared to a high rainfall site. Lower rainfall sites may also have slower litter decomposition rates (e.g. Parton *et al*, 1987) and fine roots are likely to be shorter lived and turnover more rapidly on such water stressed sites (Bartsch, 1987).

Tree growth is strongly affected by water and N availability. Rates of water loss via transpiration and CO_2/O_2 exchange (photosynthesis) by the foliage are closely linked (Cannell and Dewar, 1994). The nutrient status of the tree may also affect water relations by influencing stomatal control or the hydraulic conductance of roots (Luxmoore *et al*, 1995). Thus there are complex feedback mechanisms at work in the tree.

1.4.5 Mycorrhizal influences on belowground C allocation

Little work has been done to quantify the total carbon costs of mycorrhizal associations in mature forest systems, although the importance of mycorrhizae to growth has been well described (Vogt *et al*, 1982). Gower *et al* (1996a) suggested that combined root and mycorrhizal respiration represent a large carbon cost of between 30 and 62% of total soil respiration. Vogt *et al* (1982) estimated that mycorrhizal mass was only approximately 1% of total C biomass in both old and young fir trees, but that mycorrhizal activity represented 14 and 15% of NPP in old and young forests, respectively. Mycorrhizal and fine root carbon costs have been estimated as high as 45 and 75% in young and old fir stands respectively (Vogt *et al*, 1982).

Kozlowski (1992) suggested that although mycorrhizal fungi may make up only 4% of fine root biomass by weight, they can contribute up to 25% of CO_2

respired from fine root biomass. Mycorrhizae are an important component of soil C as they are highly active and the presence of mycorrhizae will increase the amount of carbon allocated belowground (Wardlaw, 1990). Mycorrhizae have been found in greater numbers on nutrient poor sites (Ahlstrom *et al*, 1988), indicating that belowground carbon on nutrient poor sites is likely to be increased both by greater fine root biomass and greater carbon costs of mycorrhizae. However, because mycorrhizae have a higher specific surface area than fine roots, their presence may reduce the amount of C required to support a given level of nutrient uptake.

1.5 Soil carbon storage

Soil C storage is a major factor in global carbon budgets and is becoming increasingly highlighted as political interest in the enhanced greenhouse effect heightens (Wullschleger *et al*, 1997). Carbon enters the soil system as either aboveground litterfall or input from the root system. In some systems the input of fine roots into soil detritus can exceed that of litterfall (Vogt *et al*, 1985; Vogt *et al*, 1986b; Comeau and Kimmins, 1989). Clearly such inputs must be considered when modelling soil C dynamics or soil C could be underestimated by 20-80% (Vogt *et al*, 1986b). McClaugherty *et al* (1982) have also shown the belowground system in red pine and mixed deciduous stands can have a significant input into soil organic matter.

1.6 Modelling belowground C allocation

Modelling carbon allocation belowground is a complementary approach to the difficult problem of measuring belowground productivity. Models allow:

- the examination of feedbacks in a forest system;
- the prediction of future responses to system perturbations; and
- the extrapolation of information to different sites.

Most models of carbon allocation are semi-empirical because mechanistic understanding of whole tree allocation has not yet been achieved (Santantonio and Grace, 1987). Aboveground processes in trees are much better

understood than are the belowground processes, and have been more successfully modelled.

Many stand level models are driven by climate and light capture and predict gross primary productivity (GPP) based on equations for foliar photosynthetic activity. This GPP is then converted to NPP by subtracting the C used in respiratory activity. Carbon is distributed to the aboveground portion of the stand, and in some models the remainder of the C is allocated belowground. This approach clearly fails to provide adequate representation of the belowground processes, as the belowground system is generally considered a "black box". Accurate, quantitative data on belowground systems is required to validate models. This data is generally lacking, as is a generic understanding of how carbon allocation varies with site conditions.

Belowground carbon allocation is difficult to isolate as estimates of fine root turnover in forest systems are complicated by simultaneous productivity, mortality and decomposition. The actual controls of fine root elongation, branching, cell expansion, physiological activity, senescence and abscission are unknown and have not yet been modelled accurately (Santantonio and Grace, 1987; Boone *et al*, 1998). Climate warming may have a greater impact on fine root turnover than on fine root biomass, with higher maximum temperatures conferring a greater turnover (Vogt *et al*, 1986b; Kirschbaum, 2000). At a global scale total belowground carbon allocation in mature forests has been related to aboveground litterfall (Raich and Nadelhoffer, 1989) but this relationship does not hold true within a single stand, nor for stands prior to canopy closure (Gower *et al*, 1996a).

One approach to overcoming the simultaneous production and decomposition of roots would be to view belowground carbon as two distinct systems (coarse roots and fine roots) in order to highlight the different processes occurring in each system (Santantonio and Grace, 1987). Coarse roots have a strong relationship to bole size (Jackson and Chittenden, 1981; Santantonio and Grace, 1987; Beets and Whitehead, 1996), can be more relatively easily estimated and do not suffer from simultaneous production and decomposition

as do fine roots. Presently insufficient data exist to accurately model C allocation to fine root systems at a stand level. Basic quantitative information and an understanding of the key drivers of fine root production and turnover are required before models can accurately capture belowground carbon dynamics.

1.7 Summary

Belowground C allocation and productivity are influenced by a variety of external and within-tree factors. The mechanistic understanding of fine root systems has not yet developed to a stage where fine root biomass and turnover can be accurately estimated or modelled in forest systems. Generally fine root allocation is greater on drier or nutritionally poor sites and live root mass may be shorter lived in water or nutrient-stressed systems, but insufficient data exist to generalize regarding these drivers of fine root biomass and activity.

Fine roots make up an important component of total forest production and must be viewed in the context of the whole system. The overall productivity of a system is an important driver of root activity and this is influenced by species, site fertility and climate.

The Australian National Greenhouse Advisory Committee Dedicated Grants Scheme, who supported this study, had a significant interest in the impact of climate change, and particularly the effects of elevated atmospheric CO_2, on forest productivity. The experimental work undertaken in this study investigated the influences of irrigation and fertilization on the belowground C allocation of a *Pinus radiata* plantation. The impact of an enhanced greenhouse environment on root systems must be understood in order to be able to accurately predict effects of elevated atmospheric CO_2 on total system productivity. This potential impact of an elevated CO_2 atmosphere is discussed in Chapter 2, and Chapter 9 will discuss the experimental results in the context of an elevated CO_2 environment.

CHAPTER 2. POTENTIAL EFFECTS OF ELEVATED CO_2 ON FOREST PRODUCTIVITY

2.1 Introduction

The greenhouse effect is a natural phenomenon that allows the earth to support organic life (IPCC, 1996). Greenhouse gases such as carbon dioxide (CO_2), nitrous oxide (N_2O), water vapour (H_2O), methane (CH_4), ozone (O_3) and chlorofluorocarbons (CFCs) are present in the atmosphere and cause a warming of approximately 30^oC at the earth's surface (Holdgate, 1995), which is fundamental to the current diversity and distribution of life on earth. In recent times the "enhanced greenhouse effect" has become a concern as the production and release of greenhouse gases through human activity has increased the concentration of these gases in the atmosphere. These increases in greenhouse gases in the atmosphere enhance their capacity to heat the earth. This enhanced heating capacity has been predicted to cause an increase in temperature at the earth's surface sufficient to significantly alter existing landforms and vegetation distribution (IPCC, 1996; Kirschbaum, 2000).

Greenhouse gases vary in their impact on warming. CO_2 has a relatively low greenhouse impact, but it is present in large quantities, whereas CFCs are present in very small quantities but possess a high warming capacity (IPCC, 1996). Carbon dioxide has been estimated to contribute 50% to the greenhouse effect, whereas CFCs contribute 19% (IPCC, 1996). CO_2 is fundamental to autotrophic productivity as it is the source of carbon (C) that is fixed in photosynthesis.

Atmospheric CO_2 concentration has increased from 280 μl/l in 1850, to 350 μl/l in 1994 (Wolfe, 1994) and has reached 370 μl/l in 1998 (Kirschbaum, 2000). This increase of 32% over almost 150 years is largely due to the combustion of fossil fuels and land clearing. Atmospheric CO_2 is predicted to reach 700 μl/l by the end of the 21st century (Kirschbaum, 2000).

The enhanced greenhouse effect is predicted to lead to changes in global climate through warming of the earth's surface, averaging approximately 0.7 - 2.1^{o}C by 2070 (IPCC, 1996). This corresponds to a warming of between 0.6 - 3.8^{o}C across the Australian continent by 2070, with the greatest temperature increase predicted in the interior (IPCC, 1996). Associated with this is a changing rainfall pattern with a predicted general decrease in winter continental rainfall and an inconsistent change in summer continental rainfall (IPCC, 1996).

Both climate change and increased atmospheric CO_2 are expected to influence autotrophic production through:

- direct and indirect effects of CO_2 on plant physiology and feedback processes;
- altered rates of ecophysiological processes that are temperature dependent; and
- potential effect of changing rainfall.

As there are major financial investments involved in both farming and forestry enterprises worldwide, much effort has been invested in quantifying and predicting the impact of the enhanced greenhouse effect, and more specifically the effect of elevated CO_2, on primary productivity (Fajer and Bazzaz, 1992). In addition terrestrial ecosystems play a critical role in regulating the global carbon cycle because of their large carbon storage (Ellsworth *et al*, 1995; Wullschleger *et al*, 1997).

In developing global C budgets Tans *et al* (1990) described a "missing" global carbon sink of 3 x 10^{12} tons of carbon. This "missing C sink" is now known as the "unidentified terrestrial sink" and is likely contained in the terrestrial forest ecosystem (Gifford, 1994), either in the tropical forest ecosystem (Lloyd and Farquhar, 1996) or in the northern hemisphere (Sarmiento and Wofsy, 1999). Better understanding of global carbon processes, particularly the link between terrestrial systems and the atmosphere, is essential before a realistic prediction of productivity changes due to the enhanced greenhouse effect can be made. Experimental validation data is lacking to confirm modelling theory that is

exploring the effects of elevated CO_2 on global terrestrial C dynamics (Cox *et al*, 2000).

2.2 Effects of elevated CO_2 on primary productivity

There have been several excellent reviews of the potential impacts of elevated CO_2 on terrestrial vegetation (Eamus and Jarvis, 1989; Idso and Idso, 1994; Mooney *et al*, 1999) and one specifically examining the effects of elevated CO_2 on woody plants (Ceulemans and Mousseau, 1994). The CO_2 fertilization effect is expected to influence the primary production of most plant species (Poorter, 1993; Idso and Idso, 1994). However the magnitude of this effect varies according to (modified from Idso and Idso, 1994; Mooney *et al*, 1999):

- species longevity;
- photosynthetic apparatus used by species (C3, C4 or CAM pathway);
- nutrient balance;
- water balance;
- light environment;
- temperature;
- species sensitivity; and
- other ontogenetic effects.

Studies of the effects of elevated CO_2 on primary productivity generally involve a doubling of current ambient CO_2 concentration in a greenhouse, or in field-based experiments either with open topped chambers (Leadley and Drake, 1993) or “free air carbon dioxide enriched experiments” (FACE experiments) (Hendrey *et al*, 1993). The field-based experiments simulate reality more closely by maintaining the existing vegetation *in situ*. However, there is some change to the microclimate (temperature, humidity and windspeed - Ceulemans and Mousseau, 1994) around the vegetation induced by the presence of the chamber, although these may be adjusted for by using control chambers. FACE experiments surround a group of trees or agricultural crops within a high CO_2 environment. Due to the cost of field-based experimental chambers, work has concentrated on smaller vegetation, and little work has been undertaken in

mature forest systems (Norby *et* al, 1999). Due to these considerations any field-based results may be limited to the species and interactions studied, and care needs to be exercised in extrapolating or generalising findings (Drake and Gonzalez-Meler, 1997; Pataki *et al*, 1998; Saxe *et al*, 1998; Norby *et al*, 1999).

Controlled-environment, or greenhouse, elevated CO_2 tests allow control over interactions between high CO_2 and varying temperature, nutrient, water and light levels. However only limited extrapolation to more natural forest systems is possible, as tests are often conducted on seedlings or very young plants which are likely to behave differently to older individuals (Morison, 1990; Kersteins *et al*, 1995). Many responses of younger plants to elevated CO_2 exposure have recently been identified as enhanced ontogenetic effects (Wullschleger *et al*, 1997; Saxe *et al*, 1998; Norby *et al*, 1999).

The overall effect of elevated CO_2 on forest productivity is a result of complex feedbacks and interactions between physiological and soil processes at different scales. These will be discussed according to:

1. effects of elevated CO_2 on foliar activity;
2. effects of elevated CO_2 on whole plant growth; and
3. effects of elevated CO_2 on processes affecting the ecosystem.

2.3 Effects of elevated CO_2 on foliar activity

Forest and foliar productivity is driven by photosynthesis. Instantaneous rates of photosynthesis are largely determined by ambient CO_2 concentration, radiation, stomatal conductance, transpiration and enzyme activity (Wolfe, 1994). This section will review the effect of CO_2 concentration on photosynthesis, the interaction of elevated CO_2 with foliar nitrogen, foliar water use, foliar respiration and physical foliar characteristics.

2.3.1 Photosynthesis

Physiological effects of increased carbon dioxide are frequently investigated at the foliar level. Considering only C_3 species (forest species) the reported

instantaneous photosynthesis response to a doubling of CO_2 is approximately 50-75% (Luxmoore *et al*, 1993). Separating this into deciduous and coniferous forest species, the photosynthetic stimulation to elevated CO_2 is 61% and 40%, respectively, based on 83 species of which 18 were coniferous (Ceulemans and Mousseau, 1994). A recent review by Norby *et al* (1999) found a consistent stimulation in photosynthesis of about 60% for 300 µl/l increase in CO_2 concentration based on data from field grown trees. This increased instantaneous photosynthetic rate is likely to be due to a direct stimulation in photosynthetic apparatus at the biochemical level (Ellsworth *et al*, 1995). The increased presence of CO_2 through mass diffusion into the intercellular spaces increases the competitiveness of CO_2 relative to O_2 for activation sites on the Rubisco enzyme - thus reducing the amount of photorespiration occurring in the chloroplast (Wolfe, 1994; Kersteins *et al*, 1995). However this increased photosynthetic activity does not translate ***directly*** into increased aboveground growth because of the numerous feedback effects involved in the biochemistry of the leaf. Photosynthesis may also be limited by nitrogen, water and light availability in certain environments, all of which will affect foliar response to an elevated CO_2 environment.

2.3.2 Photosynthetic acclimation

Prolonged exposure to high CO_2 has commonly led to a reduction or elimination of the enhanced photosynthetic response (Luxmoore *et al*, 1993; Ceulemans and Mousseau, 1994; Pettersson and McDonald, 1994; Wolfe, 1994; Kersteins *et al*, 1995). Several mechanisms have been advanced to explain this acclimation:

1. **sink strength** – which relates to the ability of the plant to transport carbohydrates out of the foliage and into storage or metabolically active organs. The build up of carbohydrate in the foliage may cause a depressive feedback effect on the photosynthetic machinery thereby reducing the rate of photosynthesis (Luxmoore *et al*, 1993; Wolfe, 1994; Ceulemans and Mousseau, 1994; Kersteins *et al*, 1995). Arp (1991) advanced the theory that restricted pot size, and therefore soil rooting volume, might be

responsible for reducing the root sink strength thereby causing a reduction in photosynthesis in elevated CO_2 conditions.

2. **nutrient limitation** – this occurs where either nitrogen is insufficient to maintain the activity and activation state of Rubisco (Luxmoore *et al*, 1993; Ceulemans and Mousseau, 1994; Wolfe, 1994; Kersteins *et al*, 1995) or insufficient inorganic phosphorus is present to enable energy transfer via ATP (Ceulemans and Mousseau, 1994; Wolfe, 1994; Kersteins *et al*, 1995). Pettersson and McDonald (1994) showed that where foliar N was constantly maintained there was no down-regulation of enhanced photosynthesis in an elevated CO_2 environment.

3. **increase in foliar starch content** - which could physically impede or damage foliar processes and is closely linked to foliar sink strength (Luxmoore *et al*, 1993; Ceulemans and Mousseau, 1994; Wolfe, 1994).

2.3.3 Foliar nitrogen

Norby *et al* (1999) reported that foliar N concentration decreased on average by 11% in gymnosperms when exposed to elevated CO_2. Increased foliar photosynthetic efficiency with a doubling of CO_2 is often linked with a reduction in N concentration within the foliage (Pettersson and McDonald, 1992; Coleman *et al*, 1993). Reduced foliar N concentration decreases both carboxylation efficiency and the CO_2-saturated maximum rate of photosynthesis (Pettersson and McDonald, 1994). The growth of nitrogen deficient plants is primarily limited by the absence, or reduced activity, of Rubisco (Pettersson and McDonald, 1994) and approximately 50% of foliar nitrogen is used within the Rubisco complex (Kersteins *et al*, 1995). If a constant C uptake is maintained, Rubisco activity may potentially decrease by 30% at 700 μl/l CO_2 concentration compared to 350 μl/l CO_2 concentration (Kersteins *et al*, 1995).

Other workers have questioned this CO_2-induced reduction in foliar N concentration, arguing that a decreased foliar N concentration generally occurs

where growth is accelerated, and is also a normal ontogenetic (aging) effect in N limited environments (Coleman *et al* 1993; Pettersson and McDonald, 1994), or is a result of a dilution effect through increased foliar biomass (McGuire *et al*, 1995; Norby *et al*, 1999; Gifford *et al*, 2000). Some workers have argued that total canopy N is more important than foliar N concentration in determining overall canopy productivity, and total foliar N can be approximately equal under both ambient and elevated CO_2 environments (Morison, 1990; Korner and Arnone, 1992; Gifford *et al*, 2000).

The reduced foliar N concentration also has ecosystem ramifications, where one study has shown an increase in herbivory at high CO_2 where N-reduced foliage exists (Fajer and Bazzaz, 1992; Norby *et al*, 1999). This change in herbivory pattern may affect dominance by individuals and species within forest systems and influence overall ecosystem productivity (Norby *et al*, 1999; Kirschbaum, 2000).

2.3.4 Water use

Many studies have shown an increase in water use efficiency (WUE - dry matter produced per unit water used) under elevated CO_2 conditions (Norby and O'Neill, 1991; Fajer and Bazzaz, 1992; Ceulemans and Mousseau, 1994; Idso and Idso, 1994; Ellsworth *et al*, 1995; Mooney *et al*, 1999). In the current CO_2 environment, every molecule of CO_2 that enters the stomata requires the release of between 100-500 molecules of water (Bazzaz and Fajer, 1992; Jarvis, 1995). In an elevated CO_2 environment there is a reduced requirement for stomatal opening to achieve CO_2 capture. Reduced stomatal conductance is frequently observed at elevated CO_2 though the mechanism for this is as yet unknown (Fajer and Bazzaz, 1992; Wolfe, 1994; Mooney *et al*, 1999). Some evidence indicates that stomatal density has decreased by 40% over the past 200 years in some long-lived forest trees, which has led to speculation that this is response to rising atmospheric CO_2 (Ceulemans and Mousseau, 1994; Wolfe, 1994).

Other workers have suggested that an increase in canopy leaf area could follow from the increased photosynthate production under elevated CO_2. Thus,

although leaf level WUE may be increased, overall canopy water use may not change, or may even increase, in a high CO_2 environment due to increased canopy leaf area (Ceulemans and Mousseau, 1994; Ellsworth *et al*, 1995; Kersteins *et al*, 1995). In addition, in many water-limited systems all available water may be utilised over a longer period of transpiration, despite the increase in WUE. Where the leaf area of woody plants has been measured under high CO_2, there was no evidence of an increased leaf area (Norby and O'Neill, 1991 – with poplar; Korner and Arnone, 1992 - with tropical species) although Norby *et al* (1999) reported an increase in leaf area index (LAI) in Scots pine (*P. sylvestris*) under elevated CO_2 and a greater proportion of the foliage lower in the crown. Ellsworth *et al* (1995) showed little change in stand transpiration or sap flow measurements in 11-year-old *Pinus taeda* under elevated CO_2, concluding that the increase in WUE was due to photosynthetic enhancement rather than reduced water use. Pataki *et al* (1998) similarly showed no CO_2 stimulation effect on water use in young *P. taeda* saplings, although absolute water use increased in proportion to the CO_2 stimulation of foliar and sapwood sectional area.

2.3.5 Respiration

Foliar respiration can be separated into photorespiration (light respiration), which occurs in the chloroplast, and dark respiration, which occurs in the mitochondria (Kersteins *et al*, 1995). Photorespiration is decreased under elevated CO_2 because a greater presence of CO_2 molecules enables them to out compete O_2 for activation sites on the Rubisco enzyme (Ceulemans and Mousseau, 1994). Dark respiration is reduced by approximately 20% in most plants upon exposure to double ambient CO_2, and the suggested mechanism is through a reduced enzyme activity affecting the mitochondrial electron transport system (Drake and Gonzalez-Meler, 1997).

It appears that growth respiration is unaffected by CO_2 concentration whereas maintenance respiration, which has been linked to tissue N concentration (Ryan, 1991; Ryan *et al*, 1996a) is likely to decrease in a high CO_2 environment (Luxmoore *et al*, 1993). The observed decrease in foliar N concentration under

elevated CO_2 could directly affect maintenance respiration through (Luxmoore *et al*, 1993; Drake and Gonzalez-Meler, 1997):

- high CO_2 inhibiting synthesis and activity of respiration enzymes directly;
- end product inhibition;
- interruption to mitochondrial electron transport chain (insufficient N); and
- increase in dark CO_2 fixation by non-photosynthetic carboxylation decreasing overall CO_2 output.

2.3.6 Foliar starch concentration

Many high CO_2 experiments have reported an increase in starch concentration, or an additional cell layer, in foliage exposed to high CO_2 (Korner and Arnone, 1992; Pettersson and McDonald, 1992; Ceulemans and Mousseau, 1994; Pettersson and McDonald, 1994; Curtis and Wang, 1998). This increased starch component results in a lower specific leaf area (leaf area per unit leaf weight), indicating that the carbohydrate allocated to foliage growth, which can be used to make a greater number of thin leaves, or fewer thicker, leaves, uses the latter mechanism. The formation of thicker foliage may also explain the lack of observed increase in leaf area in high CO_2 experiments (Norby and O'Neill, 1991; Korner and Arnone, 1992) although Norby *et al* (1999) have recently questioned the impact of elevated CO_2 on LAI, suggesting that in mature, closed canopy forests LAI is constrained by other environmental factors.

Many of the results described in the preceding sections are based on foliar physiological studies. The majority of physiological studies are short term and may fail to integrate the long-term feedback effects of N cycling and water use changes, which can mitigate the initial larger effects.

2.4 Effects of elevated CO_2 on whole plant growth

Studies of the effects of a doubling in CO_2 on whole plant productivity have produced variable results:

- an increase in dry matter production of 25-50% (Morison, 1990);
- an average increase of 32% in above and belowground biomass based on 70 tree species (Luxmoore *et al*, 1993);
- a 20% increase in biomass in poplar exposed to high CO_2 for 24 weeks (Norby and O'Neill, 1991);
- no increase in aboveground biomass production in a laboratory simulated tropical ecosystem (Korner and Arnone, 1992);
- 38% and 63% increase in aboveground biomass for coniferous and deciduous species respectively based on 83 species of which 18 were coniferous (Ceulemans and Mousseau, 1994); and
- a 20% increase in total biomass in *P. radiata* with a 27% increase in root allocation (Wullschleger *et al*, 1997).

Differences in reported results could relate to different species being studied, differences in the life stages of the trees being studied, differences in the length of exposure to elevated CO_2 or differences in water and nutrient limitations (Mooney *et al*, 1999). This disparity in dry matter response to elevated CO_2 indicates further long-term studies on older trees are needed to enable acclimation and ecosystem feedbacks to be investigated (Norby *et al*, 1999; Cheng *et al*, 2000; Gifford *et al*, 2000).

The following sections briefly describe issues relating to current studies of trees exposed to elevated CO_2.

2.4.1 Seedlings versus mature trees

The majority of investigations into the effects of elevated CO_2 on forest species has been done on seedlings and saplings, as these life stages are easier to work with compared to mature trees. However, seedlings and saplings do not necessarily respond in the same way to an enhanced CO_2 environment as would mature forest systems (Ceulemans and Mousseau, 1994; Ellsworth *et al*,

1995; Kersteins *et al*, 1995). Seedling/sapling experiments are likely to give an upper bound to the response to elevated CO_2 (Luxmoore *et al*, 1993; Norby *et al*, 1999) because they are in a rapid growth stage at the time of high CO_2 exposure. Caution is needed in extrapolating to mature forest systems because:

- mature trees and seedlings differ physiologically (Luxmoore *et al*, 1993);
- up-scaling from leaf level to canopy is difficult because of non-linearity and heterogeneity within a forest system (Jarvis, 1995);
- short-term photosynthetic studies may be totally inadequate to describe temporal changes in native forest systems (Morison, 1990);
- growth limiting factors may change over the lifetime of a forest stand (Gower *et al*, 1996b); and
- mature forest systems may have fully exploited the soil and light environment and may not have the capacity to respond to elevated CO_2 (McGuire *et al*, 1995; Norby *et al*, 1999).

In addition, aging or size related effects, such as decreasing relative growth rate with increasing plant size (Morison, 1990; Norby *et al*, 1999), or leaf area to total plant dry mass ratio decreasing in woody species with age (Kersteins *et al*, 1995; Norby *et al*, 1999), must be accounted for in predicting elevated CO_2 effects on tree growth.

2.4.2 Belowground allocation

The allocation of carbon belowground is the key interaction point between the carbon cycle and the water and nutrient cycles (Norby *et al*, 1999). The reported decrease in foliar N concentration under elevated CO_2 has led to speculation that a greater allocation of carbohydrates to roots would be needed in order to take up sufficient N (McGuire *et al*, 1995; Norby *et al*, 1999). Increase in root biomass under elevated CO_2 has been estimated as:

- averaging 38% for 70 woody plant species (Luxmoore *et al*, 1993);
- 68% in fine root biomass in a laboratory simulated tropical ecosystem (Korner and Arnone, 1992);
- 25-40% in yellow poplar (Norby and O'Neill, 1991);

- 65% increase in root length in one clone of poplar (Taylor *et al*, 1995);
- 135% increase in fine root mass production in 3-year old *P. sylvestris* (Janssens *et al*, 1998)

Pregitzer *et al* (1995) showed an increase in root growth in response to doubling CO_2 at both high, and low, N availability, although Pettersson and McDonald (1992) showed no root biomass response to elevated CO_2 when foliar N was constant, although specific root length increased.

Several workers have emphasised the importance of separating coarse woody root carbon (C) from fine root C (Norby *et al*, 1999; Allen *et al*, 2000; Cheng *et al*, 2000). Elevated CO_2 may increase the allocation of C belowground, but this increase belowground allocation may rapidly be released to the atmosphere through fine root turnover or it may increase the soil C storage in the form of woody roots (McGuire *et al*, 1995; Allen *et al*, 2000).

Other ratios such as root to shoot ratio, leaf area to fine root mass or length ratio have shown various responses to elevated CO_2 depending on the species examined (Ceulemans and Mousseau, 1994; Wolfe *et al*, 1994; Norby *et al*, 1999; Cheng *et al*, 2000). However these static measures of root biomass/length ignore a large carbon flux in the belowground system, related to root turn over, root exudation and respiration and C allocated to symbionts, and thus do not accurately represent belowground carbon allocation (Ceulemans and Mousseau, 1994; Pregitzer *et al*, 1995). Measuring soil respiration, the CO_2 efflux from the soil derived from root, fungal and microbial respiration, provides an indication of the activity of the total soil/root system (Raich and Nadelhoffer, 1989). Thus soil respiration is a useful parameter to measure as both static and dynamic root/soil carbon pools are involved.

It is extremely difficult to quantify a change in root C or C flux associated with root systems in mature forest systems due to large spatial and temporal variability (Luxmoore *et al*, 1993). However, decreased foliar N, stimulated by high CO_2, may lead to greater exploitation of soil resources through increased root biomass or length, or increased symbiotic effort with mycorrhizae (Ceulemans and Mousseau, 1994). Norby *et al* (1999) recently reported that

fine roots are especially responsive to CO_2 enrichment, with increases in fine root density between 60 to 140% in 6 hardwood species.

2.5 Effects of elevated CO_2 on processes affecting the ecosystem

2.5.1 Litter quality

Litter quality influences the carbon and nutrient dynamics of the forest floor and soil. Any decrease in foliar N concentration for trees grown under elevated CO_2 may cause the litter C:N ratio to increase (70 compared to 40 in 2 year old chestnut trees under doubled and ambient CO_2 respectively - Couteaux *et al*, 1991). However, Norby *et al* (1999) in reviewing the effects elevated CO_2 on tree responses indicated that, "elevated CO_2 has not been shown to consistently reduce foliar litter quality of field grown trees". In the laboratory Couteaux *et al* (1991) showed a reduced rate of "non-faunal" decomposition in high C:N litter produced under elevated CO_2, and Cotrufo *et al* (1994) showed that nutrient release from litter grown under elevated CO_2 was slower than ambient CO_2 grown litter, although this varied between species. However, Norby *et al* (1999) indicate that studies which have reported an effect of elevated CO_2 on C:N ratio of litter may be confounded by the nutrient regime used in the study.

If poorer litter quality does result under elevated CO_2, litter decomposition rates may be reduced (Fajer and Bazzaz, 1992) and the long-term availability of nutrients in the soil is also likely to be affected. These long-term impacts of elevated CO_2 on nutrient cycling are of specific concern in modelling studies where impacts over decades and centuries are investigated (Kirschbaum *et al*, 1998; Norby *et al*, 1999).

Zak *et al* (1993) suggested that the greater organic matter input to the soil under elevated CO_2 conditions might stimulate soil C and N dynamics. The C:N of forest soil organic matter in the upper layers is approximately 8 - 20, whereas the C:N of tree biomass averages approximately 60 (Gifford, 1994). It has been suggested that only a slight enhancement of N mineralisation rates could

produce the extra N required by trees grown in elevated CO_2 (Gifford *et al*, 2000). N mineralisation rates are highly dependent on soil temperature and with a predicted increase in mean global temperature with the enhanced greenhouse effect, N availability may naturally increase to satisfy tree requirements (Luxmoore *et al*, 1993; Gifford, 1994; Lloyd and Farquhar, 1996). However N mineralisation is also dependent on soil moisture and an increase in temperature alone, without a concomitant increase in soil water, may not result in greater N mineralisation in seasonally dry environments. Carbon decomposition is also highly reliant on temperature, and soil warming may also accelerate C release from the forest floor and soil, thereby affecting C:N ratios (Bonan *et al*, 1992). Further long-term studies are needed to quantify the effect of soil warming on system level C and N cycles.

2.5.2 Soil respiration

Soil respiration measurements provide information about the entire root/soil system. The CO_2 efflux from the soil is composed of root respiration, microbial/fungal respiration and decomposer respiration. The basic substrate for all respiration is organic compounds and any CO_2 produced is derived from C allocated to the belowground system through litterfall or root and root exudate input. In a laboratory simulated, double CO_2, tropical ecosystem, soil respiration almost doubled (Korner and Arnone, 1992) and Norby (1994) showed a statistically significant increase in soil respiration under elevated CO_2 conditions for both poplar and oak systems. Allen *et al* (2000) recently measured higher soil respiration for 15-year old *P. taeda* in a FACE experiment, but this increase in soil respiration was not statistically significant.

Soil CO_2 efflux could increase under elevated CO_2 conditions through several mechanisms:

- greater root biomass (Luxmoore *et al*, 1993; Norby *et al*, 1999);
- greater root exudates available as a substrate for symbionts or decomposers (Mooney *et al*, 1999);

- greater quantity of litter input through enhanced foliar production in the elevated CO_2 environment (Norby and O'Neill, 1991; Korner and Arnone, 1992); or
- greater biological activity due to soil warming. Soil respiration has been shown to be highly dependent upon soil temperature (e.g. Carlyle and Ba Than, 1988; Keith *et al*, 1997) as are nutrient mineralisation rates. Soil water also impacts both soil respiration and nutrient mineralisation rates.

2.5.3 Nitrogen fixation

It has been hypothesised that N fixation might be increased under elevated CO_2 through increased belowground allocation to N fixing systems (Fajer and Bazzaz, 1992; Gifford, 1994). Norby *et al* (1987) showed that absolute N fixed in an elevated CO_2 environment did increase, but there was no direct stimulation to the root N fixing system (i.e. the relative quantity of N fixed per root mass did not increase). More work is required before the effects of elevated CO_2 on N fixing systems can be quantified.

2.6 Modelling system responses to elevated CO_2

McMurtrie and Comins (1996), using an N-limited model, showed forest ecosystems experiencing an instantaneous doubling of CO_2 resulted in a sharp, transient CO_2 stimulated increase in growth, and a smaller longer term nutrient-limited response. Kirschbaum *et al* (1994), using a similar N-limited model, predict a 19.4% increase in net primary production (NPP) with some nutrient limitations, which corresponded to a 12.4% increase in wood produced. Luxmoore and Baldocchi (1992) also used a nitrogen-limited response and predicted a short-term increase in NPP of between 0-130% but a long term increase in NPP of between 10-50%. Taylor *et al* (1995) predicted that the increased productivity would result in a 30% increase in stem biomass for the CO_2 conditions of the next century. Kirschbaum *et al* (1998) also predicted that fire prone forests, which are dry and nutrient poor, are more likely to respond to an elevated CO_2 system than non-fire prone forest systems.

Lloyd and Farquhar (1996) used an alternative modelling approach which was respiration based, rather than N-limited, to model the effects of elevated CO_2 on forest productivity. They concluded that the response under elevated CO_2 conditions would not be nitrogen-limited, as the N system would reflect the C cycle and acclimate to achieve a similar productivity to the ambient CO_2 system. Specifically the system would adjust to the elevated CO_2 conditions and overall productivity would not be affected.

Model results are highly dependent on the modelling approach and on the assumptions used within the mathematical equations representing physiological processes and ecosystem feedbacks. The agreement of predictions between the models using the nutrient-limited approach is encouraging (Kirschbaum *et al*, 1994; Taylor *et al*, 1995), although actual values may vary as new data are incorporated into the models.

The BIOMASS model (McMurtrie *et al*, 1990a – described in more detail in Chapter 8) has been used in elevated CO_2 simulations. Ryan *et al* (1996b,c) reported results from several physiologically based stand models that simulated forest productivity under doubled CO_2 conditions. BIOMASS predicted similar increases in net primary productivity to the changed conditions over one year and over a rotation of 60 years (Ryan *et al*, 1996c). These net primary productivity predictions altered significantly when a 4^{o}C temperature increase was imposed, with a 30% increase in net primary productivity over one year, but only a 3% increase in net primary productivity after 60 years due to ecosystem feedbacks (Ryan *et al*, 1996c). This difference is largely due to the different time scales of the nutrient and carbon cycles. The coupling of soil processes to tree physiological processes has been significantly improved in more recent versions of BIOMASS, such as that used to run productivity simulations in Chapter 8.

2.7 Summary

The effect of elevated CO_2 on forest productivity is a result of complex feedbacks and interactions between various processes at different scales.

Each limitation or feedback does not act in isolation to all others (Wolfe, 1994; Mooney *et al*, 1999), but it is how each of the processes is experimentally examined. The overall impact of feedbacks on forest growth is likely to reduce the predicted impact of the short-term photosynthetic boost obtained from a doubling of CO_2 (Idso and Idso, 1994; McMurtrie and Comins, 1996). Most systems are either nutrient or water limited and this affects the absolute and relative responses to elevated CO_2 (Poorter, 1993; Norby *et al*, 1999). A more comprehensive understanding of water use and nutrient cycling and uptake by forest trees under elevated CO_2 is needed before predictions of the effects of elevated CO_2 on forest productivity become more accurate.

The experimental work undertaken to date on elevated CO_2 response largely involves comparing ambient and doubled CO_2 environments. This experimentation has been undertaken in order to quantify a response to the predicted level of CO_2 present in at the end of the 21st century (IPCC, 1996), and also to examine the physiological response of plant tissue to a large increase of CO_2. In reality atmospheric CO_2 will continue to increase gradually as it has done over the last 140 years. Photosynthetic systems may have been gradually adjusting to the changing environment and sharp increases in productivity are unlikely.

The belowground system response to elevated CO_2 requires further investigation. The root system is the intersection between the carbon and nutrient cycles and will play a key role in the overall effect of elevated CO_2 on forest productivity. Root systems may become the recipients of greater carbon allocation in a high CO_2 environment in order to capture a greater nutrient mass. Symbionts (mycorrhizae and N fixing species) may also be stimulated under elevated CO_2 and this will increase the C cost of the root system. Quantification of belowground responses is required in mature forest systems to enable better predictions of the effects of CO_2 fertilization on the existing forest estate.

The following chapters describe fieldwork undertaken on the belowground system of a *Pinus radiata* plantation in Australia, which had a range of irrigation

and fertilization treatments imposed. The work was undertaken to understand belowground C allocation in a mature, single species, forest of the same age and at a single site, but showing different productivities. The belowground dynamics examined should provide insight into possible belowground allocation responses under an elevated CO_2 environment.

CHAPTER 3. FIELD SITE DESCRIPTION AND SUMMARY OF PREVIOUS STUDIES AT THE SITE

3.1 Introduction

The Biology of Forest Growth (BFG) field experiment was established in 1983 as a multi-disciplinary project to study the effects of irrigation and nutrition on the productivity of a *Pinus radiata* plantation (Benson *et al*, 1992). The emphasis of the experiment was on understanding the underlying processes controlling forest productivity, with one outcome of the study being a detailed mechanistic model of forest growth called "BIOMASS" (Benson *et al*, 1992; McMurtrie and Landsberg, 1992; McMurtrie *et al*, 1992). A draft of this model was generated at an early stage in the project to help guide measurements required from the field site (McMurtrie *et al*, 1990b; McMurtrie and Landsberg, 1992). Intensive investigation of aboveground responses was undertaken between 1983 and 1988 (Raison and Myers, 1992). Further work, framing the basis of this thesis, and including root investigations, was conducted between 1991 and 1993.

Pinus radiata is the dominant commercial softwood species in the southern hemisphere with a total plantation area of 752,000 ha in Australia (Anonymous, 2000). These plantations cover a range of site types and qualities, most of which are subject to water and nutrient stress (Snowdon and Benson, 1992). The BFG experiment was established on a nutrient poor site that suffers water stress. The experiment manipulated irrigation and fertilization regimes to emulate standard plantation management practices, and also induced treatments that aimed to remove all water and nutrient limitations to the growth of *P. radiata*.

This chapter describes the field site and the major findings of the intensive study period between 1983 and 1988, and also describes the treatments used in the belowground carbon (C) allocation studies.

3.2 Field site

The BFG site is located in Pierces Creek Forest, approximately 20 km south west of Canberra in the Australian Capital Territory (ACT), Australia at 35^{o}21'S, 148^{o}50'E. The experimental site is approximately 620 m above sea level. The site was cleared of original eucalypt woodland in 1934 and planted to *P. radiata* in 1935. The mean annual increment (MAI) in merchantable stem volume for the first rotation was 13.1 $m^3.ha^{-1}$ (Benson *et al*, 1992). This stand was harvested in 1972 and the current *P. radiata* stand of mixed seedling origin was planted in 1973 at approximately 700 stems per hectare. The BFG experiment was established in 1983 when the trees were 10 years old. The site was thinned differentially (35-50% of basal area removed depending on standing basal area) in 1988 at age 15.

Meteorological data were collected on site and are summarised in Figure 3.1. Long term mean annual rainfall (1929-1982) for Pierces Creek Forest is 791 $mm.yr^{-1}$ (Benson *et al*, 1992), with large year-to-year variation. Rainfall occurs throughout the year with a peak in late autumn/early winter. The mean annual rainfall for the decade between 1983 and 1993 was 790mm, showing this period to be typical of the longer term. Monthly average temperatures reach a maximum exceeding 25^{o}C in summer and a minimum of less than 5^{o}C in winter, with frosts occurring on approximately 50% of mornings. The area is characterised by clear skies with an average of 5 sunshine hours in winter and 9 sunshine hours in summer (Benson *et al*, 1992).

The site is underlain by a duplex soil (sandy yellow podzolic, Dy3.61, Northcote, 1979) with a 40cm A-horizon derived from coarse granite (adamellite) (Myers and Talsma, 1992). The B-horizon extends to approximately 1 m and is characterised by poor permeability and high bulk density. The C-horizon consists of fractured granite and is penetrable by roots to a depth of at least 3m. The site is low in both organic matter and nutrient reserves (Benson *et al*, 1992).

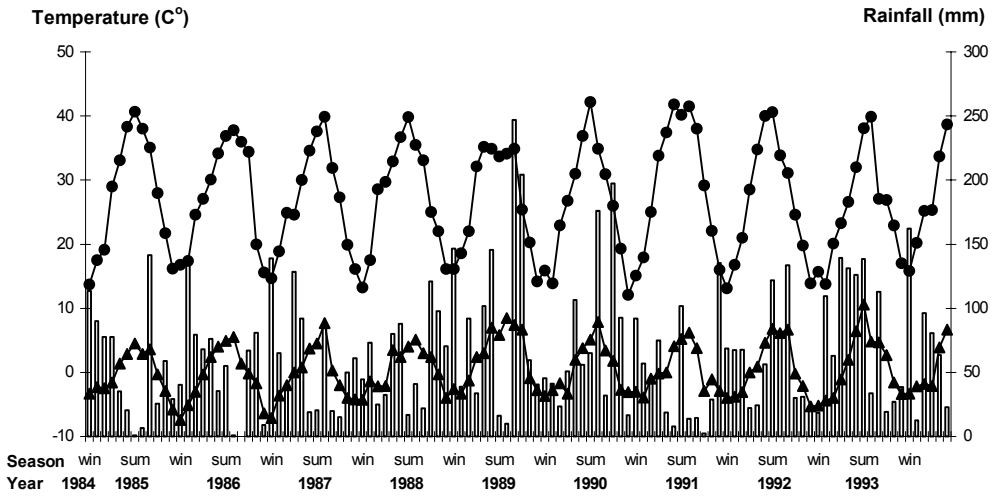


Figure 3.1: Maximum/minimum temperature (circles/triangles respectively) and rainfall (histogram) at BFG for the decade 1983 -1993.

3.3 Experimental design

The majority of treatments at the BFG site were represented by a single, large plot (0.25 ha). Generally treatments were not replicated as the aim of the BFG experiment was not to test differences between treatments at one site, but to study and model the processes of tree growth as influenced by water and nutrient availability (Benson *et al*, 1992). Two additional control plots were established adjacent to the main experiment at the beginning of the studies of carbon (C) allocation belowground in 1991. These additional control plots were smaller in area, being 0.11 and 0.06 ha, respectively.

3.4 Treatments applied

Both water and nutrients were expected to limit growth at the BFG site (Myers and Talsma, 1992), and adding fertilizer and water was expected to produce a large growth response compared to the control stand (Raison *et al*, 1992a). Treatments were selected to cover a range of managerial options or to remove either nutrient, water, or nutrient plus water limitations to growth. The treatments applied were: control (C); once-only solid fertilizer (F); irrigation only

(I); irrigation and once-only solid fertilizer (IF); irrigation and on-going liquid fertilizer (IL) and a sewerage sludge treatment. The sewerage sludge treatment did not increase aboveground growth over the initial 4 years and was not considered as a treatment in the belowground studies. The treatments were initiated in 1983/84 prior to canopy closure. By 1988, when the trees were 14 years old, several treatments had closed canopy. Benson *et al* (1992) provide further details of the treatments.

Each treatment consisted of a single large plot, except for the IL and IF treatments which each had a replicate plot. One replicate of each of these treatments was no longer irrigated after thinning in the spring of 1988. This resulted in 5 combinations of irrigation and fertilization treatments: irrigated without fertilizer (I); irrigated and once-only solid fertilizer with ongoing irrigation (IF+); irrigated and once-only solid fertilizer with irrigation terminated in 1988 (IF-); irrigated and liquid fertilizer with ongoing irrigation (IL+) and irrigated and liquid fertilizer with irrigation and fertilization terminated in 1988 (IL-); in addition to the control (C) and once-only solid fertilizer (F) treatments.

Stands were thinned in 1988 with thinning intensity varying across treatments. Lighter thinning of 30% basal area removed was imposed on stands with a high biomass (IL, IF) because of the perceived risk of excessive windthrow. Other stands had approximately 50% of basal area removed at thinning. Table 3.1 shows the different thinning intensities across the treatments. At this time the sewage sludge treatment, which had shown no increase in growth over the initial 4 years, was left unthinned (U/T). The 10 treatments shown in Table 3.1 were used for the investigations of belowground C allocation undertaken between 1991 and 1993. C1 designates the control plot initiated at the commencement of the study in 1983, C2 and C3 are the two additional control plots established at the commencement of the belowground studies in 1991.

Table 3.1: Summary of nutrients added, thinning intensity and year of establishment for plots used in belowground carbon allocation studies.

Treatment	Year treatment established	Thinning intensity@ (%)	Sum of nutrient added 1983-1994 (kg nutrient. ha^{-1})						
			N	P	K	Ca	B	S	Mg
C1	1983	50							
C2	1991	50							
C3	1991	50							
F*	1983	50	400	200	100	400	10	723	5.8
I	1984	30							
IF+*	1984	30	400	200	100	400	10	723	5.8
IF-*	1988	30	400	200	100	400	10	723	5.8
IL+	1984	30	1800	234	1170	126	3.6	162	151
IL-	1988	30	1200	156	780	84	2.4	108	101
U/T**	1988	0	176	237		2330			

*** fertilizer applied as 2 equal doses of $(NH_4)_2SO_4$ in September 1983 & November 1983**
**** Unthinned treatment received nutrient application in 1983 as 3126 kg organic sludge. Nitrogen applied was organic N.**
@ Differential thinning undertaken in 1988. Values refer to approximate % basal area removed at thinning.

Where solid fertilizer was applied (F, IF+ and IF-) two equal doses were broadcast in September and November 1983 to supply the quantities of nutrients shown in Table 3.1. This application was approximately double the quantity of nitrogen (N) and phosphorus (P) supplied in routine plantation management in the ACT (Benson *et al*, 1992). The liquid fertilizer treatments (IL+ and IL-) comprised regular applications of complete nutrient solution delivered through the irrigation system. Macronutrients were applied weekly and micronutrients every 4 weeks - the quantities varied seasonally to match tree demands and N-additions averaged approximately 300 kgN.ha^{-1}.yr^{-1}, although not all of this N would have been taken up (Benson *et al*, 1992). Because the availability of nutrients exceeded tree demand in the IL+ treatment, the liquid fertilizer additions were stopped in 1990, but irrigation was continued until the end of the belowground studies in 1993. Table 3.1 shows the total amount of nutrients added to each of the fertilized treatments.

The irrigation rate aimed to maintain the soil A horizon at field capacity, thus removing soil moisture as a growth-limiting factor. To achieve this, sprinklers were used to apply the water every 2nd or 3rd night, based on a simple water balance model (Myers and Talsma, 1992).

3.5 Results

The intensive field study between 1983 and 1988 examined various aspects of tree growth including individual needle response, stand canopy response, aboveground productivity and soil N mineralisation processes (Raison and Myers, 1992). Between 1988 and 1991 only basic growth data (diameter at breast height – 1.3m (dbh) and height) and litterfall were measured on each treatment. In 1991 soil respiration measurements were initiated as part of the studies on belowground productivity of the treatments. These studies aimed to complement the earlier work on the aboveground system.

3.5.1 Tree growth

Basal area growth showed a large increase in response to all fertilizer and irrigation treatments from 1984 to 1988 (Table 3.2). Although the differential thinning in 1988 complicates the comparison due to different numbers of trees remaining in each treatment, average basal area increments per tree of the IL+, IF+ and I treatments were 35%, 7% and 10% greater respectively, than the C plot in 1992/93 (see Table 3.2). The F treatment was growing at approximately the same rate as the C treatment.

Table 3.2: Growth achieved and growth rates for selected treatments at BFG.

Treatment	Basal area ($m^2.ha^{-1}$)			Remaining trees ($stem.ha^{-1}$)	Annual basal area increment ($cm^2.tree^{-1}$)
	1983	1988	1993*	1989	1992/93
IL+	13.0	44.3	50.3	412	92
IF+	13.1	41.3	39.2	394	73
I	11.9	31.0	28.3	303	75
C	12.5	25.6	23.6	275	68
F	12.1	26.8	25.1	279	68

*** Basal area was affected by number of stems remaining post thinning**

3.5.2 Nutrient availability

Investigation during the intensive study period (1983 – 1988) showed that tree growth at BFG was not limited by P availability. This was confirmed by the absence of response to P fertilizer (Raison *et al*, 1990) and by the low P fixing capacity of the soil (Khanna *et al*, 1992). N appeared to be the major growth limiting factor at this site (Raison *et al*, 1990).

N mineralisation rates in the 0-40 cm layer of mineral soil were measured between 1983 and 1988 using the *in situ* soil core technique (Raison *et al*, 1987; Raison *et al*, 1992a). Measured rates of N mineralisation showed a seasonal trend, with low mineralisation rates in winter and higher mineralisation rates in summer but always dominated by NH_4^+ -nitrogen (Raison *et al*, 1992a). This indicates seasonal soil activity, which should be reflected in the soil respiration measurements undertaken between 1991 and 1993. Nitrogen mineralisation in the control plot was 35 $kgN.ha^{-1}.yr^{-1}$ in 1983 and declined to 8 $kgN.ha^{-1}.yr^{-1}$ by 1988 indicating a reduction in available N for tree uptake (Raison *et al*, 1992a). All N mineralised in the unfertilized stands was estimated to be taken up by the vegetation (Raison *et al*, 1992a).

N dynamics varied markedly among the treatments (Table 3.3). For example there was a 9-fold difference in N mineralised during 1985-1987 between the

IL+ and C treatments, and a similar difference in N uptake in these treatments in 1987. This increased N availability was manifested as increased foliar N concentration immediately post fertilization and also as increased litter N concentration (Crane and Banks, 1992). The weighted mean N concentration in annual needle fall was highly correlated with estimated N uptake by stands at BFG (Raison *et al*, 1990).

Table 3.3: Aspects of N status for selected treatments prior, during and following the intensive field study at BFG.

Treatment	Cumulative N mineralised 1985-1987 ($kgN.ha^{-1}$)*	Uptake of N in 1987 ($kgN.ha^{-1}.yr^{-1}$)**	Weighted needlefall N concentration (%)		
			1983	1991	1993
IL+	180	57.5	0.61	0.73	0.62
IF+	51	26.0	0.93***	0.49	0.45
I	13	9.4	0.55	0.41	0.42
C1	20	6.0	0.65	0.41	0.45
F	50	24.0	0.80***	0.45	0.47

*** Derived from Figure 8, Raison *et al*, 1992a**
****Derived from Table 2, Raison *et al*, 1992a**
***** High needlefall N concentration as litterfall was produced post fertilization in 1983**

At the initiation of the belowground studies in 1991, the soil N mineralisation rates were unknown. However, due to the ongoing aboveground growth response and the higher litter N status (Table 3.3) it was reasoned that mineralisation remained enhanced at least on the IL+ treatment.

3.5.3 Canopy dynamics

In 1988 at the end of the intensive field study, based on the data available, there were significant differences in canopy biomass, with IL+>IF+>I=C=F, indicating that irrigation and fertilization increased canopy biomass, but irrigation alone, or fertilization alone, did not (Raison *et al*, 1992b, 1992c). These differences were reflected in projected leaf area index (LAI- m^2 leaf area per m^2 ground) measurements taken with a DEMON light interception meter (Lang *et al*, 1991, Figure 3.2). LAI was 2 units higher for IL+ and IF+ than the

control in 1993 (although the interpretation of this difference is complicated by differential thinning undertaken in 1988). Figure 3.2 also shows that the treated stands had not achieved their pre thinning LAI levels 3 years post thinning. Annual litterfall data, presented in Chapter 4, indicate that 1989, the year immediately post thinning, had a relatively high litterfall rate, but in the subsequent years 1990-1992 annual litterfall was similar to litterfall in 1987 which was the year prior to thinning. Hence the lack of an upward trend in the LAI data post thinning in Figure 3.2 is substantiated by the litterfall data.

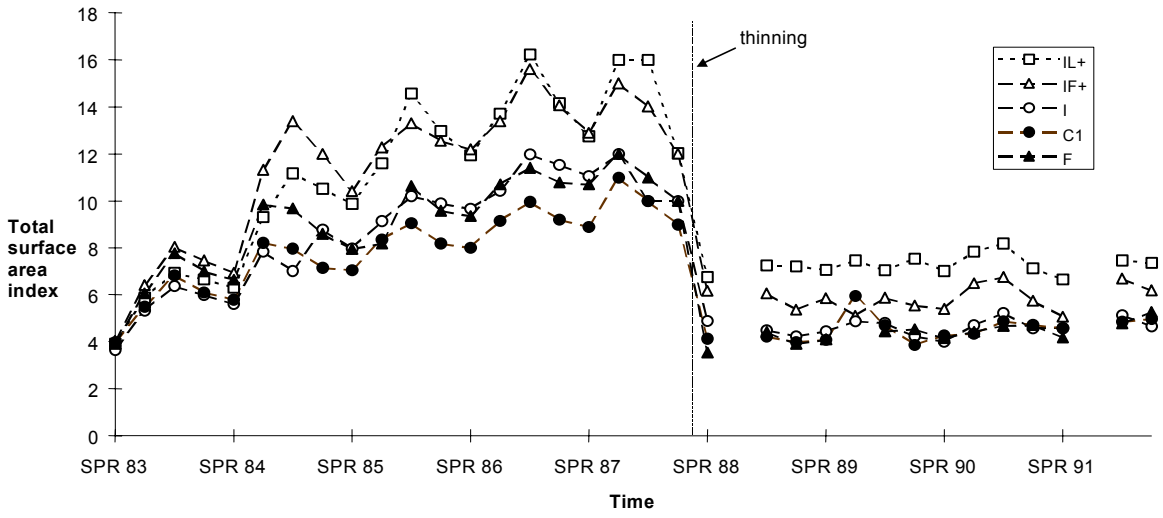


Figure 3.2: Total surface area index for foliage as estimated by the BIOMASS model prior to spring 1988, and measured using the DEMON light interception meter in treatments between 1989 and 1992.

Prior to thinning in 1988, foliage biomass held in the canopy was 50% higher in the IF+ and IL+ treatments than in the C1-control plot (Crane and Banks, 1992). Canopy mass varies throughout the year because new needle production occurs in spring and early summer whilst peak litterfall occurs in winter for irrigated sites and summer on non-irrigated sites (Raison *et al*, 1992c). This variation in canopy biomass was also reflected in seasonal variation in LAI during the year prior to thinning in 1988 (Figure 3.2).

Foliar N concentration was boosted by fertilization for all age classes of foliage measured (Crane and Banks, 1992). With fertilization there was also an increase in the absolute amount of N retranslocated prior to needle senescence, although the proportion stayed approximately the same at 40-50%

of current foliar N concentration (Crane and Banks, 1992). Table 3.3 shows the litterfall N status for 1983 and 1993. It can be seen that while the IL+ treatment maintained a higher N concentration, I has a lower needlefall N concentration than C1, which, according to Raison *et al* (1992b), is an indicator of greater N stress. This increase in N stress in the I treatment is probably due to the irrigation boosting biomass production. However with the available N unchanged, this limited available N must be diluted across the greater biomass, thereby decreasing foliar, and therefore litterfall, N concentration, and increasing N stress.

Thompson and Wheeler (1992) found no difference in net photosynthetic rates of needles in several treatments at BFG although there were large differences in needle nitrogen concentrations. Water availability appeared to affect photosynthesis more than N availability at the BFG site, with irrigated and non-irrigated treatments exhibiting different relationships between assimilation rates and stomatal conductance (Thompson and Wheeler, 1992). Irrigated treatments did show some correlation between photosynthetic rate and needle N concentration during periods of high transpiration (Thompson and Wheeler, 1992).

The canopy dynamics at BFG were intensively studied between 1983 and 1988 because photosynthesis of the canopy drives forest productivity. BIOMASS, the mechanistic model developed at the BFG site, is a canopy photosynthesis model that calculates whole stand productivity.

3.5.4 Modelling

One of the aims of the BFG experiment was to develop a mechanistic model (BIOMASS) of *P. radiata* stand growth. BIOMASS is a mechanistic model of carbon and water balance describing light interception, stomatal conductance and net foliage photosynthesis in relation to light intensity, temperature, relative humidity and CO_2 concentration (McMurtrie *et al*, 1992). Net primary production (NPP) is gross photosynthesis minus growth and maintenance respiration of tree components: stem; foliage; branches and roots. Inputs to

BIOMASS are daily maximum and minimum air temperatures, daily incident photosynthetically active radiation (PAR) and daily precipitation. Stand parameters required for the model include latitude, stocking, LAI, green crown length and average foliar N concentration. Carbon production is calculated daily and allocated monthly (McMurtrie and Landsberg, 1992). BIOMASS estimates belowground carbon allocation using the difference between calculated net primary productivity and C allocated aboveground at the BFG site (Ryan *et al*, 1996b). However the belowground C allocation module in BIOMASS is not sufficiently sophisticated to model belowground dynamics in their own right, and the model outputs of belowground allocation must be interpreted with care.

3.6 Overview

Raison and Myers (1992) summarised the major findings of the BFG experiment (Table 3.4). The upper limit for aboveground NPP was approximately 20tC $ha^{-1}.yr^{-1}$ and aboveground NPP was positively correlated to basal area increment (NPP = 3.5 +1.77 BAI - where units of NPP and BAI are tC ha^{-1} and $m^2.ha^{-1}$ respectively, $r^2 = 0.76$) (Raison and Myers, 1992). It was also found that water and N interacted positively to markedly affect a range of processes and growth. N affected the magnitude of bole growth, but water controlled both the magnitude and seasonal pattern of bole growth, with additional water extending the bole growth period in late summer/autumn. Carbon allocation was also influenced by N status, with an apparent increased allocation to branch growth with solid fertilizer addition without irrigation. This decreased the "harvest index" (ratio of harvestable wood to total wood) in the F plot (Snowdon and Benson, 1992). A limitation of the BFG experiment is the lack of replication of treatments, and so the trends in Table 3.4 can only be used a guide.

Table 3.4: Summary of effects of irrigation, fertilization and irrigation and fertilization compared with the control C1 at BFG (from Snowdon and Benson, 1992)

Stand parameter	Irrigation alone	Fertilization alone	Irrigation and Fertilization
basal area growth	increased (50%)*	increased (24%)*	increased (129%)*

soil mineralisation	unchanged	increased	increased
foliar N	decreased	increased	increased
WUE**	decreased	increased	decreased
NUE***	increased	decreased	decreased
flowering	no effect	no effect	no effect
LUE****	increased	increased	increased
allocation to branches	unchanged	increased	increased

***over 5 years**
**** Water Use Efficiency - aboveground biomass produced per unit water used**
***** Nitrogen Use Efficiency - aboveground biomass produced per unit N used**
****** Light Use Efficiency - aboveground biomass produced per unit light used**

During the intensive field study at BFG no work was undertaken on belowground carbon dynamics. The mass of fine roots was expected to be proportionally greater in the water and nutrient-stressed stands compared with irrigated and fertilized stands (Raison and Myers, 1992). Estimates of fine root biomass were made based on 3 approaches:

- correlation of fine root biomass with foliage mass;
- estimation of belowground C allocation from litterfall C; or
- using the BIOMASS model.

These estimates varied 2-3 fold between the different approaches for the C1 treatment (Raison and Myers, 1992). The lack of actual field measurements did not allow validation of any of the estimates.

3.7 Estimating belowground C allocation

Several methods exist to estimate root biomass and its change in forests including:

- mini rhizotrons (Caldwell and Virginia, 1989);
- counting root tip intersections in cores (Escamilla *et al*, 1991b);
- biomass sampling using sequential intact cores (Santantonio *et al*, 1977; Vogt *et al*, 1983; Escamilla *et al*, 1991a,b); and
- exposing a vertical soil surface and using a transparent wall where root intersections with the wall can be counted (Caldwell and Virginia, 1989).

All of the above techniques involve some form of system disturbance and none easily takes into account root turnover rates or root respiration. In addition the large spatial variation found in root systems requires extensive sampling to ensure that the observed or measured values actually represent the whole system. This spatial variation makes the task of estimating root biomass, and especially root turnover, very difficult (Vogt *et al*, 1998).

Alternatively root biomass can be correlated with aboveground stand characteristics such as basal area (BA) or aboveground biomass, but this also requires some validation of estimates. The validation process will involve site disturbance through one of the direct measurement methods listed above, and will suffer the associated problems of direct measures of root biomass.

Raich and Nadelhoffer (1989) suggested that the annual amount of carbon (C) allocated belowground to root systems could be indirectly estimated by quantifying C release from the soil and forest floor (soil respiration) and subtracting the measured amount of C entering the system as aboveground litterfall. This method is based on the premise that the system is in steady state with respect to soil and litter C, so that on an annual time scale the C flux into this unchanging C pool must equal the C flux out of it. Alternatively, if the system is not at steady state, the annual change in litter or soil C needs to be estimated and taken into consideration. Figure 3.3 is a schematic representation of this model.

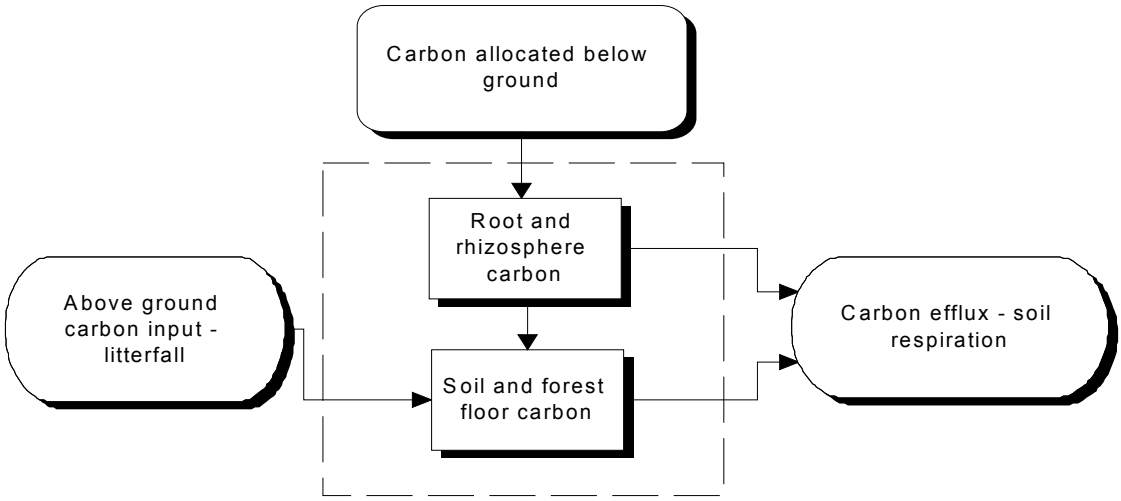


Figure 3.3: Schematic showing Raich and Nadelhoffer's (1989) principle of using soil respiration and litterfall measurements to estimate belowground carbon allocation. If carbon pools within dashed line box are in steady state, flows into must equal flows from it. The principle could still be applied if change within the pools in the box are known and could be corrected for accordingly.

Using this approach, C allocated belowground includes:

- C accumulated in root biomass (both coarse and fine);
- C exudation from roots; and
- any C respired by the roots or symbionts.

Root turnover contributes to this C flux as live roots respire C and dead roots decompose. An appropriate time scale for applying the principle is 1 year, as this enables root turnover to be estimated as CO_2 release after decomposition. This approach does not provide quantitative estimates of change in root biomass, as the C allocated belowground can increment into standing root biomass or be lost as rhizosphere and mycorrhizal respiration.

Raich and Nadelhoffer's (1989) approach requires the accurate measurement of soil respiration and litterfall, and adjustment for any change in root, soil and forest floor carbon. Chapter 4 will examine the assumptions of steady state for soil and forest floor C pools for the BFG field site, and estimate C pools in litterfall and fine and coarse roots.

Investigations into belowground carbon dynamics at the BFG site were commenced in 1991 based soil respiration measurements and litterfall data to

estimate belowground C allocation using the approach proposed by Raich and Nadelhoffer (1989) (Chapter 6). The treatments utilised include the full suite of irrigated, fertilized and irrigated and fertilized treatments available at BFG, and the two additional replicate control plots established in 1991. These measurements were continued for 2 complete years, during which time some direct measures of fine root biomass were also undertaken. Details of this work are given in Chapters 4-7 of this thesis.

CHAPTER 4. ESTIMATES OF LITTERFALL, FOREST FLOOR LITTER, ROOT AND SOIL CARBON POOLS AT THE BFG SITE

4.1 Introduction

In order to fully understand the carbon dynamics at the BFG site, carbon (C) pools and fluxes must be estimated. The C pool and/or fluxes which affect the belowground dynamics include litterfall C, forest floor C, fine and coarse root C and soil C. Each of these pools was measured:

- litterfall C was measured monthly for 10 years (1983 – 1993):
- forest floor standing litter C was measured 5 times - 1983, 1986, 1988, 1991 and 1993;
- coarse root C was estimated from an allometric relationship with diameter at breast height (dbh) for 1992 and 1993 (Jackson and Chittenden, 1981);
- fine root biomass was estimated directly in a selection of treatments in August 1992 and March 1993; and
- soil C was estimated in 1983, 1984 and 1994.

This chapter describes the size and/or change in C pool estimates of litterfall, forest floor litter, fine and coarse root biomass and soil carbon.

4.2 Annual litterfall production

4.2.1 Introduction

As described in Chapter 3 (Section 3.7) litterfall carbon is integral to the estimation of belowground C allocation using Raich and Nadelhoffer's (1989) method. Litterfall collections at BFG commenced in 1984 and were continued until the end of 1993.

4.2.2 Methods

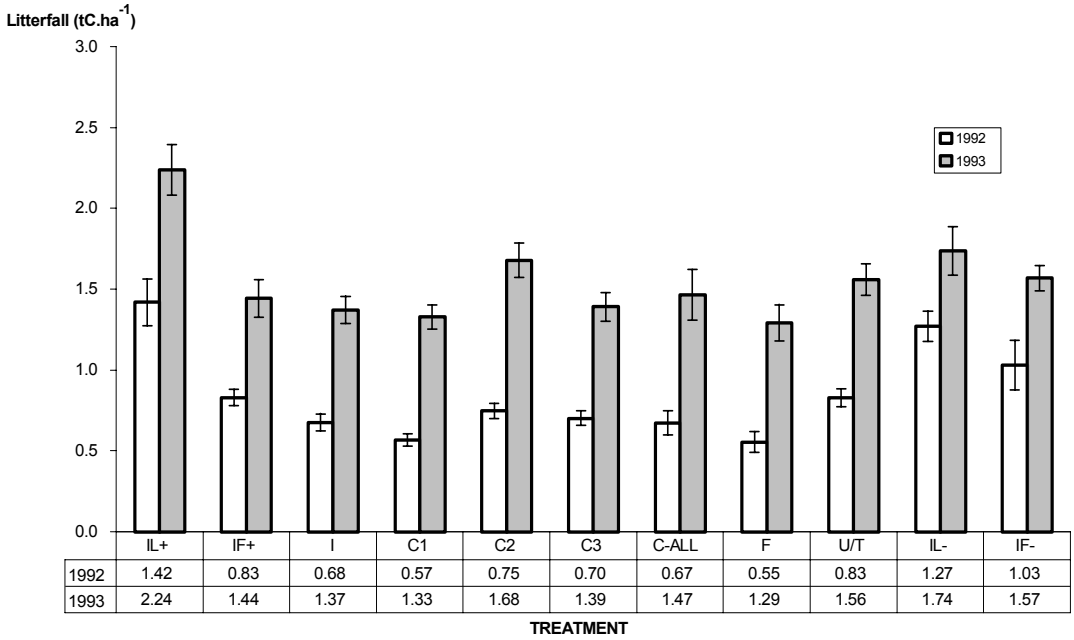
During the belowground C study (1992 and 1993) litterfall was collected monthly from within each of the 10 treatment plots. These collections were a continuation of the litterfall collections commenced in 1984 during the intensive study period, with the additional control plots (C2 and C3) commencing in 1991.

Sixteen 0.5m^2 litter traps were located within each treatment plot, and the samples collected from these litter traps were bulked up to produce 4 samples from each treatment for chemical analysis. Each collection was separated into needle litter, male cones and woody debris, with needle litter comprising the greatest mass of litter.

The biomass of the monthly collections was summed and extrapolated to a per hectare basis to estimate annual litterfall. Litterfall was assumed to be 50% carbon (Raison and Myers, 1992). Litterfall was analysed monthly for N and P using the Kjeldahl method (Heffernan, 1985).

4.2.3 Results and Discussion

Annual litterfall across the treatment plots was approximately 97% greater in 1993 compared with 1992 with the F treatment showing the greatest increase of 135% and the IL- treatment showing the least increase of 37% (Figure 4.1).



	IL+	IF+	I	C1	C2	C3	C-ALL	F	U/T	IL-	IF-
1992	1.42	0.83	0.68	0.57	0.75	0.70	0.67	0.55	0.83	1.27	1.03
1993	2.24	1.44	1.37	1.33	1.68	1.39	1.47	1.29	1.56	1.74	1.57

Figure 4.1: Annual litterfall carbon for 1992 and 1993 for 10 treatment plots at BFG. The standard deviations of the means are shown with standard errors ranging from 6 to 15%. C-ALL is the man of the three control plots (C1, C2 and C3).

Despite these large differences it was difficult to demonstrate significant differences because the data exhibited non-equal variances making standard statistical tests invalid. Additionally the small sample size and lack of replication for most of the treatments made it difficult to demonstrate statistically significant differences. The maximum difference between treatments within any year was 62% between IL+ and F in 1992 and 42% between IL+ and F in 1993.

Figure 4.2 shows the same data as Figure 4.1, with 1993 litterfall C regressed against 1992 litterfall C. The high r^2 value of 0.79 ($P<0.01$) indicates similar processes are affecting litterfall in both years, which provides confidence in the estimates obtained.

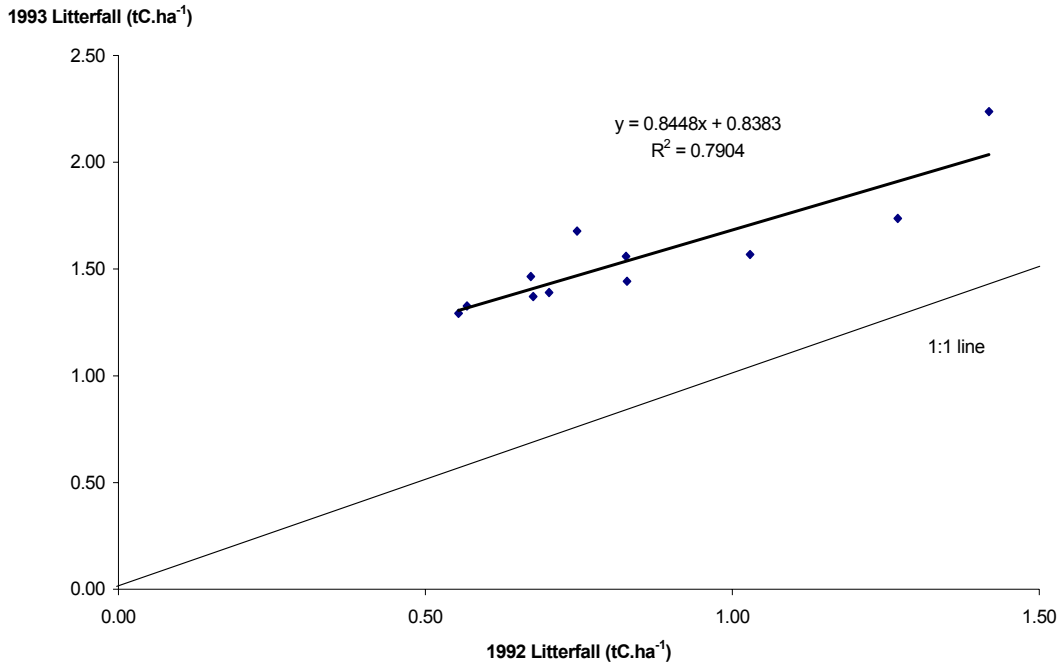
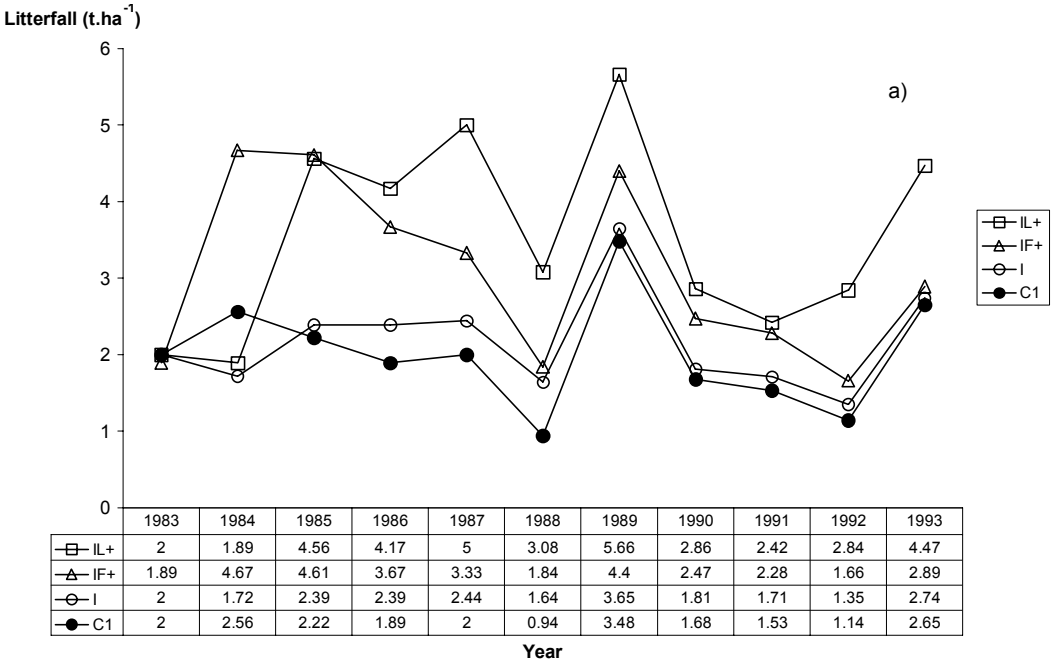
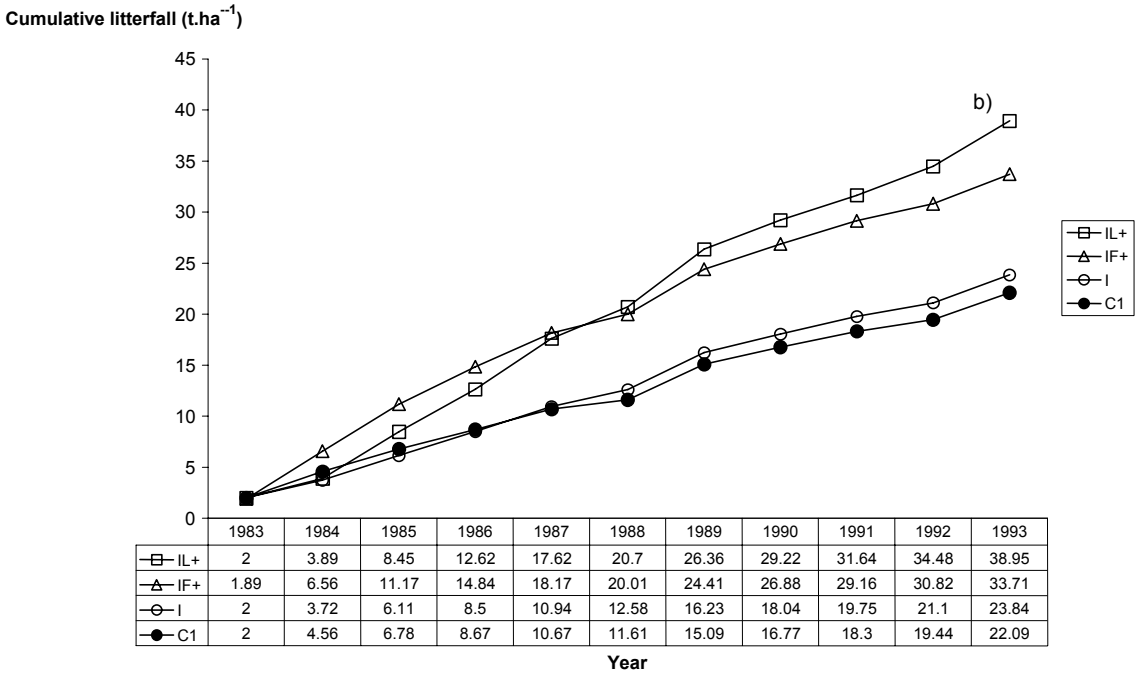


Figure 4.2: Litterfall data for 1992 and 1993 regressed against each other. The high r^2 value of 0.79 ($P<0.01$) indicates similar processes are affecting litterfall in both years.

The annual litterfall values for 1992 and 1993 range from 0.55 –2.24 tC $ha^{-1}.y^{-1}$, and fall within the range of annual litterfall experienced across different treatments at BFG between 1983-1993 (range 0.47 –2.33 tC $ha^{-1}.y^{-1}$ - Figure 4.3a). The cumulative litterfall over this 10-year period varied approximately 2 fold between IL+ and C1 as shown in Figure 4.3b.



	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
IL+	2	1.89	4.56	4.17	5	3.08	5.66	2.86	2.42	2.84	4.47
IF+	1.89	4.67	4.61	3.67	3.33	1.84	4.4	2.47	2.28	1.66	2.89
I	2	1.72	2.39	2.39	2.44	1.64	3.65	1.81	1.71	1.35	2.74
C1	2	2.56	2.22	1.89	2	0.94	3.48	1.68	1.53	1.14	2.65



	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993
IL+	2	3.89	8.45	12.62	17.62	20.7	26.36	29.22	31.64	34.48	38.95
IF+	1.89	6.56	11.17	14.84	18.17	20.01	24.41	26.88	29.16	30.82	33.71
I	2	3.72	6.11	8.5	10.94	12.58	16.23	18.04	19.75	21.1	23.84
C1	2	4.56	6.78	8.67	10.67	11.61	15.09	16.77	18.3	19.44	22.09

Figure 4.3 a) and b): Ten-year litterfall data for selected treatments (IL+, IF+, I, C1) at BFG from 1983 – 1993. a) shows annual values and b) cumulative values. Litterfall is assumed to be 0.50 C content (McMurtrie *et al*, 1992).

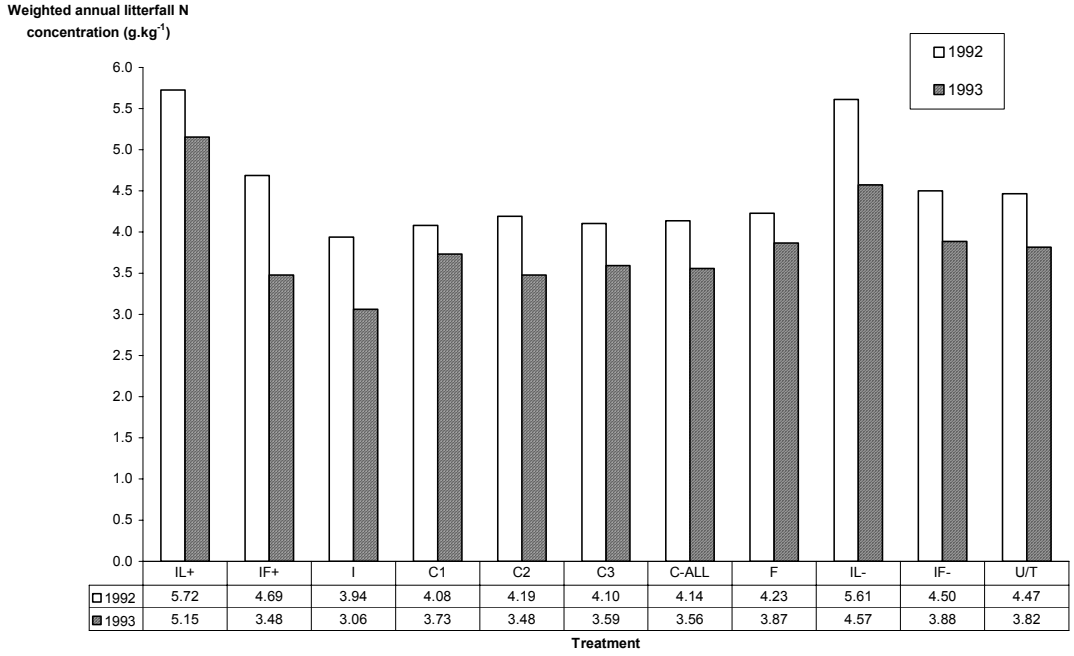
Haynes and Gower (1995) showed litterfall values of 1.10 – 1.87 tC ha^{-1} for a 31-year-old red pine stand in Wisconsin with variations of up to 37% between the years. Other pine forest types showed annual litterfall of:

- 1.8 – 3.2 tC ha^{-1} for 26 year old *Pinus elliottii* in Florida, USA (Gholz *et al*, 1986);
- 1.5 –1.9 tC ha^{-1} for 45 year old *Pinus strobus* in Wisconsin, USA (McClaugherty *et al*, 1985); and
- 0.8 – 2.4 tC ha^{-1} for 23 year old *Pinus sylvestris* in Sweden (Linder and Rook, 1984).

Raich and Nadelhoffer (1989) reported annual litterfall across different forest types, including broadleaf, tropical and needle-leafed forests, ranging from 0.75 tC ha^{-1} to 5 tC ha^{-1}. The wide range of litterfall values worldwide provides confidence in the litterfall values estimated for BFG during 1992 and 1993.

Litterfall N concentration ([N]) was examined closely because previous work (Raison *et al*, 1990) had shown that the weighted mean annual litterfall needle N concentration correlated strongly with N uptake, and, when water availability was adequate, with aboveground biomass production.

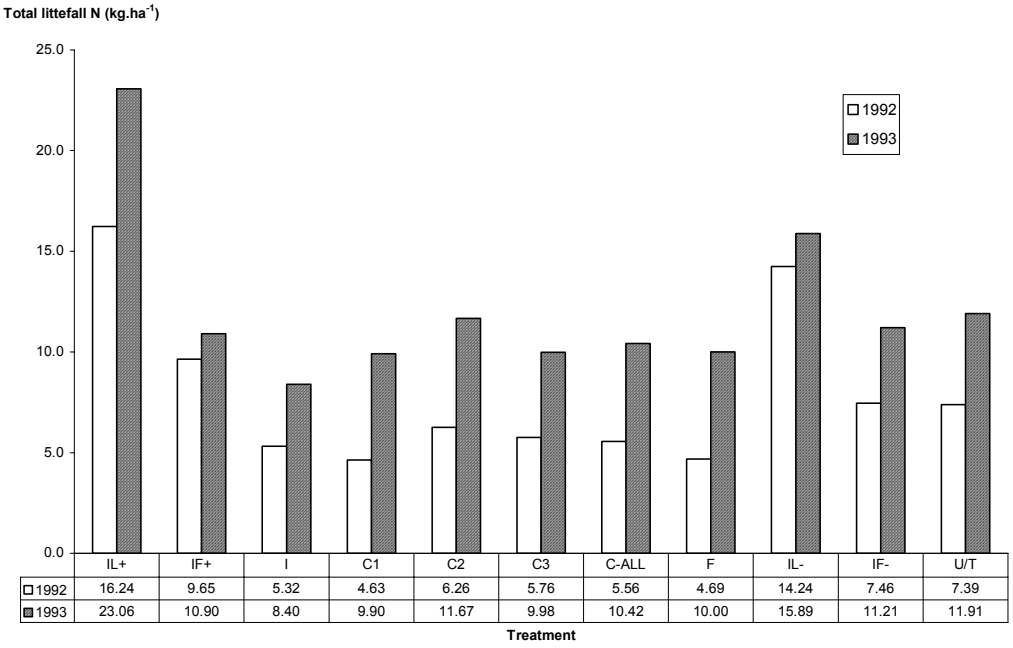
The weighted annual litterfall [N] ranged from a high of 5.72 g.kg^{-1} for IL+ in 1992 to a low of 3.01 g.kg^{-1} for the I treatment in 1993 (Figure 4.4). The IL+ treatment had the highest litterfall [N] for both 1992 and 1993. Similarly the I treatment had the lowest annual litterfall [N] for both years. Litterfall [N] was approximately 18% lower across all treatments in 1993 compared with 1992 (Figure 4.4).



	IL+	IF+	I	C1	C2	C3	C-ALL	F	IL-	IF-	U/T
1992	5.72	4.69	3.94	4.08	4.19	4.10	4.14	4.23	5.61	4.50	4.47
1993	5.15	3.48	3.06	3.73	3.48	3.59	3.56	3.87	4.57	3.88	3.82

Figure 4.4: Weighted annual litterfall [N] for each of the BFG treatments for 1992 and 1993.

The total N in the litterfall is a measure of stand N availability and was also examined (Figure 4.5). This parameter was calculated using the total litterfall mass multiplied by the average weighted annual litterfall [N]. In general there was approximately 70% more N in the litterfall in 1993 compared with 1992, although the IL- and IF+ treatments showed lower increases in the mass of N in the litterfall for 1993. The change in litterfall mass (approximately 97% increase between 1992 and 1993) was largely responsible for the increase in N in the litterfall, although the approximate 18% decrease in litterfall [N] did reduce the overall increase in total litterfall N.



	IL+	IF+	I	C1	C2	C3	C-ALL	F	IL-	IF-	U/T
1992	16.24	9.65	5.32	4.63	6.26	5.76	5.56	4.69	14.24	7.46	7.39
1993	23.06	10.90	8.40	9.90	11.67	9.98	10.42	10.00	15.89	11.21	11.91

Figure 4.5: Total N in litterfall for 1992 and 1993 across all treatments.

Both weighted annual litterfall [N] and total litterfall N were examined with respect to basal area increment for the 10 treatments for 1992 and 1993. Table 4.1 shows the correlations between weighted annual litterfall [N], and total litterfall N against basal area increment for the 10 treatments for 1992 and 1993. There is a distinct difference between the years, with 1992 showing a significant positive correlation between weighted annual litterfall [N] and basal area increment (r^2 =0.78, P<0.01), whereas the relationship between basal area increment and weighted annual litterfall [N] in 1993 is not significant. Where both years' data are combined there is a significant positive correlation between basal area increment and weighted annual litterfall [N], with an r^2 of 0.55, P<0.01.

Table 4.1: Relationship between basal area increment and weighted annual litterfall [N] and total litterfall N for 1992 and 1993

	Litterfall [N]	Total litterfall N
1992	0.78 (P<0.01)	0.84 (P<0.01)
1993	ns	ns
1992 and 1993 combined	0.55 (P<0.01)	ns

*ns = not significant

The relationship between total litterfall N and basal area increment also showed distinct between year differences (Table 4.1). The correlation between total litterfall N and basal area increment was significant for 1992 (r^2=0.84, P<0.01) and not significant for 1993 and the combined 1992 and 1993 data. This analysis indicates significant between year variation in growth and N status of the stands. It would appear that litterfall [N] is a stronger driver of basal area increment than total litterfall N at BFG. This supports Raison *et al* (1990) who also showed that litterfall [N] was related to N uptake and aboveground biomass productivity when water was adequate. As 1992 experienced higher than average rainfall (1008 mm compared to the average of 790mm), there may have been sufficient water to ensure the relationship between litterfall [N] and aboveground productivity persisted.

4.3 Forest Floor Carbon

4.3.1 Introduction

Another important carbon pool affecting soil respiration measurements and the use of Raich and Nadelhoffer's (1989) methodology is the forest floor litter layer. At the BFG *Pinus radiata* site the litter layer is composed mainly of needles, with some twigs and male and female cones. The litter layer is built up by the continual input of litter from the forest canopy and depleted by decomposer activity. Temperature, moisture and the quality of the standing

litter (Singh and Gupta, 1977) influence decomposer activity. When the system is in steady state the annual input of litter approximates the decomposition rate.

At the outset of the BFG experiment in 1983 the plantation was ten years old and canopy closure had not yet been achieved. With the initiation of the treatments in 1983/4 standing litter was measured in the IL+, IF+, I, C1, F, and U/T treatments. To determine temporal change in the standing litter, 5 estimates were made of the accumulated standing litter between 1983 and 1993.

4.3.2 Methods

To measure standing litter, eight randomly located, 0.5m^2 quadrats were sampled in each of the IL+, IF+, I, C1, F and U/T treatments in 1983, 1986, 1988, 1991 and 1993. In 1991 and 1993, at the beginning and end of the soil respiration studies, quadrats were also sampled in the IL-, IF-, C2 and C3 plots. These samples were separated into:

- structural litter - green foliage, dead needles > 2cm in length, male cones;
- decomposed litter - smaller components of needles, decomposing male cones, and
- woody litter - twigs, branches and female cones.

The litter fractions were oven dried at 70^{o}C to constant weight and weights were recorded. C content was estimated as 0.45 of standing litter (McMurtrie *et al*, 1992). Subsamples of the litter were ground and N was measured following Kjeldahl digestion (Heffernan, 1985) by automated colorimetry (Technicon TRAACS – 800, Bran and Luebb Analysing Technologies Inc., 1986). These concentrations were converted to mass of N held in the litter layer for each of the treatments so that C:N ratios of the litter could be examined. These measurements were taken for the 1983, 1986, 1988, and 1993 samples. In 1991 only the C of standing litter was measured.
As different researchers collected the forest floor samples between 1983 and 1993, differences in interpretation between structural litter and decomposed

litter, and in identifying the interface between the litter and soil surface could not be avoided. Thus it was only possible to estimate a single standing litter value comprising both structural and decomposing litter, but excluding woody litter, for each treatment at BFG.

4.3.3 Results and Discussion

4.3.3.1 Forest Floor Litter Mass

Figure 4.6 shows the change in mass of standing litter on the forest floor between 1983 and 1993 for 6 treatments. Over the decade the forest floor has significantly accumulated in all treatments, with the greatest mass of 27.5 $t.ha^{-1}$ (dry weight) occurring in the IL+ treatment in 1993. The litter layer at BFG at age 20 (in 1993) ranged from 11.4 (I) to 27.5 (IL+) $t.ha^{-1}$ which compares with that of 11 to 27 $t.ha^{-1}$ beneath *Pinus radiata* aged 30 - 40 years on a range of soil types reported by Lamb (1976). Under 16 - 20 year old *P. radiata* in New Zealand a litter layer of 18 $t.ha^{-1}$ was measured (Will *et al*, 1983), while under an 8 year old *P. radiata* stand in New Zealand the litter mass was 18.9 $t.ha^{-1}$ (Frederick *et al*, 1985).

The age at which steady state litter mass is achieved is dependent on many factors such as site, soil type, climate, quality of litter and the input of litter (Lamb 1976; Berg *et al*, 1980; Cromer *et al*, 1984). Lamb (1976) suggested that *P. radiata* stands in southern Australia reached steady state at approximately age 30. At BFG the litter layer appeared to approach steady state for the majority of treatments by 1991 at age 18. However the lack of regular litter layer estimates, and the thinning input in 1988 providing an additional input into the litter layer, prevent the accurate determination of the age at which steady state was achieved (Figure 4.6).

Table 4.2 shows the C content of standing litter on all ten treatment plots used in the soil respiration studies between 1991 and 1993. The irrigated and fertilized plots (IL+, IL- and IF+) had the greatest C content in both 1991 and 1993. There was no significant difference for the IL+, IL-, IF-, IF+, I, C1, F and

U/T treatments between 1991 and 1993. There was a significant increase in standing litter C recorded between 1991 and 1993 for C2 and C3 of 3.20 ± 2.30 and 2.67 ± 1.96 tC ha^{-1} respectively. When the three control replicates were averaged the increase in standing litter C of 1.97 tC ha^{-1} between 1991 and 1993 remained significant (Table 4.2). The increase in standing litter in C2 and C3 will need to be adjusted for when determining belowground C allocation using Raich and Nadelhoffer's (1989) approach.

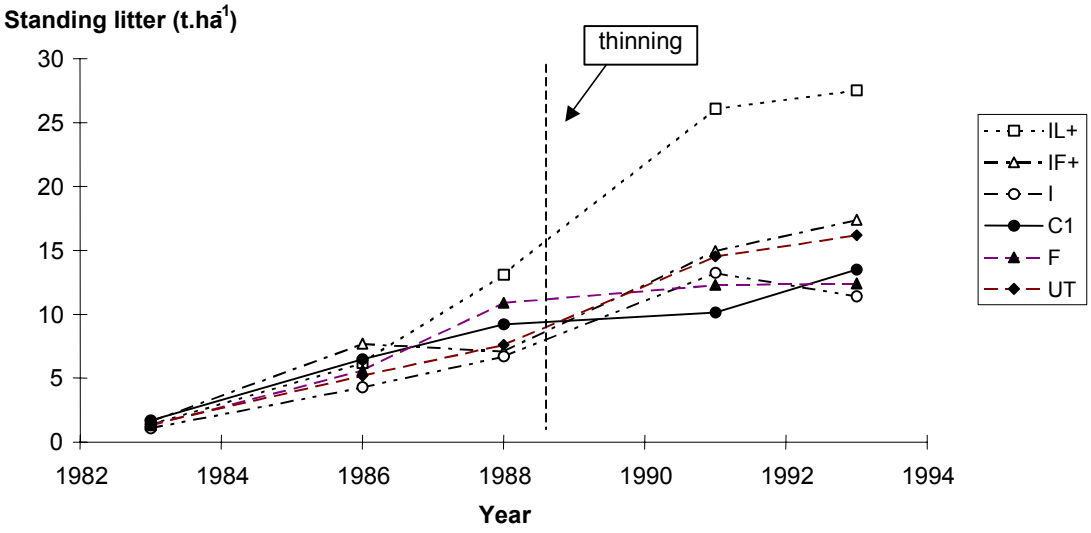


Figure 4.6: Temporal change in standing litter mass under several treatments at the BFG site between 1983 and 1993. Thinning in spring of 1988 provided an additional input into the litter layer.

Table 4.2: Standing litter C content in differently treated BFG stands between 1991 and 1993. Values within each year having the same letters were not significantly different (n=8, P>0.05). C-ALL is the mean of three replicate control plots. C content was estimated as 0.45 of standing litter (McMurtrie *et al*, 1992)

	litter carbon content ($tC\ ha^{-1}$)		
Treatment	**1991**	**1993**	**Change (P>0.05) between 1991 and 1993**
IL+	11.75 a	12.38 a	NS
IL-	11.01 a	11.86 a	NS
IF-	7.98 b	9.42 b	NS
C2	5.41 b	8.61 b	increase
C3	5.44 b	8.11 b	increase
IF+	6.72 b	7.82 bc	NS
U/T	6.54 b	7.29 bc	NS
C-ALL	5.27 b	7.24 bc	increase
C1	4.56 b	6.08 c	NS
F	5.52 b	5.59 c	NS
I	5.96 b	5.14 c	NS

Table 4.3 shows the litter input, litter accumulation and apparent decomposition of the forest floor over the decade 1983 to 1993 for the IL+, IF+, I, C1 and F treatments. The lowest decomposition (39%) occurred in the IL+ treatment which also had the greatest litter input over the decade. This treatment was continually irrigated and received the greatest input of nutrients over the 10 years (see Table 3.1, Section 3.4). The greatest decomposition occurred in the I treatment where 64% of the litter added to the system apparently decomposed. Lamb (1976), Berg and Tamm (1991) and Weinand and Stock (1995) have reported that litter with higher N concentrations have proportionally lower decomposition rates, which coincides with the IL+ treatment litter showing the lowest apparent decomposition rate at BFG (Table 4.3). Cromer *et al* (1984) showed a higher decomposition rate in irrigated compared to non-irrigated 15 year old *P. radiata* stands, which also agrees with the I treatment having the highest apparent decomposition rate at BFG (Table 4.3).

Table 4.3: Litter input, litter accumulation and apparent decomposition between 1983 and 1993.

Plot	mass C balance of forest floor (tC ha^{-1})					
	standing litter 1983	litter input 1983-1993*	input from Thinning**	total input	standing litter 1993@	% decomp#
IL+	0.6	17.52	2.13	**20.25**	12.38	39.0
IF+	0.7	15.17	2.19	**18.06**	7.83	56.6
I	0.5	10.73	3.11	**14.34**	5.13	64.2
C	0.8	9.94	2.92	**13.66**	6.08	55.5
F	0.6	9.96	2.82	**13.38**	5.58	58.3

* measured in litter traps over 10 years (described in Section 4.2)
**estimated from foliage biomass – BA relationship of felled trees (Snowdon and Benson, 1992)
@ standing litter layer measured 1993
# calculated by (total input-standing litter 1993)/total input x 100

4.3.3.2 Forest Floor C:N

The C:N ratio of the forest floor can provide an indication of decomposer activity in the forest floor. An examination of this ratio allows a more in-depth interpretation of standing litter development in the BFG treatments.

The forest floor C:N ratio for the IL+, IF+, I, C1, F and U/T treatments in 1983 and 1993 ranged between 43 - 93 (Figure 4.7). There appears to be a decline in the litter C:N ratios over the decade across all treatments. The litter layer C:N of conifer systems varies widely: 29 for 8 year old *P. radiata* (New Zealand, Frederick *et al*, 1985); 72 for 45 year old mixed stand of *P. palustris* and *P. elliottii* (USA, Lee *et al*, 1983); 84 for 22 year old *P. radiata* (Australia, Baker and Attiwill, 1985) and 89 for 90 year old *P. contorta* (Prescott *et al*, 1992).

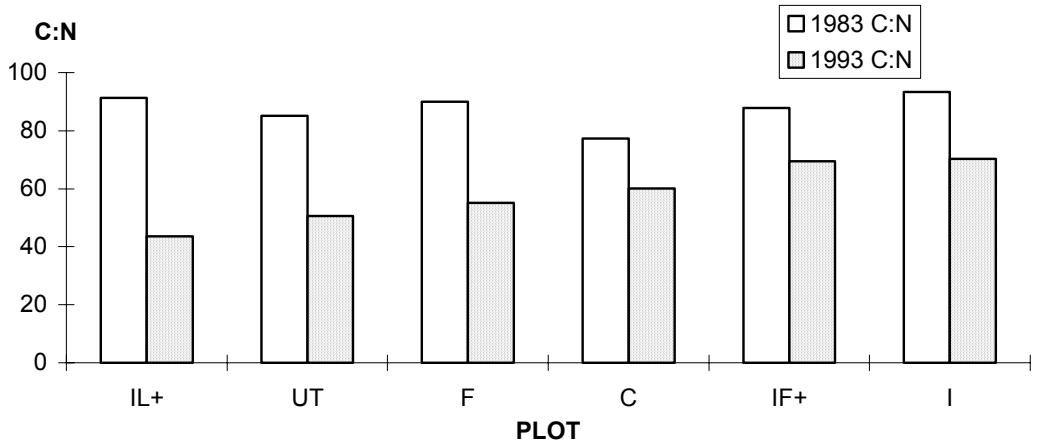


Figure 4.7: The C:N ratio of forest floor litter in IL+, IF+, I, C1, F and U/T treatments in 1983 and 1993. C estimated to be 0.45% of standing litter (McMurtrie *et al*, 1992).

The standing litter C:N of the IL+ and F treatments (the apparent lowest and a relatively high decomposing treatment) was 44 and 70, respectively, in 1993. The C:N ratio of standing litter in C2 and C3 was 51 and 53, respectively, in 1993, which falls between the C:N ratios quoted above for IL+ and F treatments. Both the IL+ and F treatment remained in steady state with respect to standing litter between 1991 and 1993 (Table 4.2), but C2 and C3 recorded an increase in standing litter, despite having C:N ratios within "normal" decomposition ranges.

As the standing litter C did not change over the period 1991 to 1993 for the majority of the treatments, there was no adjustment for changes in forest floor C in belowground C allocation calculations for 1992 and 1993. The increase in forest floor litter in the C2 and C3 treatments, which appears unusual due to the steady state nature of the other treatments, was adjusted for in the 1992 and 1993 belowground C allocation calculations (see Chapter 7).

4.4 Annual coarse root production

4.4.1 Introduction

The Raich and Nadelhoffer (1989) aproach for estimating belowground C allocation includes all belowground respiratory contributions (fine and coarse root respiration, mycorhizal and decomposer respiration) but does not take into

account long-term carbon storage belowground in the form of coarse roots. However, the belowground C picture is incomplete without consideration of the coarse root C pool and this was estimated for BFG between 1991 and 1993.

4.4.2 Methods

Direct estimates of coarse root production at BFG during 1991 and 1993 were not undertaken due to insufficient resources. Preliminary work in 1983 at the BFG site found the biomass of roots greater than 10mm diameter to be between 4.3 and 26.9 kg.tree^{-1} and that these weights were highly correlated with basal area of individual trees (Bent Jakobsen[1], unpublished, 1983). This equated to a coarse root biomass (>10mm) of approximately 11.3 t.ha^{-1} in 1983. An estimate of "fine" root biomass undertaken during this preliminary work in 1983 using a traditional soil coring method was 11t.ha^{-1} for roots <10mm.

Jackson and Chittenden (1981) undertook extensive root biomass sampling in *Pinus radiata* stands in New Zealand to develop a relationship between easily measurable aboveground attributes and coarse root biomass. For roots >2mm diameter a relationship:

$$\text{Weight coarse roots} = 0.00597 \times (\text{dbh})^{2.8068} \qquad r^2 = 0.899$$

(Equation 4.1)

was developed (coarse roots in oven dry kilograms, dbh in centimetres Jackson and Chittenden, 1981). This relationship was based on 97 excavations of young *P. radiata* trees, and verified using 150 additional *P. radiata* trees from range of soil types and fertilities across New Zealand.

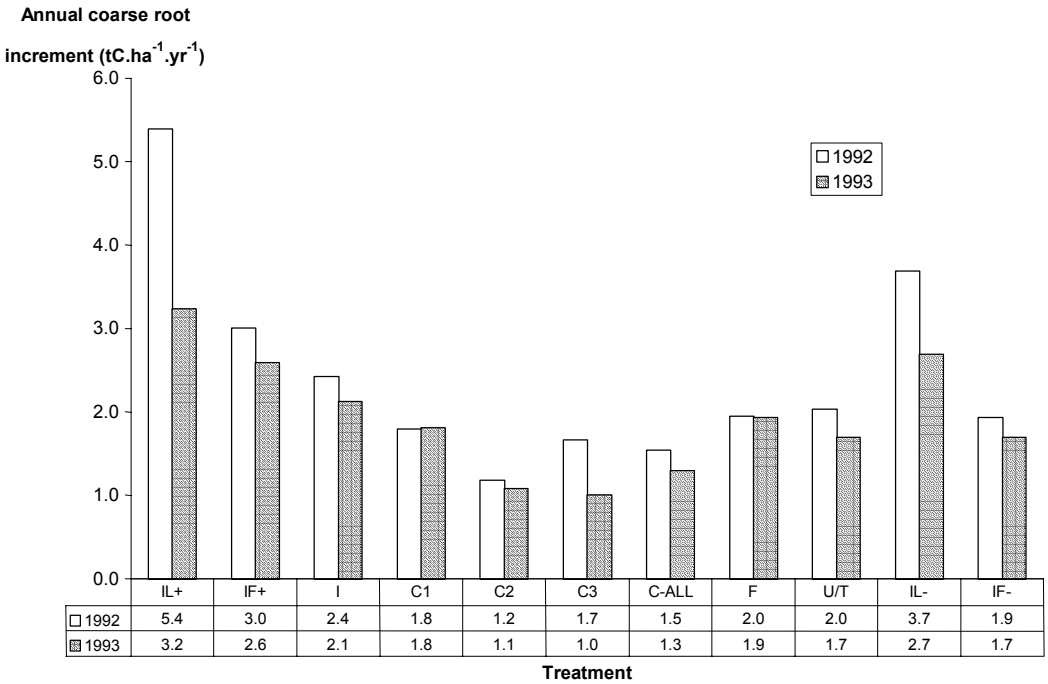
Will (1966) established a similar relationship between coarse root weight and branch weight for 18-year-old *P. radiata* in New Zealand. However this work was based on only 8 trees, and provided quite different results than the Jackson and Chittenden (1981) method. The robustness of Jackson and Chittenden's (1981) approach, which was based on a much larger number of

[1] Bent Jakobsen, CSIRO Division of Forestry, Research Scientist

samples, and the similarity of preliminary results of root work undertaken at BFG (Bent Jakobsen, unpublished, 1983), indicate that this relationship was appropriate to estimate the coarse root biomass of the 10 treatment plots at BFG.

4.4.3 Results and Discussion

Coarse root production for 1992 and 1993 is shown in Figure 4.8. Coarse root production in 1992 ranged from 5.4 to 1.2 tC ha^{-1} for the IL+ and C2 treatments respectively, and from 3.2 to 1.0 tC ha^{-1} for the IL+ and C3 treatments respectively in 1993. Coarse root production generally decreased in 1993 compared with 1992, however this could not be statistically tested because only a total coarse root biomass for each treatment could be calculated. Large differences occurred between treatments and this was proportional to stand annual basal area increment.



	IL+	IF+	I	C1	C2	C3	C-ALL	F	U/T	IL-	IF-
1992	5.4	3.0	2.4	1.8	1.2	1.7	1.5	2.0	2.0	3.7	1.9
1993	3.2	2.6	2.1	1.8	1.1	1.0	1.3	1.9	1.7	2.7	1.7

Figure 4.8: Coarse root production for 10 treatments for 1992 and 1993 calculated using Jackson and Chittenden's (1981) relationship between dbh and coarse root weight (> 2mm diameter). Coarse roots assumed to be 0.5 C (McMurtrie *et al*, 1992).

Other research has shown annual coarse root productions of:

- 0.2 – 0.45 tC $ha^{-1}.y^{-1}$ for roots greater than 5 mm in diameter in *Pinus contorta* (Comeau and Kimmins, 1989);
- 0.3 – 0.45 tC $ha^{-1}.y^{-1}$ for roots greater than 10 mm in *Pinus resinosa* in Wisconsin, USA (Haynes and Gower, 1995);
- 1.25 – 1.35 tC $ha^{-1}.y^{-1}$ for roots greater than 2 mm diameter in Douglas fir (Keyes and Grier, 1981);
- 0.35- 0.8 tC $ha^{-1}.y^{-1}$ for roots greater than 5 mm *Abies amabilis* in Washington, USA (Grier *et al*, 1981); and
- 0.7 - 1.9 tC $ha^{-1}.y^{-1}$ for roots greater than 5 mm in 7 – 11 year old *Pinus radiata* in New Zealand using Jackson and Chittenden's (1981) relationship (Beets and Whitehead, 1996).

Coarse root production was significantly greater at BFG compared to other published values of coarse root production. One of difficulties in comparing root data involves the different definitions of coarse root production (roots greater than 5 mm or greater than 2 mm in diameter) and in the extensive differences in root systems between species - both between genera and between other *Pinus* species. Apart from the New Zealand estimates (Beets and Whitehead, 1996) destructive harvesting of root systems were used to derive the coarse root estimates quoted above.

The proportion of coarse root production to stem wood production in the data cited above varies from 4.8% in the *Pinus contorta* (Comeau and Kimmins, 1989) to 62% in *Abies amabilis* (Grier *et al*, 1981). This wide range is likely to be due to differences in coarse root production at different life stages within the stand, site differences and differences between species. The proportion of coarse root to stem wood production was not estimated at BFG during 1991 and 1993 due to lack of specific allometric relationships for the site.

4.5 Estimate of fine root biomass

4.5.1 Introduction

Soil respiration studies undertaken between 1991 and 1993 at BFG indicated treatment and seasonal differences in soil respiration estimates (Chapter 6). Soil respiration is comprised of root, symbiont and decomposer respiration and in order to help partition soil respiration into that derived from fine root respiration and that due to other sources, fine root biomass was estimated at contrasting periods and across at least 3 treatments.

4.5.2 Methods

Fine root biomass was estimated from samples collected by soil cores. Preliminary studies using cores of 51mm internal diameter and 40cm in length sampled in August 1992 indicated that 85% of the fine root biomass (<2mm diameter) was located in the upper 20cm of soil and that 12 cores per treatment plot provided a standard error of 10% in fine root biomass estimates.

Fine root biomass was sampled in August 1992, at a time of low soil respiration and again in March 1993 when soil respiration was high (Chapter 6). In August 1992 two high soil respiration plots (C1, I) and a low soil respiration plot (IL+) were sampled with 12 cores taken at random from each selected treatment. In March 1993 six treatments: IL+, IF+, I, C1, F and U/T were sampled using the same protocol.

Intact soil cores were returned from the field and separated into three depths:

1. litter – 0.05 m
2. 0.05 m – 0.10 m
3. 0.10 m – 0.20 m.

Roots were extracted from these samples using a floatation root washing machine. Roots and litter were captured on the fine mesh while the soil washed away. Each sample was labelled and frozen for later sorting into the following 4 diameter size classes:

1. < 0.5 mm;

2. 0.5 – 1.0 mm;
3. 1.0 – 2.0 mm;
4. >2.0 mm;

and 3 viability classes:

1. live/white;
2. live/brown
3. dead.

This resulted in 12 possible classes for each root sample and 432 possible root samples (12 cores x 3 depths x 4 root diameters x 3 viability classes) from each treatment. Each sample was oven dried to constant weight for 24 h at 70^{o}C and weighed. The mean weight of each class for each treatment was calculated, not on an ash free basis, and the fine root biomass was scaled up to per hectare values.

Some chemical analysis of white, brown and dead root samples from 0-0.05m and 0.05-0.1 m depth classes from both sampling periods was undertaken. Nitrogen (N) was assessed following Kjeldahl (acid) digestion (Heffernan, 1985) and automated colorimetry (Technicon TRAACS - 800, Bran and Luebb Analysing Technologies Inc., 1986), and multiplied by root biomass to provide estimates of root N content in kilograms per hectare.

Direct measures of fine root respiration were undertaken using an IRGA at the BFG site in 1993 (Ryan *et al*, 1996a) and this provided a basis for estimating contribution of fine roots to total soil respiration. In the field Ryan *et al* (1996a) placed samples of intact smaller roots in a cuvette attached to the IRGA and measured the increased CO_2 concentration over time within the cuvettes. Once the field measurements were completed the roots contained within the cuvette were detached from the main root system, and taken to the laboratory for drying, weighing and chemical analysis.

4.5.3 Results and Discussion

The fine root sampling in August 1992, during a period of low soil respiration, and again in March 1993, during a period of high soil respiration, provided an indication of the variation in fine root biomass throughout the year.

Figure 4.9 shows the total mass of fine roots <2.0mm in each sampled plot at both sampling periods. Fine root biomass for the IL+, I and C1 treatments was lower in March 1993 compared with August 1992, with the greatest reduction of 27% in the C1 treatment. March 1993 was a period of high soil respiration, so the lower fine root biomass could indicate a limited contribution of fine roots to total soil respiration.

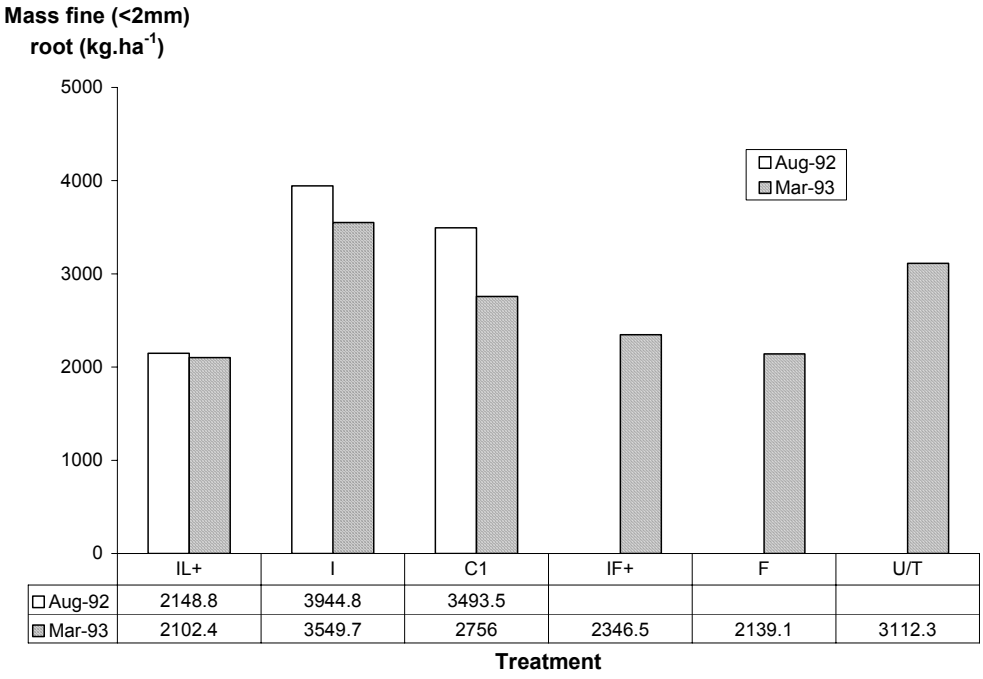


Figure 4.9: Mass of fine (< 2.0mm) roots across several treatments in August 1992 and March 1993. The mass shown combines white, brown and dead roots down to a depth of 0.20 m.

Figures 4.10 a) and b) show the biomass of the 3 types of fine roots in the < 0.5mm diameter class. In August 1992 (Fig 4.10a), a low soil respiration period, the contribution of the white type to total fine root biomass was less than 10% for all three treatments. In the C1 treatment biomass was dominated by dead fine roots, the I treatment had a greater mass of live/brown fine roots, and

the roots in the IL+ treatment were equally distributed between live/brown and dead roots. In March 1993 (Fig 4.10b), a high soil respiration period, the contribution of the white roots was still minor, but live/brown roots dominated the remainder of the root biomass in all treatments. The impact of differing moisture conditions in the treatments at the time of sampling may have influenced the rate of soil andor fine root respiration per unit mass.

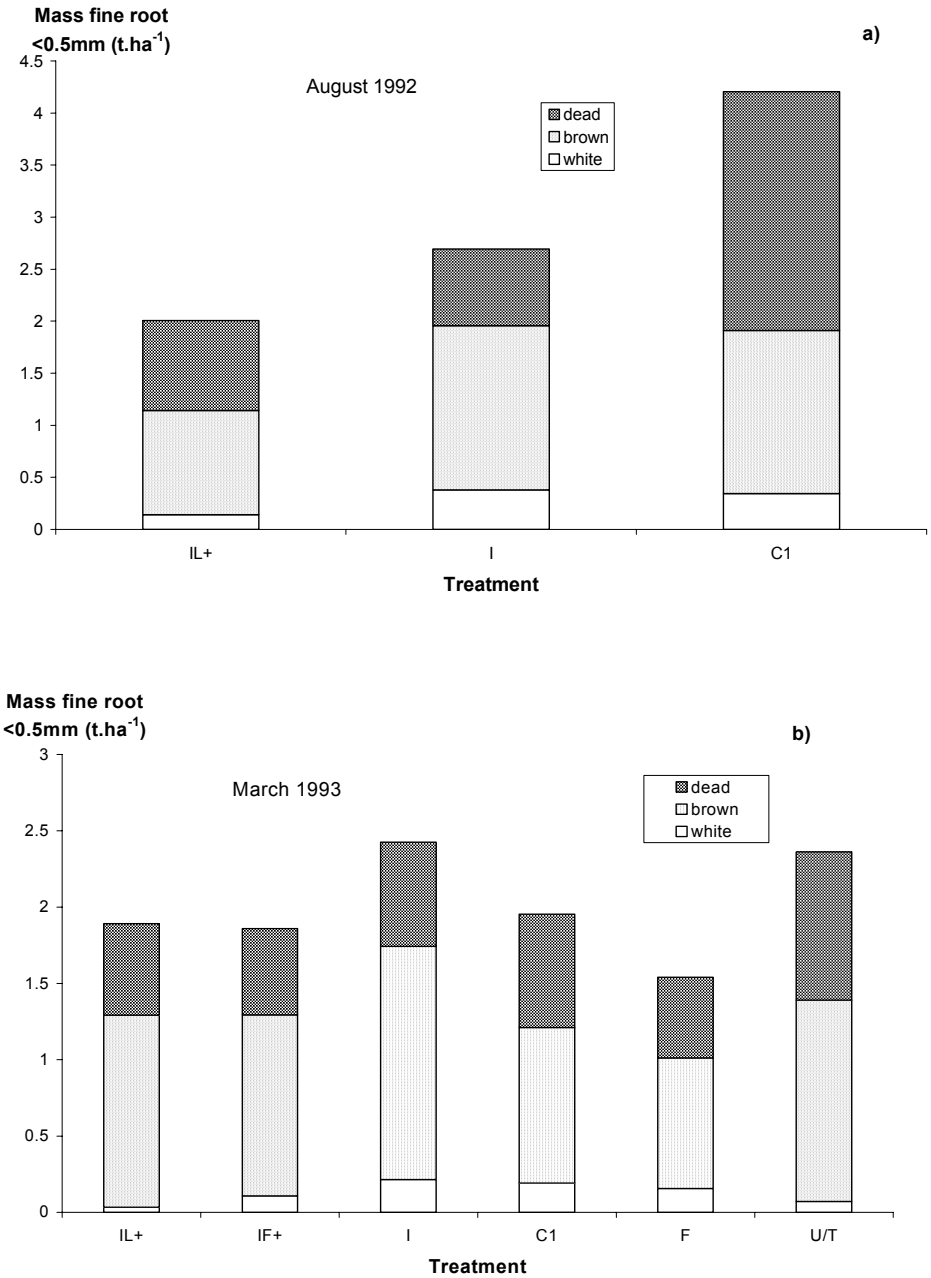


Figure 4.10 a and b: Fine root mass less than 0.5mm diameter across all treatments in August 1992 (a) and March 1993 (b). Roots are distinguished into white, brown and dead root types. Note the reduced scale in (b) compared with (a).

White, brown and dead roots less than 0.5 mm diameter were analysed for nitrogen concentration [N] (Table 4.4). The limited data makes it difficult to distinguish statistically significant differences. The white roots had an [N] approximately 50% that of the brown and dead roots. The brown and dead roots showed no difference in [N].

Table 4.4: Mean nitrogen concentrations (mgN.g^{-1}root) for fine roots <0.5mm diameter down to 10cm depth for sampled treatments in 1992 and 1993. Standard deviation of the mean is shown in parentheses.

	Live (white)		Live (brown)		Dead	
	August 92	**March 93**	**August 92**	**March 93**	**August 92**	**March 93**
IL+	4.046 (0.29)	4.687 (-)	10.985 (1.67)	11.455 (1.42)	12.905 (0.89)	12.655 (0.92)
IF+		4.499 (0.24)		8.327 (0.69)		8.636 (0.75)
I	4.352 (0.51)	5.268 (0.77)	7.130 (0.70)	6.156 (1.19)	7.887 (0.63)	7.124 (0.51)
C1	5.186 (0.45)	5.955 (0.36)	8.251 (1.31)	8.580 (0.71)	9.288 (0.86)	8.659 (0.90)
F		5.441 (0.72)		9.952 (1.51)		10.181 (0.83)
U/T		6.767 (0.47)		7.976 (1.53)		8.636 (1.33)

The spot estimates of fine root biomass, taken on a limited number of treatments at BFG in 1992 and 1993, provided some information relating to the link between soil respiration and actual root biomass. Fogel (1983) pointed out the limitation of spot measurements of fine root biomass in determining annual trends, and that the labour involved in obtaining these spot estimates does not justify the limited information to be obtained from the results. Nambiar (1983) showed that fine root density was independent of distance from stem by age 2 or 3 in *Pinus radiata* stands in sandy soils, so that random selection of soil cores should have captured the inherent variation across the site.

There is a major difficulty in comparing root biomass estimates from different studies due to the non standard definitions of fine roots. Biomass of fine roots (<2mm) estimated at BFG ranged from 2.1t.ha^{-1} (IL+, March 1993) to 3.9t.ha^{-1} (I, August 1992). There appeared to be a decrease in fine root biomass between August 1992 (period of low soil respiration) and March 1993 (high soil respiration). Santantonio and Hermann (1985) did not find any seasonal changes in fine root biomass in a Douglas fir forest, but this may have been obscured by the natural variation across the site. The BFG root data also exhibited large variation, and statistical tests could not show significant differences either between the sites or within the two measurement periods. Santantonio and Hermann (1985) also found no difference in biomass of live fine roots across dry and wet sites, but found a much larger mass of dead fine roots on the dry site, which is corroborated by the data at BFG, where in August 1992 the C1 treatment was dominated by dead roots compared to the irrigated plots (IL+ and IF+, Figure 4.10a). In the March 1993 sampling, the proportion of dead roots to total root biomass in the non-irrigated plots was 38% compared to 30% in the irrigated plots (Figure 4.10b).

The BFG data showed that [N] from the IL+ treatment was higher than those from the I and C1 treatments, but there was little difference in the [N] of any of the root viability classes between the August 1992 and March 1993 samples. Nambiar (1987) also found no seasonal pattern in N concentration of fine roots, nor difference in [N] of live and dead fine roots. There was little difference in the biomass of fine roots in the irrigated plots (IL+ and I) between the two sampling periods, whereas the fine root biomass in the C1 plot was reduced by 27% between August 1992 and March 1993.

The limited root data at BFG makes it difficult to define any general relationships between easily measurable parameters at BFG and fine root biomass. A thorough examination of fine root biomass at BFG would have involved many more sampling periods in order to capture maximum and minimum biomass and root turnover, and limited resources prevented this occurring. The Raich and Nadelhoffer (1989) model to estimating belowground C allocation overcomes the difficulties in capturing the changes in fine root

biomass by treating the fine root biomass as a “black box” and estimating the flux difference between C inputs and losses.

4.6 Soil Carbon

4.6.1 Introduction

The Raich and Nadelhoffer (1989) model of estimating belowground C allocation assumes soil C is in steady state. To validate this assumption, soil C was measured for the treatments at BFG. Measuring soil carbon in the forest is not in itself a difficult task given modern instruments, but the large spatial variation in field samples makes it difficult to quantify a temporal change in soil C (Ruark and Zarnoch, 1992), where short-term changes in soil C are difficult to detect against background values. The BFG field site was established in 1983, and for this reason trend in soil C was evaluated over an eleven-year period (1983 –1994) at BFG. Data were used to infer possible change in soil C during the 2-year period when soil respiration was monitored.

4.6.2 Methods

Three estimates of soil C were taken at the BFG site.

1. Soil C was measured when the BFG soils were characterised during the site survey stage prior to the treatments being applied in 1983. This was undertaken for the IL+, IF+, I, C, F and UT proposed treatments, and employed a random sampling of 24, 0.4 m cores across the identified treatments. Three cores were bulked to give a total of 8 samples per plot that characterised the soil prior to treatments being applied. This data is referred to as survey data.

2. In 1984 a more complete reference study of soil C was undertaken. Four 2x2m permanent subplots within each of the main treatments were isolated and six, 0-30cm cores were taken from within each of these subplots. Thin walled cores were used to prevent compaction within the core and to

provide accurate bulk density estimates. These cores were separated into five depths: 0-0.25; 0.25-0.5; 0.5-0.10; 0.10-0.20 and 0.20-0.30 m, and three cores bulked to give 2 samples for each subplot, and a total of 8 representative samples from each treatment. Ruark and Zarnoch (1992) showed that bulking soil samples maintained accuracy in measured soil parameters while reducing the number of samples to be processed. The sites of core extraction were marked for future reference.

The samples were air dried and sieved through a 2 mm screen. The total weights of both fine (< 2mm) and coarse (> 2mm) fractions were measured, gravimetric moisture content was determined by drying to a constant weight at 105^{o}C and subsamples were finely ground for C analysis. Soil carbon was measured using combustion methods.

3. In October 1994 the reference subplots within the treatments sampled in 1983 (IL+, IF+, I, C, F, UT) were relocated. A sampling similar to that described above was repeated, taking care to avoid the locations initially sampled. Four 2x2m subplots were located on the other four treatments used in the soil respiration studies (IL-, IF-, C2, C3), and six, 0-0.4 m cores were taken in each. A modified electric jackhammer was used to collect the cores. The cores were again separated into depths 0-0.25; 0.25-0.5; 0.5-0.10; 0.10-0.20, 0.20-0.30 and 0.30-0.40 m and three cores were bulked to give a total of eight samples by six depths per treatment. These samples were passed through a 2 mm sieve, roots >1mm diameter were removed and weighed, weight of fine (<2mm) and coarse (> 2mm) fractions, and moisture content were measured. A sample of the fine soil (<2mm) was ground and used to measure soil C using combustion methods (LECO CHN - 1000, Leco Corporation, 1991).

4.6.3 Results and Discussion

Figure 4.11 shows the total soil carbon to a depth of 0.3 m for different treatments in 1983 with site survey data, in 1984 with reference soil samples and in 1994 when reference soil samples were resampled. There is no statistical difference (P>0.05) between the 1984 and 1994 sampling periods for any treatment. There was an apparent (but not significant) large increase in carbon in the F treatment over the ten years from 23.51 to 35.83 tC ha^{-1}. However there is some possibility of an error in 1984 data for the F treatment. The 1983 soil survey samples for the F treatment gave total soil carbon to depth of 0.30 m of 36.93 tC ha^{-1}, which is very similar to the 1994 value (Figure 4.11). Survey sample soil C contents for the other treatments are similar to the 1984 reference soil values (Figure 4.11). Because of the discrepancy in soil carbon between the survey (1983) and reference (1984) data for the F treatment, it is not clear whether the soil C in the F treatment has changed over the period 1983-1994. A change seems unlikely given the relatively stable soil carbon in all other treatments over the decade, despite a large increase in aboveground biomass.

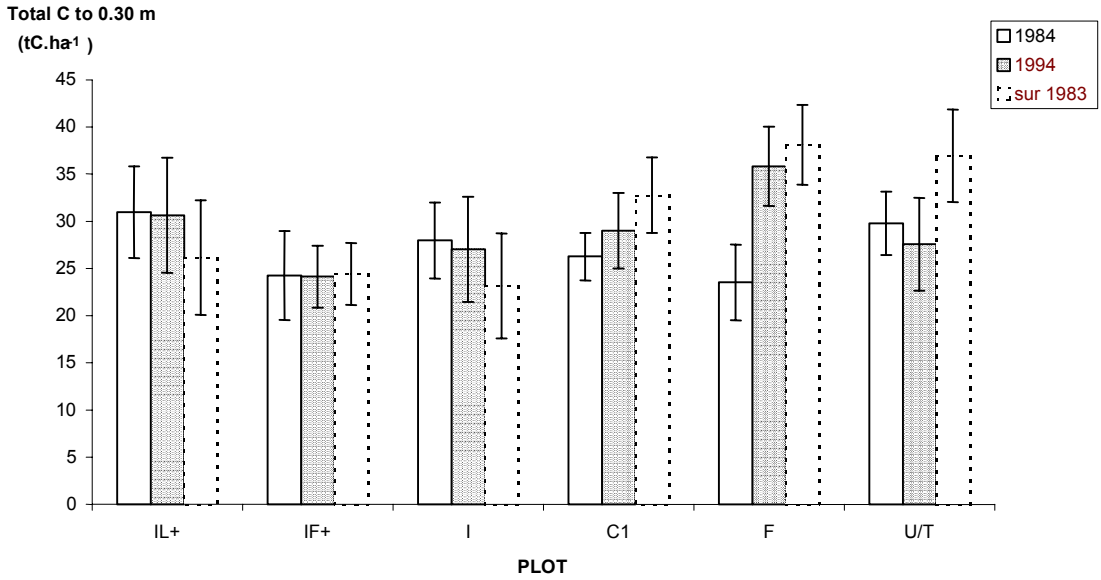


Figure 4.11: Soil carbon content to depth of 0.30 m for IL+, IF+, I, C1, F and U/T treatments in 1983 (dashed bars), 1984 (clear bars) and 1994 (shaded bars). Standard deviations are also shown. Dashed line bars represent the 1983 survey soil C content.

Johnson (1992) concluded that an increase in soil C concentration with fertilizer application is usual, but this did not occur in the sandy soils at BFG. Soil C may be increased by the incorporation of litter C and root C into the soil system, and soil C is decreased by increased decomposition. Substrate quality, and environmental conditions such as temperature, moisture and soil pH, influence the soil microbial population dynamics (Singh and Gupta, 1977; Johnson, 1993). Fertilization is likely to enhance litter inputs (volume) and quality (litterfall [N]) and thus will increase the rate of C turnover in the soil system. However soil C will only increase in the long term if the soil has the capacity to "protect" additional C from microbial degradation, and this is related to which C pool ("bound" or labile) the added C enters (Parton *et al*, 1987).

Carlyle (1995) reported a mineral soil carbon content of 30.2 $t.ha^{-1}$ to 0.30 m depth in a duplex soil (yellow podzol) which is similar to that found at BFG. In an earlier study Carlyle (1993) showed that in sandy soil systems 70% of soil C was present as chemically stable compounds and that only 30% of soil C was non-stable, labile C. Because an increase in soil C is likely to occur only in the labile C pool in sandy soils, the added C may not be enough to be detected as an increase in soil C (Carlyle, 1993). This may explain why there is no change in measured soil C at BFG over 10 years despite a large increase in aboveground biomass.

The overall conclusion from this study is that soil C change on an annual basis is likely to be very small at the BFG site and showed no particular trend. Thus no correction was made for soil C change when applying Raich and Nadelhoffer's (1989) approach in estimating belowground allocation of carbon.

4.7 Conclusions

Litterfall C at BFG ranged from 0.47 to 2.28 $tCha^{-1}$ between 1983 and 1993. During the period of belowground study (1992 and 1993) litterfall values ranged from 0.55 to 2.24 tC ha^{-1}, which is within the 10 year values of annual litterfall at BFG. The litterfall was approximately 97% greater in 1993 compared with 1992

across all treatments. These annual litterfall estimates fall within the global estimates collated by Raich and Nadelhoffer (1989).

The litter layer had accumulated significantly in all plots over ten years between 1983 and 1993. However treatments IL+, IL-, IF-, IF+, I, C1, F and U/T showed no change in the mass of standing litter between 1991 and 1993, during the period of soil respiration study. No adjustments are required for the standing litter carbon pool in these treatments when applying the Raich and Nadelhoffer (1989) model of estimating belowground C allocation. The C2 and C3 treatments showed a measured increase in mass of standing litter of 1.60 and 1.33 tC $ha^{-1}.yr^{-1}$ respectively, despite having C:N ratios in the mid range of C:N ratios experienced at BFG. The increment in standing litter in C2 and C3 cannot exceed the measured input in litterfall. Since the litterfall is accurately measured, this was taken as the upper limit for correction. Because of this increase in standing litter mass, belowground C estimates for C2 and C3 have been calculated using two scenarios:

1. measured change in forest floor carbon pool; and
2. no change in forest floor carbon pool (Chapter 7).

The coarse root (>2 mm diameter) C allocation, which was calculated using Jackson and Chittenden's (1981) allometric relationship between dbh and coarse root biomass, ranged from 5.4 tC ha^{-1} in the IL+ treatment in 1992 to 1.0 tC ha^{-1} in the C3 treatments in 1993, and was generally lower in 1993 compared with 1992. This coarse root C allocation was proportional to the basal area increment of the treatments in 1992 and 1993.

Fine root biomass (<2 mm diameter) measurements taken at BFG during 1992 and 1993 showed little difference within measured treatments during periods of high soil respiration and low soil respiration, respectively. There appeared to be a difference between the treatments at each sampling period with the IL+ treatment exhibiting a lower biomass compared to I and C1.

Over a period of 10 years there has been no significant change in the soil carbon pool for the IL+, IF+, I, C1, F and U/T treatments. Since these

treatments represent the extremes of forest growth and litter inputs at the site, it is assumed that there was no change in the soil carbon pools in the intermediate IL-, IF-, C2 and C3 treatments. Hence no adjustments were made to account for change in soil C when estimating belowground carbon allocation by using the C budget approach by Raich and Nadelhoffer (1989).

Chapter 7 relies on the C estimates provided in this chapter, in conjunction with soil C flux estimates described in Chapter 6, to estimate belowground carbon allocation at BFG based on Raich and Nadelhoffer's (1989) approach.

CHAPTER 5 SOIL RESPIRATION METHODOLOGY

5.1 Introduction

In order to investigate belowground carbon (C) dynamics at BFG an approach developed by Raich and Nadelhoffer (1989), which is described more fully in Chapter 3, Section 3.7, was utilised. This approach involves measuring CO_2 efflux from the soil (soil respiration), measuring soil C input through litterfall, and understanding the C status of the soil and forest floor, in order to estimate belowground C allocation. To use this approach however, an accurate means of measuring soil respiration is required.

Soil respiration, CO_2 evolution from the soil, provides information on carbon (C) metabolism in the soil and forest floor (Singh and Gupta, 1977). Soil CO_2 evolution is composed of fine and coarse root respiration and decomposer respiration. It can be indicative of nutrient mineralisation rates and, under specified conditions, may be used to estimate the allocation of C belowground (Raich and Nadelhoffer, 1989; Haynes and Gower, 1995). Soil respiration measurements were undertaken *in situ* at the BFG site between 1991 and 1993 to determine how irrigation and nutrition affected belowground carbon allocation.

Soil respiration may be measured either in the laboratory or in the field. Laboratory incubations can be used to examine the effects of moisture and temperature on respiration. *In situ* field-based estimates of soil CO_2 evolution are spatially and temporally variable because of variability in substrate quality, microbial populations and root activity, and because of changing environmental conditions, particularly temperature and moisture (Naganawa, 1990; Rochette *et al*, 1991). To quantify field rates of soil respiration reliable methods are needed to cope with variability in space and time.

The most common techniques for measuring soil respiration *in situ* employ either alkali absorbents (Tesarova and Gloser, 1976; Edwards 1982; Ewel *et al*, 1987a; Raich *et al*, 1990; Nay *et al* 1994; Haynes and Gower 1995; Norman *et*

al, 1997; Pongracic *et al*, 1997; Janssens *et al*, 2000) or infra red gas analysis (IRGA) (Witkamp, 1969; Ewel *et al*, 1987b; Nay *et al* 1994; Haynes and Gower 1995; Norman *et al*, 1997; Rochette *et al,* 1997; Janssens *et al*, 2000). These typically are characterised by the absence or presence of airflow in the measurement chamber, and may be referred to as static (alkali absorbent) or dynamic (IRGA) respectively. The IRGA can also be used in the absence of airflow to monitor CO_2 build up over time in the measurement chamber (Ewel *et al*, 1987a; Nay *et al* 1994; Haynes and Gower 1995; Norman *et al*, 1997).

The alkaline absorption method generally involves placing granular soda lime within an airtight chamber set in the soil and leaving it to absorb evolved CO_2. The advantages of this technique are:

- it is relatively inexpensive and simple to undertake, allowing extensive spatial replication;
- long periods of field measurement (up to 24 hours) are possible; and
- it can be used with larger chambers that allow integration of microscale variation in CO_2 efflux.

The IRGA technique generally utilises a closed loop airflow system to take short-term measurements (up to 1 min) of CO_2 evolution into a chamber or collar set in the ground. IRGA measurements are repeated several times throughout the day and are scaled up to give daily flux estimates (Ewel *et al*, 1987b; Haynes and Gower, 1995). This technique is more labour intensive; generally uses smaller chambers/collars; and is highly sensitive to pressure changes within the chamber (Witkamp, 1969; Kanemasu *et al*, 1974; Rayment and Jarvis, 1997; Fang and Moncrieff, 1998).

Several studies (Table 5.1) have concluded that estimates of soil respiration measured by soda lime differ from those measured with an IRGA (Cropper *et al*, 1985; Ewel *et al*, 1987b; Nay *et al*, 1994; Haynes and Gower, 1995; Jannsens *et al*, 2000). Generally, results from field measurements showed that at high rates of CO_2 efflux, the soda lime methodology provided lower estimates of soil respiration and that flux rates from the two methods were highly correlated through an exponential relationship (Ewel *et al*, 1987b; Haynes and

Gower, 1995). Ewel *et al* (1987b) indicated that the exponential relationship could be used to scale soda lime soil respiration estimates to IRGA-equivalents, and this was supported by work undertaken by Haynes and Gower (1995). Rochette *et al* (1997) and Jannsens *et al* (2000) both indicate that soda lime can accurately estimate soil respiration when the technique is appropriately applied and that the soda lime method is particularly useful where spatial variability is large.

Table 5.1: Comparisons of soil CO_2 efflux measured by soda lime and IRGA techniques. Actual IRGA methodologies vary between studies.

% increase in estimated CO_2 efflux by IRGA compared with soda lime	temporal scale	Forest System	Reference
-12 to 105	monthly	slash pine *Pinus elliotii*	Cropper *et al*, 1985
-20 to 107	daily	slash pine *Pinus elliotii*	Ewel *et al*, 1987b
-50 to 57	daily	laboratory	Nay *et al*, 1994
11 to 70	annual	red pine *Pinus resinosa*	Haynes and Gower, 1995
10	daily	Scots pine *Pinus sylvestris*	Jannsens *et al*, 2000

Nay *et al* (1994) compared the CO_2 flux estimates from the soda lime and IRGA techniques within a laboratory-based artificial soil system. Results showed that soda lime did not accurately measure soil respiration predicted by a theoretical flux model. At zero "soil" efflux rate, head space analysis showed that soda lime was drawing CO_2 out of ambient air and at high flux rates soda lime allowed a significant build up of CO_2 in the head space. On the other hand, the IRGA method consistently underestimated the calculated CO_2 flux rate by approximately 15% (Nay *et al*, 1994), but did not record any CO_2 flux at zero soil flux. This study showed that neither method accurately measured the predicted CO_2 flux, but that IRGA estimates showed a consistent bias.

The work undertaken at BFG was initiated in 1991 before there was controversy about the relative accuracy of soda lime and IRGA methodologies. Soil

respiration measurements at BFG were undertaken using an adapted soda lime methodology that utilised large, well sealed, permanently located measurement chambers, inert soda lime dishes (glass Petrie dishes were used) and soda lime "blanks" to account for CO_2 absorbed during handling and transport to the field. This approach ensured that many of the previous criticisms of the soda lime methodology, such as instantaneous disturbance through non-permanent measuring collars, small collar size, CO_2 leakage around the lids to the collars and the soda lime chemical interacting with the holding container, did not occur.

Several initiatives were taken to ensure that soil respiration estimates obtained from BFG were realistic. A comparison of the soda lime and IRGA techniques was undertaken in 1994 and 1995. The impetus for this comparison arose from the very high CO_2 efflux rates estimated using the soda lime technique at the *Pinus radiata* site in Australia (Chapter 6). Applying the soda lime-IRGA conversion described in Ewel *et al* (1987b), predicted a carbon flux from the soil of approximately 40 tC $ha^{-1}yr^{-1}$ in the most active BFG treatment (I - irrigated) in 1992. Such rates are clearly unrealistic for this system where estimated annual gross primary productivity (GPP) is approximately 27 tC $ha^{-1}.yr^{-1}$ for the (I – irrigated) treatment (McMurtrie *et al*, 1992; Raison and Myers, 1992; Ryan *et al*, 1996a).

Ryan *et al* (1996a) developed a detailed carbon budget for *Pinus radiata* growing under several treatments at BFG site. Their model, based on detailed respiration measurements of various plant tissues, indicated the total belowground C in the irrigated treatment (I) comprising coarse and fine root respiration, plus coarse and fine root production, was 10.4 tC $ha^{-1}.yr^{-1}$ in 1992/93. These estimates took no account of fine root turnover and were approximately 25% less than estimates of belowground carbon allocation based on the approach of Raich and Nadelhoffer (1989) - described in Chapter 3. Ryan *et al*'s (1996a) study also suggested that root respiration dominated soil CO_2 efflux. Root respiration rates of fine roots were directly measured using an IRGA and fine root biomass was measured. The resultant estimated fine root respiration was up to 60% of the measured soda lime estimates of soil

respiration at the BFG site. Based on this empirical evidence, the soda lime soil respiration measurements obtained from BFG seemed credible.

To understand more about soda lime and IRGA techniques for measuring soil CO_2 flux controlled laboratory work was undertaken to:

- determine if soda lime can effectively absorb all CO_2 present, and
- examine the pattern of CO_2 absorption by soda lime.

This laboratory work was supported by field studies in two forest types - a Canadian boreal forest and the BFG *Pinus radiata* plantation in Australia. The fieldwork examined:

1. direct comparisons of soda lime and IRGA techniques at both the boreal forest and *Pinus radiata* plantation;
2. the effect of chamber size on rate of CO_2 absorption by soda lime;
3. the effect of chamber size on rate of CO_2 efflux by IRGA;
4. the diurnal patterns of CO_2 evolution using IRGA monitoring, and
5. the effects of disturbance and pressure changes on IRGA estimates of soil CO_2 evolution.

The remainder of this chapter describes the results of the laboratory work and the field studies comparing the soda lime and the IRGA techniques for measuring soil respiration. The following studies were published as Pongracic *et al* (1997).

5.2 Methods and Field Sites

5.2.1 Laboratory studies of the efficiency and pattern of CO_2 absorption

The efficacy of CO_2 absorption by soda lime was examined in the laboratory by:

1. adding a known amount of CO_2 to a sealed chamber with and without moisture present; and
2. using an IRGA to track how chamber headspace CO_2 concentration changes with time.

To test the capacity of soda lime to take up CO_2, soda lime granules and a source of moisture were placed in a sealed, 7.8L chamber containing ambient air. Approximately 40g of oven dried 40-60 mesh soda lime were held in a glass Petrie dish 0.1m diameter by 0.015 m height, providing an exposed surface area of at least 7850 mm^2. Actual granule surface area would have been much greater. The moisture source is required as the soda lime requires a moistened outer surface to absorb CO_2 but it is uncertain how much moisture is sufficient to ensure that soda lime adequately absorbs all CO_2 present. The moisture source was provided by moist filter paper within the chamber, and changing the size of moist filter paper exposed from 0 to 7500 mm^2 varied the moisture source. A known amount of CO_2 gas (food grade, 99.8% pure, BOC gases) was bled into this sealed chamber over four hours using a mass flow controller (MFC) calibrated against a bubble meter. The mass of CO_2 added (1.1g CO_2) was approximately equivalent to the expected flux over 24 hr in a similar sized chamber set in sandy soil beneath a *Pinus radiata* stand. The limitations of the MFC required that this volume of CO_2 be bled in over 4 hours rather than 24 hours. After a lag time of two hours (total absorbency time 6 hours) the soda lime was removed from the chamber and weighed. The efficiency of absorption was determined by comparing the amount of CO_2 added with that taken up by the soda lime.

An IRGA (LICOR 6000) was used to monitor the CO_2 concentration of the head space of a sealed chamber containing soda lime into which CO_2 was being bled. This was replicated three times. This was undertaken with 7500 mm^2 of moist filter paper exposed. Monitoring began once the CO_2 inflow had been switched off, and was continued until the CO_2 concentration within the chamber approached zero. Two small fans were installed in the chamber to facilitate air mixing for IRGA field measurements. However the fans were not activated during this laboratory study because typical field conditions for soda lime CO_2 absorption were being simulated.

5.2.2 Field studies in a Canadian boreal forest

A direct comparison between IRGA and soda lime methodology was undertaken at two field sites. The initial work was done as part of the Boreal Ecosystem and Atmosphere Study (BOREAS) in August 1994 (Sellers *et al*, 1994). Three sites in the boreal forest in northern Manitoba were chosen - aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) with and without an alder (*Alnus crispa*) understorey. These sites covered a range of boreal forest productivity with aspen being more productive and jack pine less so. Work here also looked at the effect of chamber size on both IRGA and soda lime estimates of soil CO_2 flux.

5.2.2.1 Comparison of soda lime and IRGA estimates of soil CO_2 flux

Six 5 m x 5 m plots were established at three sites in the boreal forest. The three sites comprised an aspen stand and two jack pine stands one with, and one without, an alder understorey. These plots were used to examine the effects of chamber size on soda lime and IRGA estimates of soil CO_2 efflux, and also for comparison of soda lime and IRGA estimates of soil CO_2 efflux.

Six chambers of each of the large surface area-large volume and large surface area-small volume chambers (see Table 5.2) were installed in pairs to a depth of 0.03 -0.04 m in the 5 m x 5 m plots at least two weeks prior to CO_2 efflux measurement. The two different chambers were installed as pairs (within 0.3 m of each other) to minimise any spatial variability that may have been present within the 5 m x 5 m plots. The paired chambers were used to directly compare the effects of different chamber sizes on IRGA and soda lime estimates of CO_2 efflux for the same microsites. One chamber of the pair was used for soda lime on the initial day, with the IRGA method used in the other chamber. The measurement methods were swapped between the chambers for the second measurement in order to minimise any problems of microsite differences. Efflux rates on different days were corrected with a temperature response function derived by Kirschbaum (1995), allowing a better comparison of efflux rates on different days.

A LICOR soil respiration collar (small surface area – small volume) was also installed in each of the six 5 m x 5 m plots 2 weeks prior to the commencement

of measurements. Because of the small size of the LICOR soil respiration collar (see Table 5.2), soda lime measurements could not be taken in these collars.

The soda lime soil respiration estimate involved exposing approximately 40g of oven dried soda lime in 0.07 m diameter by 0.03 m high tins in each of the large surface - large volume and larger surface area – small volume chambers. Five "blanks" were used to account for any CO_2 absorption during handling. Measurement periods of 8 hr were used.

Table 5.2: Description of chamber types used to compare soil CO_2 efflux by soda lime absorption and IRGA methods

Chamber type	surface area exposed soil (m^2)	volume of chamber (L)	site used	measurement method
large surface area-large volume*	0.0638	31.1	boreal forest: aspen, jack pine	soda lime, IRGA
large surface area-small volume**	0.0471	6.3	boreal forest: aspen	soda lime, IRGA
small surface area-small volume***	0.0072	1.2	boreal forest: aspen, jack pine	IRGA
largest surface area-intermediate volume****	0.0779	7.8	*Pinus radiata* plantation	soda lime, IRGA

* used by Haynes and Gower, 1995
** similar to chamber used by Pongracic *et al*, 1997
*** LICOR commercially available soil respiration chamber
**** used by Pongracic *et al*, 1997 and Ryan *et al*, 1996a

IRGA measurements were taken with a LICOR 6200 using a closed system with a flow in excess of 1L min^{-1}. The LICOR chamber measurement was taken by passing the air within the chamber through a CO_2 scrubber to draw down the CO_2 in the air to below ambient levels (approximately 350 $\mu g.g^{-1}$) as per the method of Norman *et al* (1992). CO_2 was then allowed to build up to approximately 15 $\mu g.g^{-1}$ below ambient and then every change of 5 $\mu g.g^{-1}$ of

CO_2 was logged for 5 incremental periods. CO_2 efflux was calculated from the CO_2 increase in the chamber and the time taken to achieve this increase.

This method was used for the smaller volume chambers (large surface area – small volume and small surface area – small volume (Table 5.2)). The measurements were taken three times during the day, usually at 0900, 1300 and 1700 hours and were scaled to 8 hr equivalents by assuming the first second and third measurements apply to the periods 0900-1100, 1100-1500 and 1500-1700 respectively.

The IRGA measurement technique for the large surface area-large volume chambers was slightly different to that described above as it was impossible to scrub the air within the large surface area chambers to below ambient with available LICOR pumps. The chamber was flushed with ambient air and the lid gently placed upon the chamber to minimise soil disturbance and pressure changes. Again increases of 5 $\mu g.g^{-1}$ CO_2 were logged for five periods and CO_2 efflux calculated as above.

5.2.2.2 Effect of chamber size on chamber headspace CO_2 levels

A two-way chamber comparison was undertaken in the aspen stand of the boreal forest to test the effects of differences in chamber size on CO_2 headspace levels, and by extension on the rate of CO_2 uptake. A large surface area-large volume and a large surface area-small volume chamber were used. Dimensions of the chambers are given in Table 5.2.

40g of oven dried soda lime was exposed in 0.07m diameter by 0.03m high tins for 24 hr in each of the paired chambers. Five “blanks” were used to account for CO_2 absorption during handling. A sample of the chamber headspace gas was taken through rubber seals in the chamber lids just prior to removing the soda lime. Each syringe was flushed with headspace gas, and the samples analysed using gas chromatography.

5.2.2.3 Effect of chamber size on rate of CO_2 evolution estimated by IRGA

To test the influence of chamber size on IRGA measurements a three-way comparison was set up in the aspen stand of the boreal forest. Three types of chambers were used: large surface area-large volume; large surface area-small volume, and small surface area-small volume chambers (Table 5.2). The IRGA method was identical to that described above, but some 24 hr estimates of soil CO_2 flux were calculated, by taking more measurements during the day.

5.2.3 Field studies at the BFG site in Australia

The second field site involved *Pinus radiata* stands in the Biology of Forest Growth (BFG) study described in Chapter 3 (Benson *et al*, 1992). Earlier work at the site had shown a wide range of soil CO_2 efflux values between control and irrigated/fertilized stands (see Chapter 6). Permanent, large surface area-intermediate volume respiration chambers (7.8L in volume) were installed to a depth of 0.03-0.04 m at the site in 1991. This soil respiration methodology work, undertaken in December (summer) 1995, involved:

- direct comparisons of soil CO_2 efflux estimated by soda lime and IRGA methods;
- measuring diurnal fluctuations in CO_2 evolution; and
- investigating whether chamber disturbance effects could be causing a discrepancy between soda lime and IRGA measurements.

Full descriptions of the chambers and their placement in the field are given in Section 6.3.1.1.

5.2.3.1 Comparison of soda lime and IRGA estimates of soil CO_2 flux

A direct comparison of the CO_2 efflux rates estimated using a continuous flow IRGA and the soda lime method was undertaken in *Pinus radiata* stands. Two of the largest surface areas – intermediate volume chambers (Table 5.2) were established within 0.3 m of each other to minimise spatial variability. One of the chambers had been installed in 1991, the second in 1995, two weeks prior to measurement. During the initial measurement one of the pair was used for soda lime measurements whilst the other was being measured with the IRGA over 24 hours. On the second day the measurement techniques were swapped

on these paired chambers. CO_2 flux rates were standardised to 15^o Celsius using the temperature function described in Kirschbaum (1995) and the microsites were directly compared.

For soda lime measurements, approximately 40g of oven dried 40-60 mesh soda lime granules were exposed in a glass Petrie dish 0.1m diameter and 0.015m height, providing an exposed surface area of at least 7850 mm^2. Five "blanks" were used to account for any CO_2 absorbed during handling. Soda lime was exposed for 24 hr.

An open flow IRGA system was set up in order to monitor soil CO_2 efflux continuously. A MFC was used to pass zero grade air (< 1 mg.g^{-1} CO_2, BOC gases) through the chamber, via a desiccant and onto a LICOR 6000 IRGA. CO_2 concentration of the air passing from the chamber was monitored, with the only source of CO_2 being the forest floor. The chamber lid was fitted with the LICOR 6000 photosynthesis sensor head in addition to having two small fans to ensure adequate mixing of chamber air. CO_2 concentration was logged every minute for the initial diurnal measurement and every 4 min during 3 additional 24 hr measurements. CO_2 flux was calculated from IRGA flow rate multiplied by CO_2 concentration.

5.2.3.2 Diurnal patterns of CO_2 evolution

The continuous flow system described above was used to monitor diurnal fluctuations in soil CO_2 efflux over 24 hr periods. Soil temperature at 0.01 m and 0.10 m depths and meteorological data were also logged. These diurmal patterns can provide an indication of how "spot" measurements taken during the day can over- or under estimate actual CO_2 flux.

5.2.3.3 Effects of disturbance and pressure changes on IRGA estimated soil CO_2 flux rates

The influence of disturbance and pressure changes on soil CO_2 efflux was investigated at the *Pinus radiata* site using the IRGA continuous monitoring method described above. Disturbance involved moving the chamber around within the soil, but not breaking the "seal" with the soil. This was initially half a turn of the chamber within the soil and was increased to approximately five turns. Altering the ratio of gas flow in, to gas flow out, of the chamber and monitoring the subsequent changes in apparent CO_2 efflux were attempted to induce pressure related changes in CO_2 efflux.

5.3 Results and Discussion

5.3.1 Laboratory studies on the efficiency and pattern of CO_2 absorption

The amount of moisture available to the soda lime had an effect on the efficiency and the absolute value of CO_2 uptake (Table 5.3), as the reaction between hydroxide and CO_2 is facilitated by the presence of water. In the presence of adequate moisture soda lime absorbed 98% of added CO_2 without any air movement within the chamber. Without added water the amount of CO_2 uptake was highly variable and averaged only 58% of CO_2 added. The high variation may have been caused by the variation in initial laboratory humidity. This relative test did not quantify the absolute amount of water required to ensure maximum uptake of CO_2 by soda lime, but provided an indication of the importance of this factor.

Edwards (1982) also emphasised the importance of water with the soda lime technique. Edwards (1982) indicated that in the field, moisture derived from the soil and forest floor may be sufficient to allow adequate uptake. However in work undertaken at the BFG during 1992 and 1993, in dry summer periods in the non-irrigated treatments the soda lime was sprayed with water prior to being set out in the field to ensure efficient absorption of CO_2 (Chapter 6).

Table 5.3: Percentage of added CO_2 absorbed by soda lime with different moisture regimes. Values are means with standard errors shown in brackets. Means with the same letter exhibit no significant difference at the 90% level.

moisture regime (mm^2 moist filter paper)	n	average % CO_2 absorption
0	4	58 (28) a
375	5	78 (16) ab
750	4	90 (9) bc
7500	12	98 (4) c

Figure 5.1 shows the temporal pattern of CO_2 absorption in the chamber headspace. As the maximum reading possible with the LICOR 6000 IRGA was 1100 $mg.g^{-1}$ the draw down in CO_2 concentration over the initial 20 - 30 minutes could not be logged due to instrument limitations. The CO_2 concentration within the chamber approached zero approximately 2.5 hr after the initiation of monitoring, indicating that soda lime was able to absorb virtually all CO_2 present in the chamber.

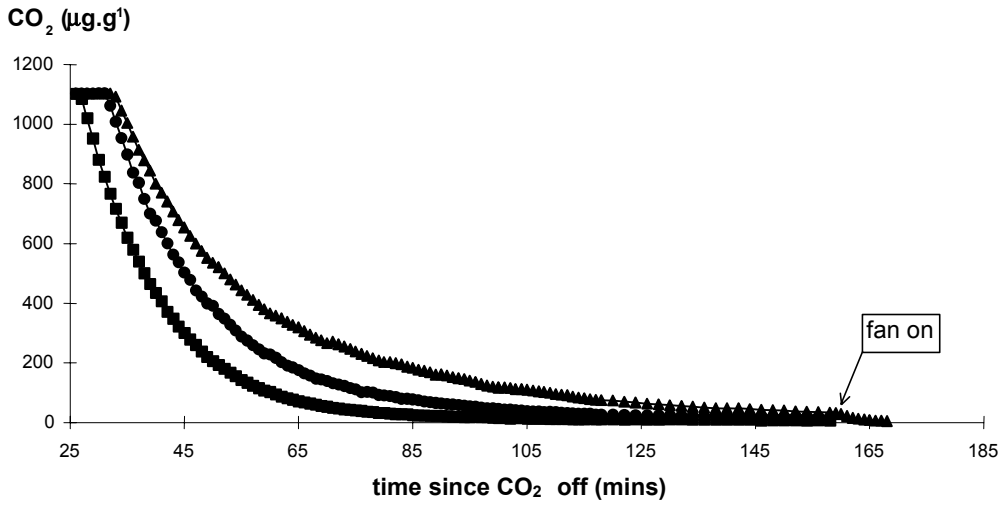


Figure 5.1: Temporal absorption of CO_2 by soda lime in sealed chambers in the laboratory. The X-axis is the time since CO_2 addition was turned off. Each line represents a study on a different day, values over 1100 $\mu g.g^{-1}$ were off scale. Chamber head space was measured with a LICOR 6000.

Figure 5.1 shows that CO_2 uptake by soda lime is gradual, with diminishing rates of CO_2 absorption with decreasing concentrations of CO_2 in the head space. CO_2 must be at the soda lime granule boundary before it will be taken up by soda lime and air movement within the chamber is likely to be slow where

turbulence is solely reliant on external heat differences to initiate air movement. This is of particular significance in stable laboratory conditions. The upper trace shows the small fans installed in the chamber were switched on after 160 minutes, which increased the rate of CO_2 absorption (Figure 5.1). Fans were not used in initial traces as field chambers used to estimate soil respiration at the BFG site during 1992 and 1993 did not have fans to aid air mixing. A possible consideration for field measurements with soda lime could be the addition of fans to the chambers to ensure better air mixing.

The results indicate that rate of CO_2 absorption by soda lime is influenced by the concentration of CO_2 in chamber, and by air mixing. Under field conditions, external heat differences may be sufficiently variable to ensure adequate air movement, and therefore mixing, within the chamber.

5.3.2 Comparison of soda lime and IRGA estimates of soil CO_2 flux - boreal forest

Soda lime and IRGA estimates of soil CO_2 flux were compared directly over 8 hr in the aspen and jack pine stands of the boreal forest. The flux rates were temperature corrected using equations from Kirschbaum (1995) and directly compared. Figure 5.2 shows the comparison on an individual chamber basis using the large surface area - large volume and large surface area - smaller volume chambers. The average IRGA CO_2 flux reported for the northern study site of BOREAS for the aspen stand in 1994 was 1426 $mgCO_2.m^{-2}.hr^{-1}$, which correlates well with the IRGA measurements in this study (Sellers *et al*, 1994). IRGA estimates were larger than those for soda lime but the correlation between the two was not significant ($r^2 = 0.05$, n=23). There was no evidence of the exponential relationship found by other workers (Ewel *et al*, 1987b; Haynes and Gower, 1995) despite spanning a similar range of soda lime efflux rates. On average individual chamber IRGA estimates were 4 fold higher than for soda lime (Figure 5.2). This may have been due to the short time frame (8 hr) not allowing soda lime to efficiently absorb the CO_2 respired during the time of maximum respiration (see diurnal patterns of CO_2 efflux later, Section 5.3.7). Rochette *et al* (1997) also showed that where shorter measurement periods (9

hr) were used, the differences between static and dynamic methods were larger than for longer measurement periods (24 hr).

When IRGA and soda lime estimates were compared on a plot average basis, and IRGA measurements of the small surface area-small volume (LICOR) chamber were included, the correlation between the two methods was improved, but still not significant (r^2 = 0.35, n=10, data not shown,). The 8 hr integration period may not have been sufficient to allow the soda lime to work at its full potential. Unfortunately time restrictions did not allow further testing at this site.

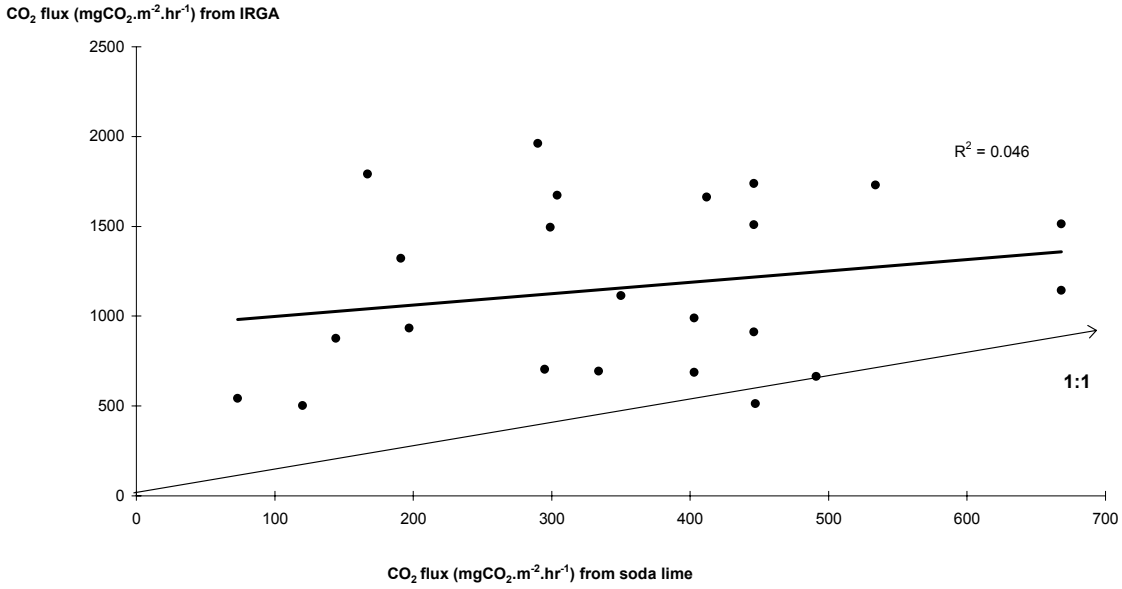


Figure 5.2: Relationship between soil CO_2 efflux estimated by IRGA (LICOR 6200) and that estimated from absorption by soda lime in aspen and jack pine in boreal forest over 8 h. Rates standardised to 10° C (r^2 = 0.05).

5.3.3 Effect of chamber size on rate of CO_2 absorption by soda lime - boreal forest

Different sized chambers could be predicted to have an influence on the measured CO_2 efflux as the soil to soda lime surface area ratio influences the

rate at which soda lime can absorb CO_2. Haynes and Gower (1995) had used a large surface area - large volume chamber which showed a difference between soda lime and IRGA estimates of soil CO_2 flux. Earlier work by Pongracic (unpublished) had used large surface area - intermediate volume chambers which produced high CO_2 flux estimates using the soda lime method which could not realistically be converted to IRGA equivalents using the exponential relationship derived by Haynes and Gower (1995).

Results from the aspen stand in the boreal forest showed chamber size had no consistent effect on the measured CO_2 efflux rates measured using the soda lime method (Table 5.4 - chamber dimensions in Table 5.2).

Table 5.4: The effects of chamber geometry on rates of soil CO_2 efflux (mg $CO_2.m^{-2}.hr^{-1}$) measured by soda lime absorption within the aspen stand of the boreal forest. Standard errors shown in brackets. There was no consistent difference between chamber types at the 95% level using the students T-test.

date	n	large surface area-large volume (mg CO_2 $.m^{-2}.hr^{-1}$)	large surface area-small volume (mg CO_2 $.m^{-2}.hr^{-1}$)	period of exposure (hours)
5-8-1994	6	581 (114)	618 (53)	24
11-8-1994	3	390 (96)	354 (0)	8
18-8-1994	3	408 (14)	310 (110)	8

The CO_2 concentration after 24 hours in the head space of the large surface area-large volume chamber was 1362 $mg.g^{-1}$ (se = 90) compared with 1109 $mg.g^{-1}$ (se = 76) in the large surface area-smaller volume chamber. The difference was significant only at $P<0.10$, using a student's T-test. However CO_2 build up in the head space of chambers can only explain between 1.4 and 6.9 % of evolved CO_2, and is much less than the observed discrepancy between early work on CO_2 flux rates estimated by soda lime and IRGA techniques (Ewel *et al*, 1987b; Haynes and Gower, 1995). Recent studies with improved soda lime techniques, have indicated that the difference between soda lime and IRGA estimates of soil CO_2 efflux are lower (Rochette *et al*, 1997; Jannsens *et al*, 2000) and the measured build up in the headspace may be a significant contributor to this difference.

5.3.4 Effect of chamber size on rate of CO_2 evolution estimated by IRGA- boreal forest

Chamber size had little influence on the rates of CO_2 efflux estimated by IRGA in the boreal forest types (Figure 5.3), with measurements taken at four times throughout the day showing no consistent difference. No discrimination between the chambers was evidenced in the aspen stand on two successive days (second day not shown), and this was supported by the work undertaken at the jack pine site. There was no significant difference between the chamber types at either $P<0.05$ or $P<0.10$. This similarity in soil CO_2 efflux with different chamber sizes was also described in Jannsens *et al* (2000).

Differences in IRGA measurement technique did not appear to have any effect on apparent efflux rate. The LICOR chamber used a scrub down technique to measure CO_2 efflux whilst the larger volume chambers used an "ambient air" method. The main difference between these techniques was the initial CO_2 concentration within the chamber. In general, the larger surface area chamber in which the head space was not being scrubbed of CO_2 had slightly higher than ambient initial CO_2 concentration (380 - 450 $mg.g^{-1}$), but these values are within the range of CO_2 concentrations experienced approximately 1m above the soil surface at night (Ryan, Hubbard, Grauel, Pongracic, 1994, unpublished). Figure 5.4 indicates no significant relationship between measured efflux rate and the initial chamber CO_2 concentrations ($r^2= 0.08$).

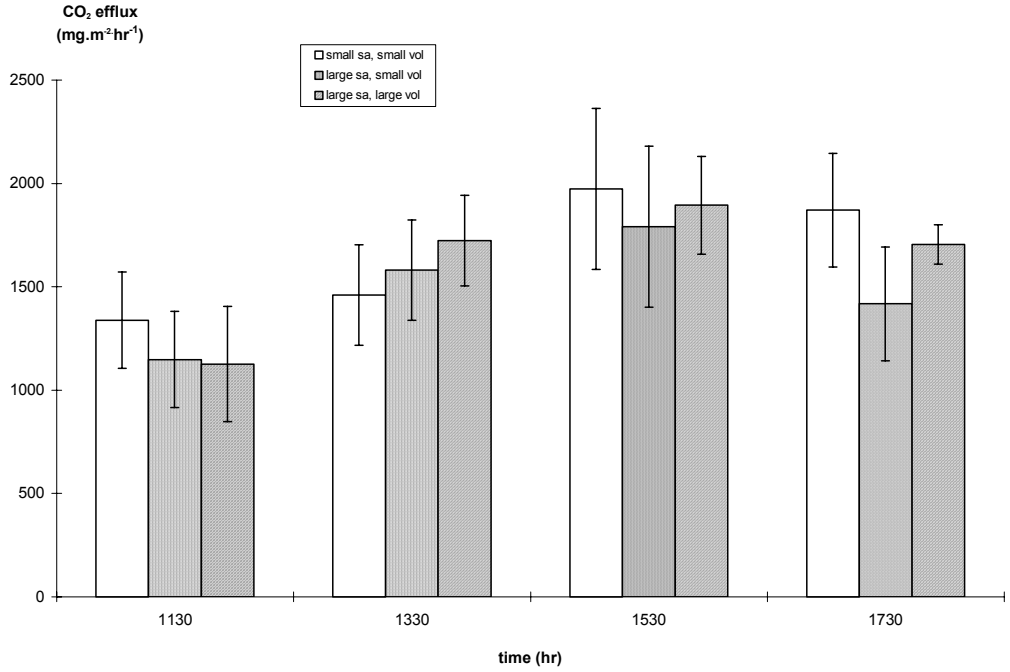


Figure 5.3: Effects of chamber surface area and volume combinations on the CO_2 efflux rates estimated using the LICOR 6200 in the boreal forest.

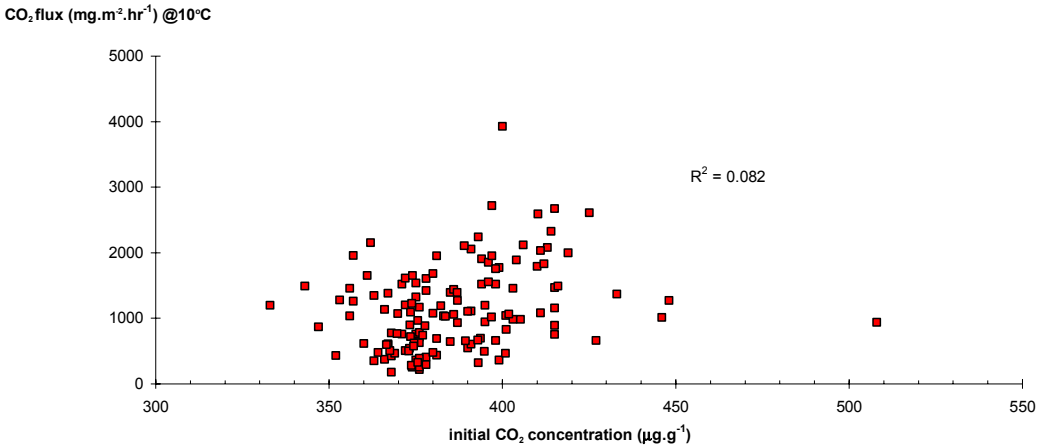


Figure 5.4: Influence of initial CO_2 concentration within the chamber on CO_2 flux rates estimated using IRGA (LICOR 6200, r^2 = 0.08).

5.3.5 Comparison of soda lime and IRGA estimates of soil CO_2 flux – BFG Australia

To compare IRGA fluxes to soda lime equivalents the IRGA fluxes were scaled up by summing each one or four minute measurement for the full 24 hr. This 24 hr IRGA estimate of CO_2 production was then compared to the 24 hr soda lime measurement. Although only four 24 hr measurements were taken, soda lime and IRGA estimates of soil CO_2 flux were much more similar in this system, compared to the data from the boreal forest. For three out of four measurements IRGA values were higher than those for soda lime, and the average difference was 40% (Figure 5.5), but the difference between the methods did not increase with increasing flux rates. Using the strict conditions for IRGA measurement with a continuous flow, and the soda lime method used for the 1992 and 1993 measurements in the *Pinus radiata* stand (see Chapter 6), there were not large differences between the estimates of soil respiration. Hence there is no basis for converting soda lime estimates of soil CO_2 efflux measured in 1992 and 1993 to IRGA equivalents using the exponential relationship developed by Ewel *et al* (1987b) and Haynes and Gower (1995), which was the recommendation of the literature at the time this field work was undertaken.

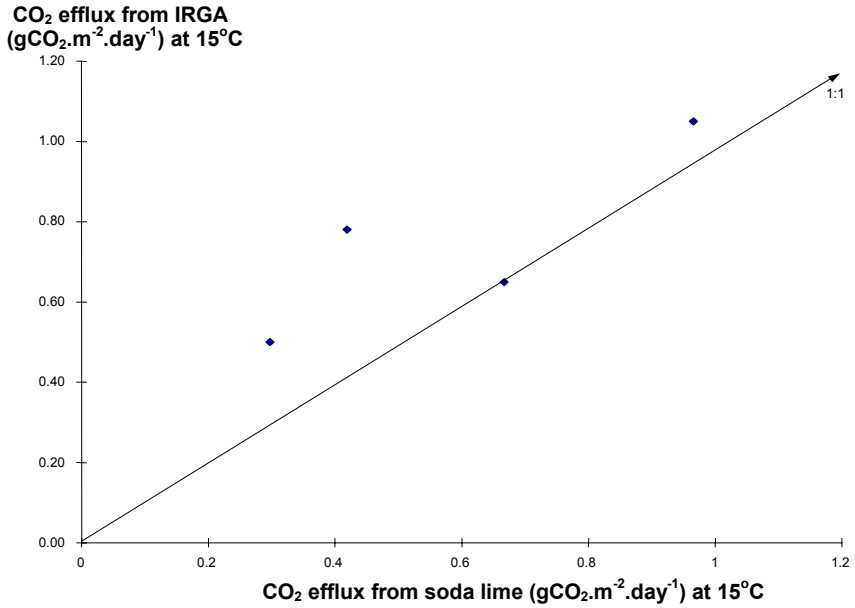


Figure 5.5: Relationship between soil CO_2 flux rates estimated by IRGA (LICOR 6000) and absorption by soda lime from the same microsite in a stand of *Pinus radiata*.

5.3.6 Effects of disturbance and pressure changes on IRGA estimated soil CO_2 flux rates – BFG Australia

There is some disturbance associated with taking IRGA measurements due to the chamber lid being placed on the collar immediately prior to taking the measurement. Soil disturbance through chamber movement can cause a stimulation in CO_2 evolved from the soil (Ewel *et al*, 1987b). In addition placing the chamber lid on the collar induces slight pressure changes that may influence the CO_2 efflux. A disturbance stimulation of CO_2 efflux did not occur in the *Pinus radiata* stand despite repeated movements of chambers (Figure 5.6). This lack of "disturbance simulation" could be due to a small "edge effect" of disturbance in the largest surface area-intermediate volume chambers (Table 5.2), or the CO_2 flux in these chambers being dominated by root respiration rather than decomposer respiration (Ryan *et al*, 1996a).

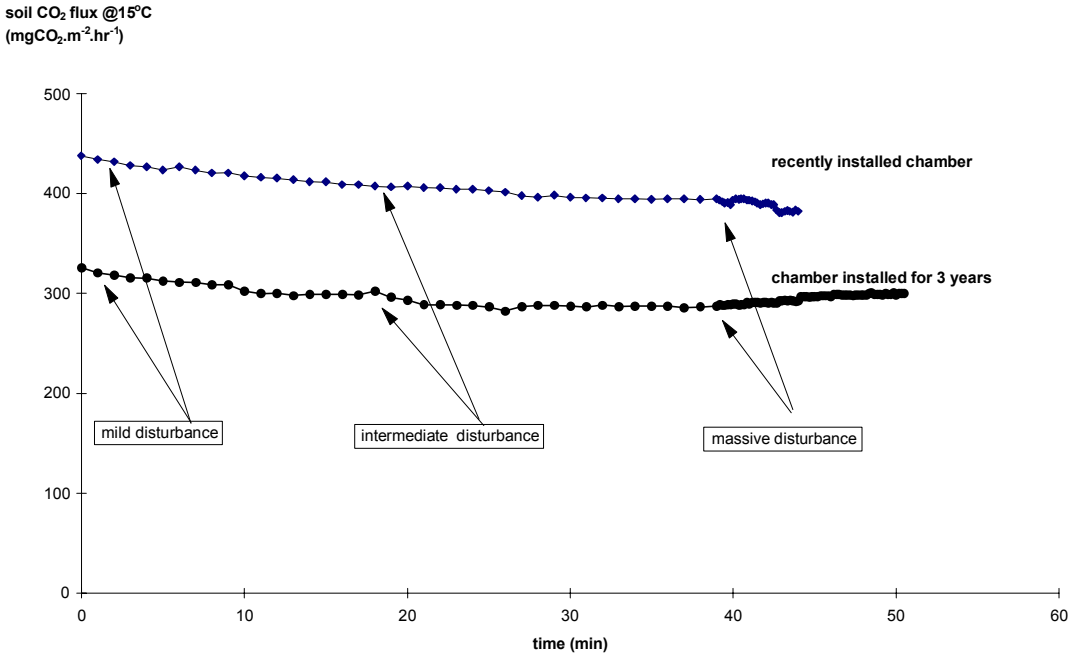


Figure 5.6: Influence of varying degrees of disturbance on soil CO_2 efflux estimated using IRGA (LICOR 6000) for a recently installed chamber and one that had been installed for three years.

Pressure build up in the field chamber could not be measured due to the "leakiness" of the soil (i.e. a good seal could not be obtained between the chamber and the soil). Pressure build up could, however, be demonstrated in a "false bottomed" (perspex based) chamber. Changing the ratio of air flow in to air flow out produced intriguing results (Figure 5.7), but we cannot be certain that this change in measured CO_2 rates were due entirely to stimulating or repressing soil CO_2 efflux, because of the lack of a good seal. However the effects of pressure and suction were marked (as shown in Figure 5.7) which may potentially introduce large errors into scaled up IRGA estimates of soil respiration. Kanemasu *et al* (1974) estimated that a suction as small as 25 mbars could cause a significant increase in apparent CO_2 efflux rates. Similarly Fang and Moncrieff (1998) showed significant impact on soil CO_2 efflux of a 1 Pa negative pressure within the chamber. Short term pressure changes caused by taking IRGA measurements could have a significant effect on the scaled up estimates of CO_2 efflux because only a very small fraction of the day is actually monitored. Considering a 2 hourly measurement period from 8 am to 8pm with 2-minute measurements, only 14 minutes are actually measured over a 24 hour

period. Any stimulation of this 1% of CO_2 efflux could have a significant impact on the scaled-up values.

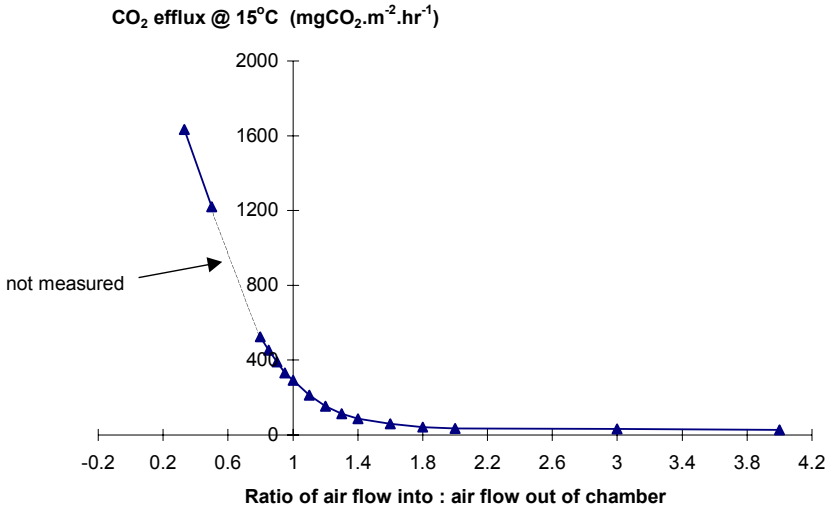


Figure 5.7: Effect of varying the ratio of in-flow to out-flow (suction and pressure build up) in a large surface area-intermediate volume chamber set in the ground.

5.3.7 Diurnal patterns of CO_2 evolution – BFG Australia

A diurnal trace of CO_2 evolution is shown in Figure 5.8 for a well watered, well fertilized site. Similar diurnal patterns were found for three other chambers, one other in a well-watered fertilized treatment and two others in a non–irrigated, non-fertilized treatment. Figure 5.8 shows the CO_2 flux ranging from 395 - 640 mg CO_2 .m^{-2}.h^{-1} with the high flux rate associated with high temperature at 1600. The 60% variation in efflux rate throughout the day was significantly correlated with soil temperature at 1cm depth ($P<0.10$). The variation in CO_2 efflux is also likely to be influenced by plant photosynthesis and respiration, which varies throughout the day in response to changes in radiation.

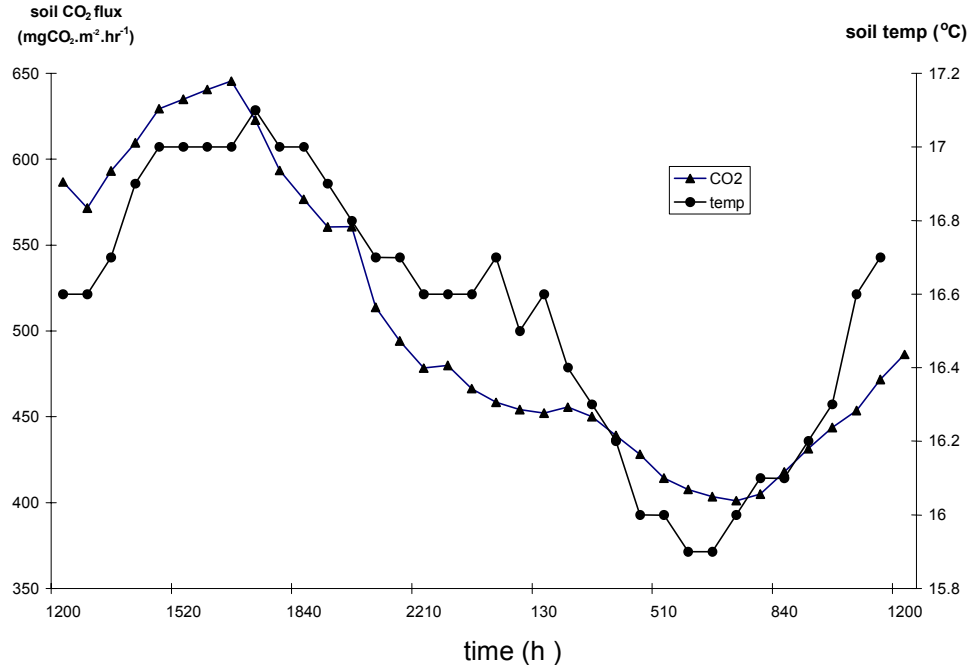


Figure 5.8: Diurnal pattern of soil CO_2 efflux (LICOR 6000) and soil temperature at 0.01m depth for a chamber in an irrigated and fertilized stand of *Pinus radiata*. The two variables were linearly correlated (r^2=0.65, p<0.1).

Because of diurnal variation in CO_2 efflux, scaling up short term IRGA measurements may overestimate this flux, particularly if CO_2 production during measurement was stimulated through chamber disturbance or from pressure changes. By choosing four times within our diurnal traces (0800, 1200, 1600 and 2000) and scaling up to 24 h we found that the 24 h CO_2 estimate overestimated on average by 7% (range 1.7 to 12%). This is clearly insufficient to account for differences between IRGA and soda lime estimates quoted in the literature. However the system in the *Pinus radiata* stand was not typical, as the 24 hr monitoring system was very stable with the continuous flow through monitoring ensuring **no** disturbance effects. The issue of artifacts created during short term flux measurements using an IRGA in a typical measurement regime may be much more important.

The importance of soil temperature in driving the soil respiration system is shown in Table 5.5. Four 24 h diurnal traces were taken with the IRGA continuous flow system, two in the control (non-fertilized, non-irrigated)

treatment and two in the IL+ (irrigated, liquid-fertilized) treatment. The r^2 values for soil temperature at 1 cm related to soil respiration over the 24 h period ranges from 0.65 to 0.96 with a similar variation exhibited in the irrigated, well fertilized treatment and the non-irrigated, non-fertilized treatment. The relationship between soil respiration and soil temperature at 0.10 m depth was weaker.

Table 5.5: r^2 values for soil respiration and temperature at 0.01 m depth and 0.10 m depth respectively, as measured over 24 hours with an IRGA (ns = not significantly correlated at P<0.05).

	Control Chamber 1	Control Chamber 2	IL+ Chamber 1	IL+ Chamber 2
Soil Temp @ 0.01 m depth	0.78	0.96	0.65	0.94
Soil Temp @ 0.10 m depth	0.58	0.93	ns	0.77

5.4 Conclusions

This study did not clearly resolve why field measurements of CO_2 efflux estimated by soda lime and IRGA can differ markedly. Soda lime in the laboratory was shown to efficiently absorb all CO_2 present, provided adequate moisture was available. The size of chamber used for IRGA and soda lime estimates of CO_2 flux was unimportant over the range of flux rates estimated. Field estimates of soil CO_2 efflux using an IRGA were greater than those using soda lime and the discrepancy was particularly large when the measurement period was short - 8 h compared to 24 h. The use of fans to aid air mixing in soda lime chambers may overcome some of the discrepancy between these soda lime and IRGA estimates of soil respiration. However fans may also cause significant boundary pressure gradients at the soil surface, and should not be used until their full implication on soil surface flux has been evaluated. Diurnal variation in CO_2 efflux also requires that care be taken in scaling up short- term measurements to daily values.

The exponential relationship between soda lime and IRGA measures of CO_2 flux described by Ewel *et al* (1987b) and Haynes and Gower (1995) could not be repeated in the boreal forest nor in the *Pinus radiata* plantation. The exponential relationships between soda lime and IRGA estimates of soil CO_2 efflux published in the literature at the time field measurements for this work were being undertaken, are based on limited data and these relationships appear not to be generic and should not be applied without prior evaluation. Based on the work described in this chapter, no adjustment was made to the soil respiration rates estimated using the soda lime technique at the BFG site during 1992 and 1993.

More recently other workers (e.g. Rochette *et al*, 1997; Jannsens *et al*, 2000) have indicated that soda lime can adequately measure soil respiration, and is particularly useful where large spatial variability exists. Rochette *et al* (1997) and Jannsens *et al* (2000) could not conclusively explain why they still found differences between dynamic and static estimates of soil respiration, although Rochette *et al* (1997) did indicate that the physical soil system may play an important role.

CHAPTER 6 SOIL RESPIRATION MEASUREMENTS

6.1 Introduction

Soil respiration (CO_2 efflux) studies at BFG began in January 1992 using the soda lime technique to measure soil CO_2 efflux as described in Chapter 3. Preliminary work in the laboratory had shown that soda lime adequately absorbed added CO_2 (Chapter 5) and initial fieldwork in 1991 provided an indication of the spatial variability in CO_2 efflux estimates (Pongracic *et al*, 1997). Soil CO_2 efflux measurements were taken every 2 or 4 weeks over 2 full years from January 1992 through till December 1993. Soil temperature and soil and litter moisture contents were also estimated. This chapter will describe the measurements undertaken during the major field study component of this work (1991-1993) and relate the measurement results to biotic and abiotic influences.

6.2 Experimental Layout

Eight combinations of irrigation and fertilization at BFG were used for the soil respiration studies. In addition 2 extra control treatments were established in 1991 to estimate between-stand variability, making a total of 10 treatments for the soil respiration studies. The treatments are described in Chapter 3 (Table 3.1). At the commencement of the soil respiration studies in 1991 large differences in aboveground growth were still apparent, and the soil respiration studies were expected to reflect this.

Each treatment had an internal plot area (excluding buffers) of 0.25 ha. Preliminary soil respiration work in October 1991 showed the variability across the control plot (C1) required 12 soil respiration chambers to encompass 90% of the variability 95% of the time. Slash coverage was estimated for each treatment, as thinning slash deposited in 1988 may have affected soil respiration rates within slash compared to non-slash areas. Each treatment was stratified into slash and non-slash areas with slash coverage per treatment ranging from 0 (U/T) to 64 (IL-)% of plot area (Table 6.1). The number of soil respiration chambers located in each stratum (slash or non slash) in each

treatment is shown in Table 6.1. The chambers were randomly located across the treatments within each of the strata, and permanently located for the 2-year study.

Table 6.1: Distribution of chambers among slash strata. The irrigated treatments had the irrigation pipes removed during thinning and replaced post thinning. This led to the thinning slash being relocated away from the irrigation lines and spread more or less evenly away from the irrigation lines.

	Number of Chambers		
Plot	Slash	Non slash	% slash coverage
IL+	3	9	30*
IL-	8	4	64
IF-	5	7	42
IF+	4	8	30*
I	4	8	30*
C1	6	6	50
F	4	8	30
C2	1	11	12
C3	1	11	10
U/T	0	12	0

* irrigated treatments with evenly spread slash

6.3 Materials and Methods

6.3.1 Soil Respiration Measurements

6.3.1.1 Soil Respiration Chambers

Soil respiration chambers were constructed from 20L, 3-5 mm thick, white plastic nappy (diaper) buckets. These buckets had tight fitting lids that were easily removed and replaced during measurement, which ensured minimum disturbance to the chambers. White buckets were chosen to minimise heating within the chamber during soil respiration measurements. The thickness of the plastic ensured no CO_2 could diffuse through the plastic itself. The buckets were cut approximately 0.12 m from the upper rim to provide a “ring” (soil respiration chamber) of 0.32 m diameter at the soil surface. The soil respiration chambers enclosed a surface area of 0.08m^2 of forest floor. This relatively large forest floor area within the chamber provided an integration of microsite variability of CO_2 efflux.

A steel ring template with a 0.32 m diameter (identical to the lower edge of the soil respiration chamber) was used to cut through the litter into the soil so that soil respiration chambers could be inserted 0.025 cm into the soil without causing major soil/litter disturbance. Because of the different depths of the litter layers across treatments there was some difference in chamber headspace volume. The greatest headspace was in the irrigated only (I) treatment (0.3682 m^2), with the smallest headspace in the irrigated and fertilized treatment (IL+), at 0.1227 m^2. Chambers were "weeded" as necessary between measurements to remove herbaceous vegetation that would otherwise fix some CO_2 by photosynthesis.

The upper rims of the soil respiration chambers were coated with high vacuum grease to ensure a tight seal between the chamber lid and the chamber. This grease was periodically re-applied as necessary.

The soil respiration chambers were left uncovered to allow the area within the chamber to experience the same conditions as the rest of the treatment plot. Chambers were covered only for the 24 h of soil respiration measurement every 2-4 weeks depending on the season.

6.3.1.2 Soil Respiration Measurements

Approximately 40g of 30-40 mesh granular soda lime was weighed out into 120, 0.10m diameter glass Petrie dishes. Glass dishes were used in preference to tin containers (used by Haynes and Gower, 1995) to prevent soda lime reacting with the metal. The weighed dishes were placed in an oven at 105^oC for at least 12 hours to drive off moisture from the soda lime. As the dishes were removed from the oven, lids were placed on the dishes and the dishes allowed to cool. The cooled dishes were weighed and sealed with PVC (electrical) tape to prevent any flow of air onto the soda lime, and to allow easy transport to the field.

In the field dishes containing soda lime were distributed in a systematic order at each measurement to maintain the period of exposure of soda lime in the field

to as close as possible to 24 h. The Petrie dish was opened, and the bottom of the Petrie dish containing the soda lime was placed on the lid in the centre of the chamber, and the time of distribution was recorded. During the summer months a mist sprayer filled with water was carried and all chambers were visually assessed as dry or sufficiently moist. In the chambers assessed as dry, the soda lime was sprayed with a fine mist of water to ensure the soda lime would absorb CO_2 from the soil. The lid of the soil respiration chamber was gently placed on the chamber, minimising chamber disturbance. A brick was then placed on the closed chamber to ensure the seal between the lid and the chamber was maintained via the vacuum grease for the full 24 h. The lid formed a good seal with the chamber, confirmed by studies using an infrared gas analyser (Chapter 5).

The soda lime filled Petrie dishes were collected from the chamber 24 h later in the same order as they were distributed. The soil respiration chamber was opened, the Petrie dish closed and sealed with PVC tape and transferred to the laboratory. In the laboratory the dishes were placed in an oven at 105^{o}C for approximately 24 h, cooled and weighed. The mass of CO_2 absorbed was determined by the weight of soda lime post-exposure minus the weight of soda lime pre-exposure, and multiplied by a "water factor". The water factor is due to the H_2O produced by conversion of NaOH to Na_2CO_3 and $Ca(OH)_2$ to $CaCO_3$ and is approximately 1.41 (Edwards, 1982). Recently Grogan (1998) indicated that the theoretically correct water factor should be 1.69, rather than the empirically derived 1.41. However the 1.41 factor is repeatable in the laboratory for a known mass of added CO_2 (Edwards, 1982), and Chapter 5 in this thesis, and was used in this study.

For each field measurement 15 "blanks" (controls) were used to adjust for any CO_2 absorbed during handling and transport, and to account for ambient CO_2 in chamber headspace. These controls were treated in exactly the same manner as the Petrie dishes used to measure soil CO_2 efflux, except that in the field they were exposed in respiration chambers with a Perspex base so that the only CO_2 absorbed would be from the chamber atmosphere. Because of the

lack of a water source, the controls were sprayed with a fine mist of water at each measurement.

The mass of CO_2 absorbed by soda lime in the field was calculated as:

$$mass_{CO2} = (w_{post} - w_{pre} - w_{control}) \times wf \quad \textbf{(Equation 6.1)}$$

where w_{post} = mass of soda lime post exposure

w_{pre} = mass of dried soda lime pre exposure

$w_{control}$ = mass change in control dishes

wf = water factor = 1.41 (Edwards, 1982).

The CO_2 efflux values were analysed by stratum (slash, non slash) and also averaged by treatment. These rates were converted to an area-based flux using the exposed surface area of forest floor within the chamber ($0.08m^2$). Respiration rates were adjusted upwards by 2.4% (Pongracic *et al*, 1997) to allow for unabsorbed CO_2 in the chamber headspace at the end of the measurement period.

Soil respiration measurements were taken every fortnight within the spring/summer period when soil CO_2 flux was expected to be high, and monthly during winter months. This resulted in a total of 18 measurements per year.

6.3.2 Soil Temperature

Soil temperatures were taken with a probe thermometer at 0.01 and 0.1 m depth into the mineral soil within 0.10m of each soil respiration chamber. Soil temperatures were taken each measurement date between 9 and 10 am, after the soda lime had been placed in the chambers. The 12 temperatures per treatment were averaged. Because of the difference in canopy cover between treatment plots, there were often measured soil temperature differences between the treatment plots.

6.3.3 Litter moisture content

Litter moisture contents were also measured at each soil respiration measurement date. Several handfuls of litter ('grab' samples) were collected from 8 random sites within each treatment plot. The litter included both unfragmented litter and duff components down to mineral earth. These litter samples were placed in paper bags, kept cool and quickly returned to the laboratory where they were weighed, and then dried at 70^{o}C for 24 to 48 h to constant weight. The dry litter was weighed and moisture content calculated by:

$$\text{Litter moisture content} = \frac{(\text{litter}_{wet} - \text{litter}_{dry})}{(\text{litter}_{dry} - \text{averagebagweight})} X100$$

(Equation 6.2)

The 8 samples were averaged to provide a plot litter moisture content.

6.3.4 Soil moisture content

Soil moisture was measured by collecting 8 randomly located, 0.1 m diameter, 0.20 m depth soil cores in each treatment during each measurement period. Intact cores were returned to the laboratory and separated into 0 - 0.05m, 0.05 - 0.10m and 0.10 -0.20m soil depths. Sub-samples of soil from each of these depths from each core were placed in vials, weighed and oven dried to constant weight at 105^{o}C.

Soil moisture content was calculated by:

$$\text{soil moisture content} = \frac{(\text{soil}_{wet} - \text{soil}_{dry})}{(\text{soil}_{dry} - \text{averagevialweight})} X100$$

(Equation 6.3)

These moisture contents were averaged across soil depths and treatment plots to produce plot average values. Soil moisture content measurements were discontinued for the final 12 soil respiration measurements (from May – December 1993) after analysis of the initial 24 measurements indicated a poor relationship with soil respiration.

6.3.5 Litter Manipulation

The mass of litter within the soil respiration chambers was expected to influence the soil respiration measurements. In May 1993 a litter manipulation experiment was undertaken in all 10 treatments. The litter layer was removed from half of the chambers (6 chambers) in each treatment plot in order to determine the contribution of the litter layer to soil respiration. During the previous 24 measurements individual chambers within treatment plots maintained a fairly consistent ranking in terms of soil CO_2 efflux. (Figure 6.1 – described later). Each chamber was ranked according to its contribution to the average treatment soil respiration estimate. The chambers ranked 2, 4, 6, 8, 10 and 12 within each treatment had the litter within the chamber removed. This enabled an estimate of treatment mean soil respiration to continue to be obtained from the remaining undisturbed (retained litter) chambers that approximated the mean estimate obtained from the original 12 soil respiration chambers. The litter layer was "replaced" with 3-4 mm depth of inert, alkathane beads, to prevent any large fluctuations in soil temperature and moisture content within the chamber. The beaded chambers were treated the same as the undisturbed chambers for the remaining 12 measurements in 1993.

6.4 Results and Discussion

6.4.1 Influence of slash from thinning operations on soil respiration estimates

To test the influence of slash presence on soil respiration rates in each of the treatments an Analysis of Variance test was undertaken using slash presence as the factor on three contrasting measurements:

- the initial measurement (measurement 1 – 17/18 December 1991);
- measurement 4 (18/19 February 1992 - summer) with the highest soil respiration rates measured in 1992; and
- measurement 11 (15/16 August 1992 -winter) with the lowest soil respiration rates measured in 1992.

Figure 6.1 shows the soil respiration rates from 7 treatments from chambers situated within slash and not in slash remaining on the ground from the thinning operation in 1988. Table 6.2 shows that there was no significant difference

between the average soil respiration rates for chambers located within thinning slash and non-slash chambers. The subsequent treatment average was determined as the average of the 12 chamber soil respiration measurements.

Table 6.2: Significance levels of slash vs. non-slash chamber soil respiration measurements across all treatments. P values are not significant at 95% significance level. Treatments C2 and C3 were not included as only one chamber was situated within the slash strata.

		One Way ANOVA P value		
Treatment	**% slash**	**Mment 1**	**Mment 4**	**Mment 11**
IL+	30	0.0879	0.8651	0.9312
IL-	64	0.9018	0.8979	0.7672
IF-	42	0.6100	0.2201	0.2569
IF+	30	0.3847	0.0911	0.1352
I	30	0.6429	0.6033	0.2574
C1	50	0.9645	0.5758	0.5826
F	30	0.7992	0.9153	0.7221

The lack of difference between slash and non-slash soil respiration rates was not surprising as the slash had been produced in the late 1988 thinning. Much of the readily decomposable needle material should have been decomposed by the time soil respiration measurements commenced in 1991. The majority of the slash in 1992 was woody material with low decomposition (CO_2 evolution) rates and the small amounts of needle material remaining should not have added significantly to respired CO_2.

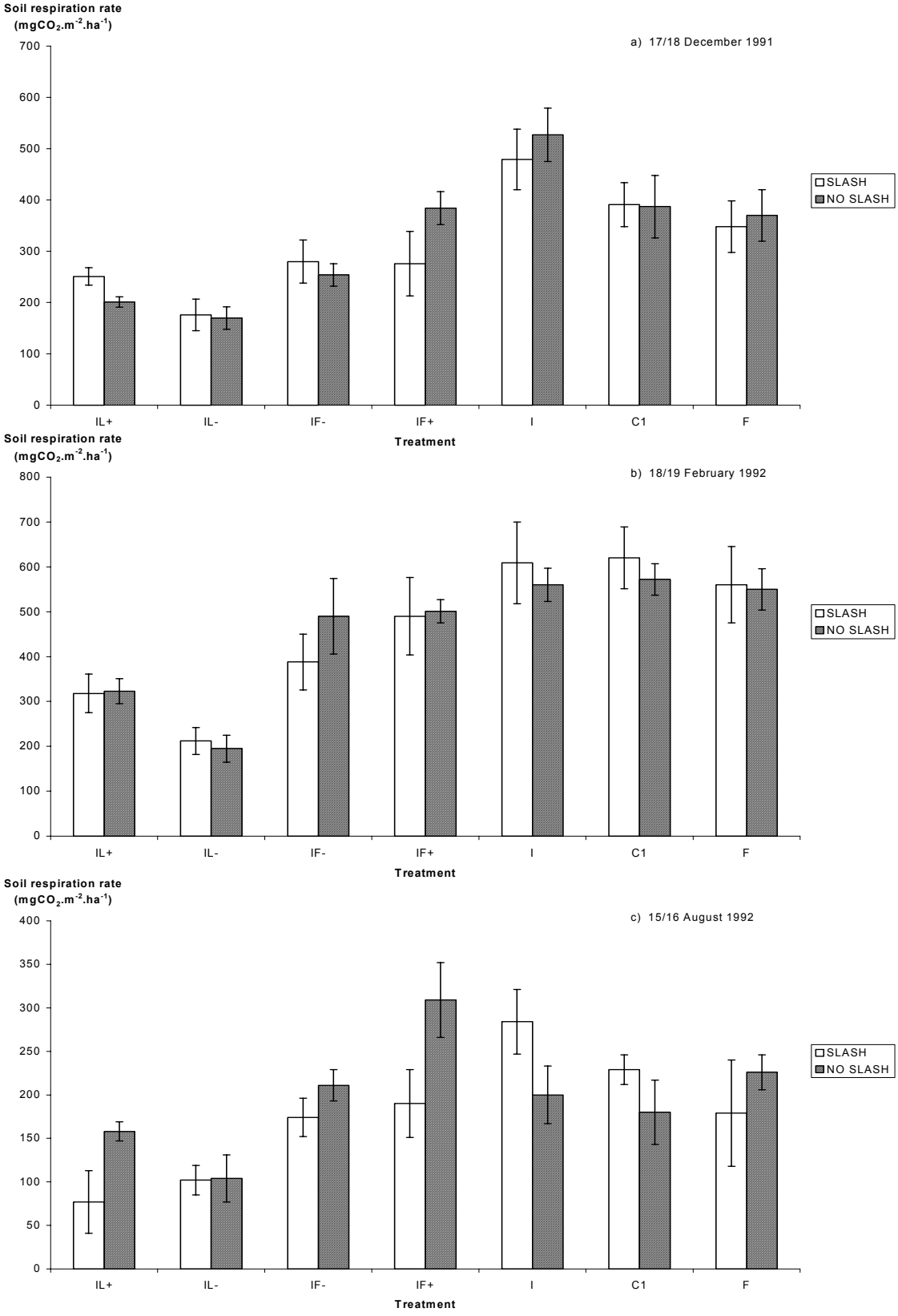


Figure 6.1: Comparison of soil respiration rates from chambers situated in slash and not in slash from thinning operations. Three dates are shown: a) Measurement 1 –18/19 December 1991, b) Measurement 4 – 18/19 February 1992 and c) Measurement 11 – 15/16 August 1992). Note the different scales on the Y-axis between the graphs.

6.4.2 Spatial variation in respiration between individual chambers in treatments

A guide to the number of chambers distributed in each treatment was determined by an initial measurement undertaken in October 1991 on the control plot (C1) that showed that 12 chambers captured 90% of the variation in soil respiration measurement with a probability of 95%. This resulted in 12 chambers being placed in each treatment. Thus at any one measurement 12 soil respiration rates were averaged to produced a treatment average for the measurement, once there was shown to be no difference between slash and non-slash chambers (Section 6.4.1). The difference in soil respiration estimates in each of the 12 chambers within a treatment provided an indication of the spatial variability in soil respiration across the treatments.

The soil respiration rates of individual chambers within treatments were plotted for the highest and lowest average respiration rates in 1992 and 1993. Figure 6.2 shows individual chamber soil respiration rates plotted for the control plot (C1), unthinned (U/T), irrigated only (I) and irrigated plus liquid fertilized (IL+) treatments.

In general, on the treatment plots with higher respiration rates (C1, U/T and I) chambers maintained their hierarchy in soil respiration rates between the measurements. There is little crossover in the chambers at either the highest or lowest respiration measurement. The chambers in the IL+ treatment have a less clear distinction between the chambers. The IL+ treatment consistently had low soil respiration rates. The variability during measurements at the lower respiration rates was higher with standard errors ranging from 7 – 47%, whereas at higher respiration rates the standard errors range from 6-16% (data not shown).

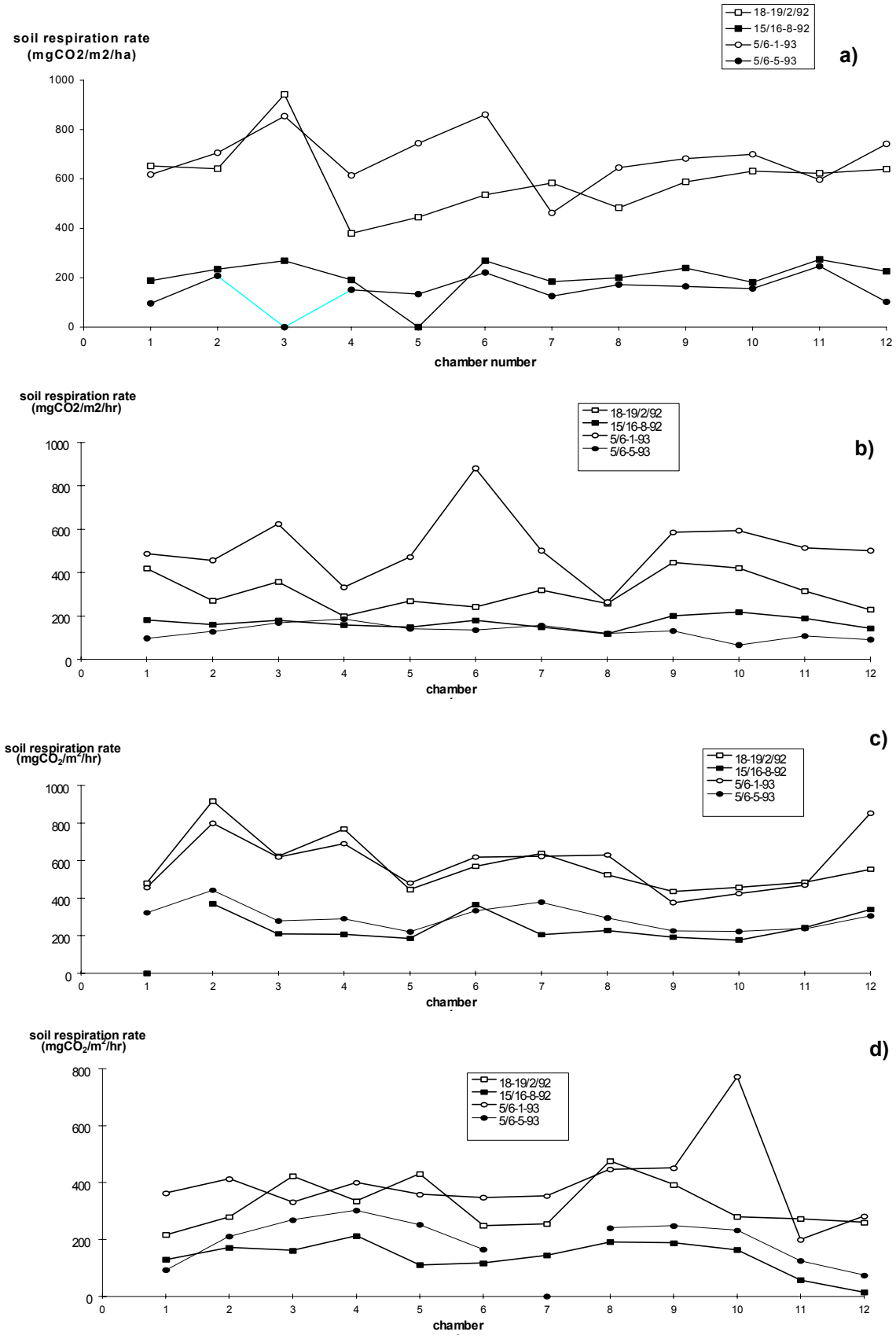


Figure 6.2: Individual chamber soil respiration rates for the lowest and highest average measurements in 1992 and 1993, for treatments C1 (a), U/T(b), I(c) and IL+(d). Note that the vertical scale on IL+(d) only extends to 800 $mgCO_2.m^{-2}.h^{-1}$. Where measurements are missing this resulted from spillage, stolen chambers or chamber disturbance.

6.4.3 Variability between Control Plots

When belowground C allocation studies were commenced in 1991, the BFG experiment had no replicates of any of the treatments. In 1991 two extra control plots were established to enable between plot variation in the control stand to be examined. The average soil respiration estimates for each of the control plots (C1, C2, and C3) over 2 years is shown in Figure 6.3. It can be seen that the 3 control plots follow a very similar pattern over the 2 years, although C1 has slightly higher soil respiration rates. Over the two years of measurements C2 and C3 estimated respiration rates were 11% and 22% lower, respectively, than C1 estimates.

The soil respiration measurements from the replicate control plots (C2 and C3) were compared with the original control plot (C1) over the entire 36 measurements. It was found:

- the variance between the 3 control replicates was not significantly different at the 95% confidence level according to Cochrans C test (P=0.6098) or Bartletts test (P=0.2431);
- there was no significant difference between the means of each of the control plots at the 95% level (P=0.0675); and
- the medians of each of the control plots were not significantly different at the 95% level (P=0.0759) according to the Kruskal-Wallis test.

Hence there is no statistically significant difference in soil respiration rates between the three control plots. From this it may be inferred that inherent between plot variation was not excessive at the BFG site and that treatment differences were due to imposed irrigation and fertilization. Raison and Myers (1992) reached similar conclusions for the aboveground processes at BFG. Where the results from the 3 control plots are combined they are labelled “C-ALL” in the following presentation of results and discussion. Where individual control plots are discussed C1 is used for the control plot established in 1983, and C2 and C3 for the replicate control plots established in 1991.

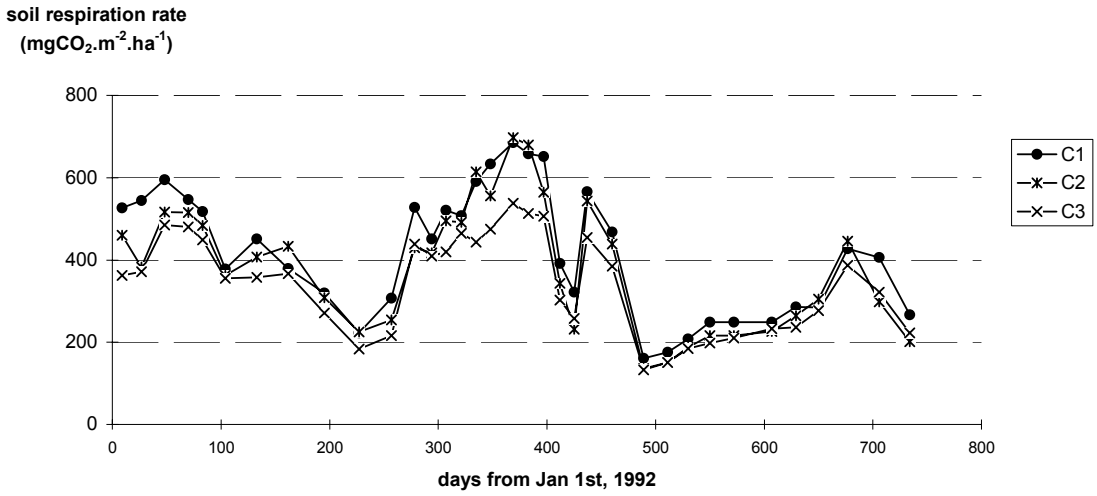


Figure 6.3: Soil respiration flux from the three control plots over 24 months throughout 1992 and 1993. C1 was the control plot established in 1983/84, C2 and C3 were established in 1991. Each point represents the mean of 12 chambers. Typical standard errors are 7.1%, 8.1% and 7.8% for C1, C2 and C3 respectively.

6.4.4 Soil respiration measurements over 2 years

6.4.4.1 Individual measurements

Figure 6.4 shows the mean soil respiration flux from all treatments in 1992 and 1993. There appear to be distinct seasonal patterns across all treatments with summer highs and winter lows in soil respiration rates. Soil respiration rates ranged about 6-fold between treatments from a high of 785 $mgCO_2.m^{-2}.hr^{-1}$ in the summer of 1992 on the I treatment to a low of 137 $mgCO_2.m^{-2}.hr^{-1}$ in the IL+ treatment in the winter of 1993. This seasonal pattern was consistent across all treatments and throughout the year. There was an occasional exception to the pattern such as the summer of 1993 where a dip in soil respiration rates between February and March (days 412 and 427 from Jan 1st 1992) was observed across all treatments. The reason for this reduction in soil respiration is not readily apparent, but may have been caused by rainfall or temperature variation.

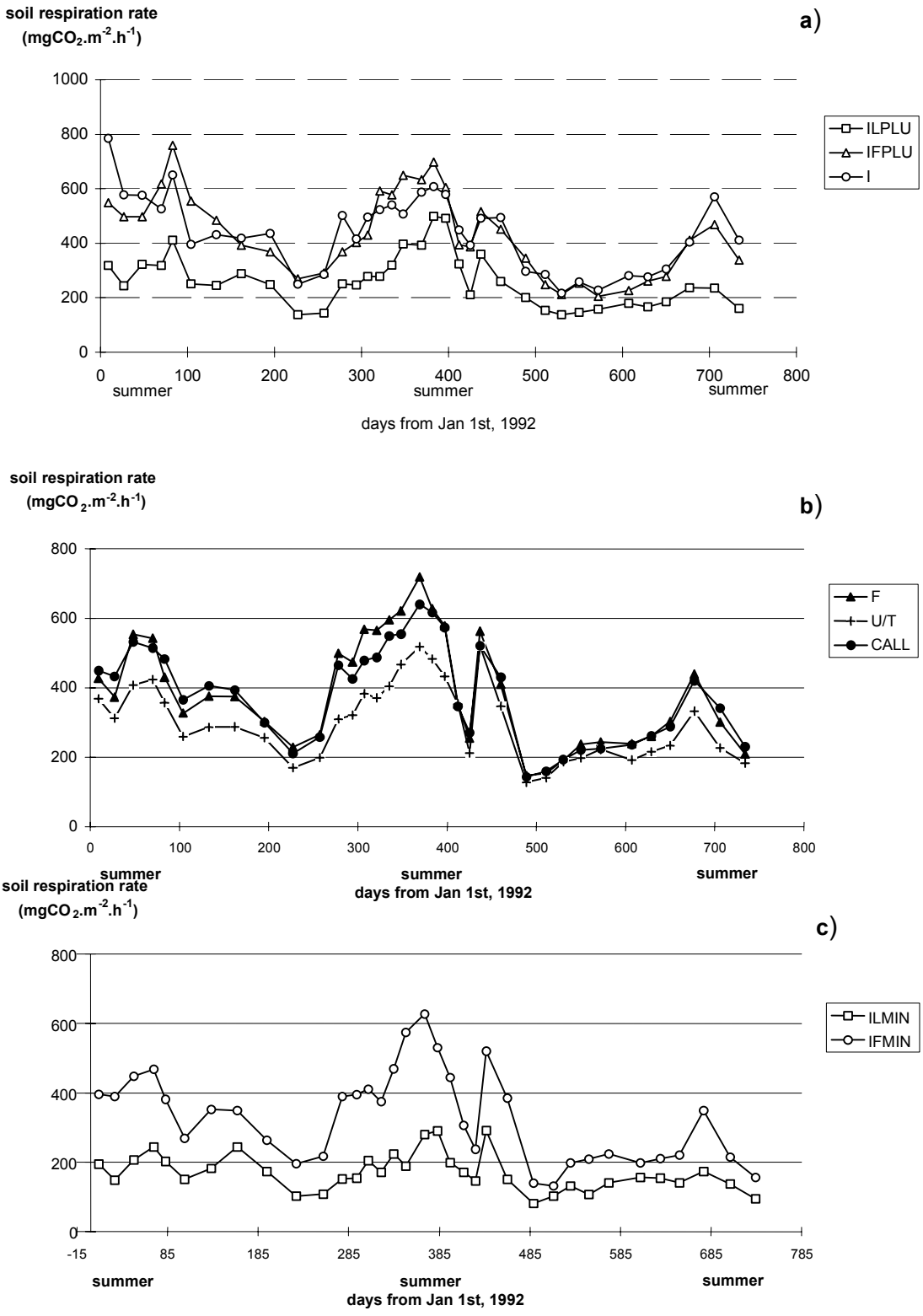


Figure 6.4: Pattern of soil respiration flux from all treatments over 1992 and 1993. Each point represents the mean soil respiration of 12 chambers in that treatment. Figure 6.4(a) represents the irrigated treatments, 6.4(b) the non-irrigated treatments and 6.4(c) represents the treatments that were irrigated until 1988. Typical percentage standards errors range from a low of 7.0% for the U/T treatment to 12.8% for the IL- treatment. Note that the maximum Y-axis scale in Figure 6.4(a) is 1000.

The treatments at BFG were not replicated. Thus it is impossible to test whether statistically significant differences occurred between the treatments. The rankings of lowest soil respiration median to highest soil respiration median were: IL-, IL+, U/T, IF-, C-ALL, F, IF+ and I. The box and whisker plot in Figure 6.5 is a graphical representation of the data. The IL- treatment had the lowest respiration compared with all other treatments, and that the IL+ and U/T treatments had overlapping median ranges.

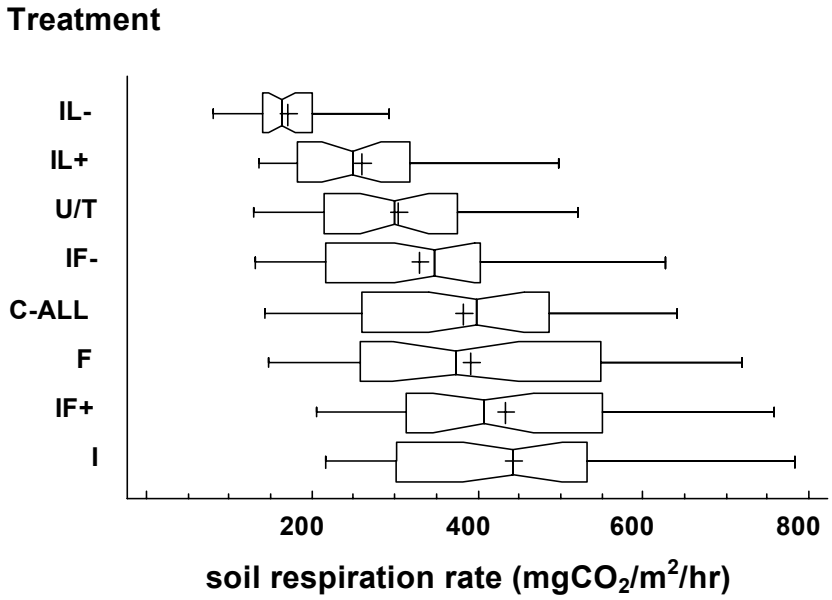


Figure 6.5: Box and Whisker Plot of the 2 year soil respiration data for the 8 treatments. The boxes, which are notched at the median, represent the middle 50% of the data while the sides of the boxes are upper and lower quartiles. The whiskers show the range of the data. The length of the notches around the median show the approximate 95% confidence interval for the median. The data mean is represented by the +.

Figure 6.6 is a more familiar plot of mean soil respiration rates with their associated standard error values. Standard statistical tests could not be undertaken on the data as the treatments were not replicated, and had only a single value for comparison. However Figure 6.6, similarly to Figure 6.5, does show that the I and F+ treatments showed the highest mean soil respiration rate followed by F and C-ALL. U/T and IF- were ranked above IL- and IL+, but showed lower mean soil respiration rates compared to F and C-ALL.

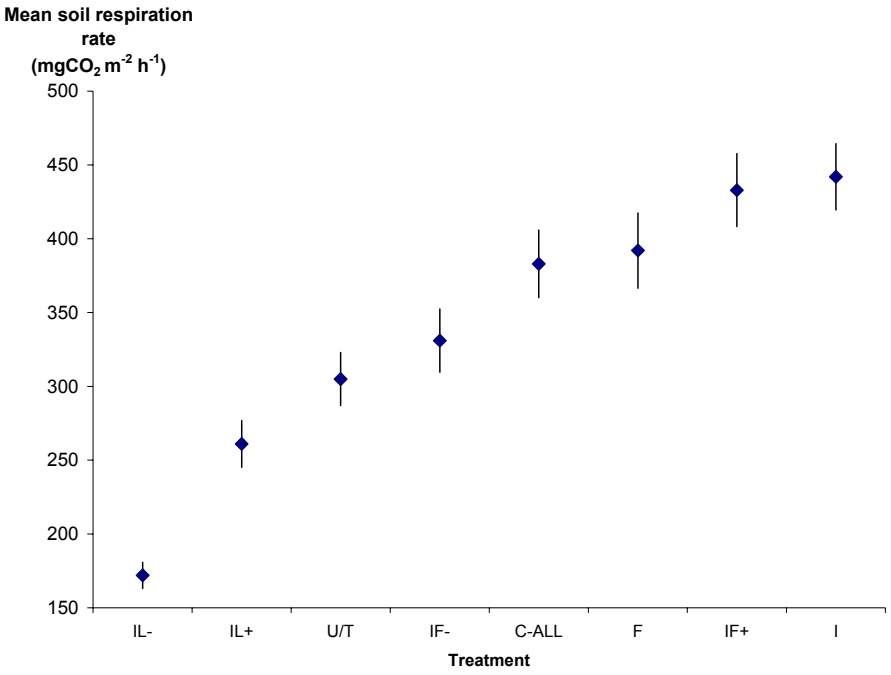


Figure 6.6: Plot of means of treatments with similar variances. Bars indicate least significant differences.

6.4.4.2 Cumulative curves

Cumulative soil respiration curves provide an alternative representation of the 2-year soil respiration data (Figure 6.7). The cumulative soil respiration curves were derived by linear interpolation - summing the average soil respiration for each measurement period for each treatment, and plotting the cumulative total at each subsequent measurement date. This approach emphasises the difference between treatments over the course of a single year, or two years, and also shows seasonal differences by the steepness of the curve.

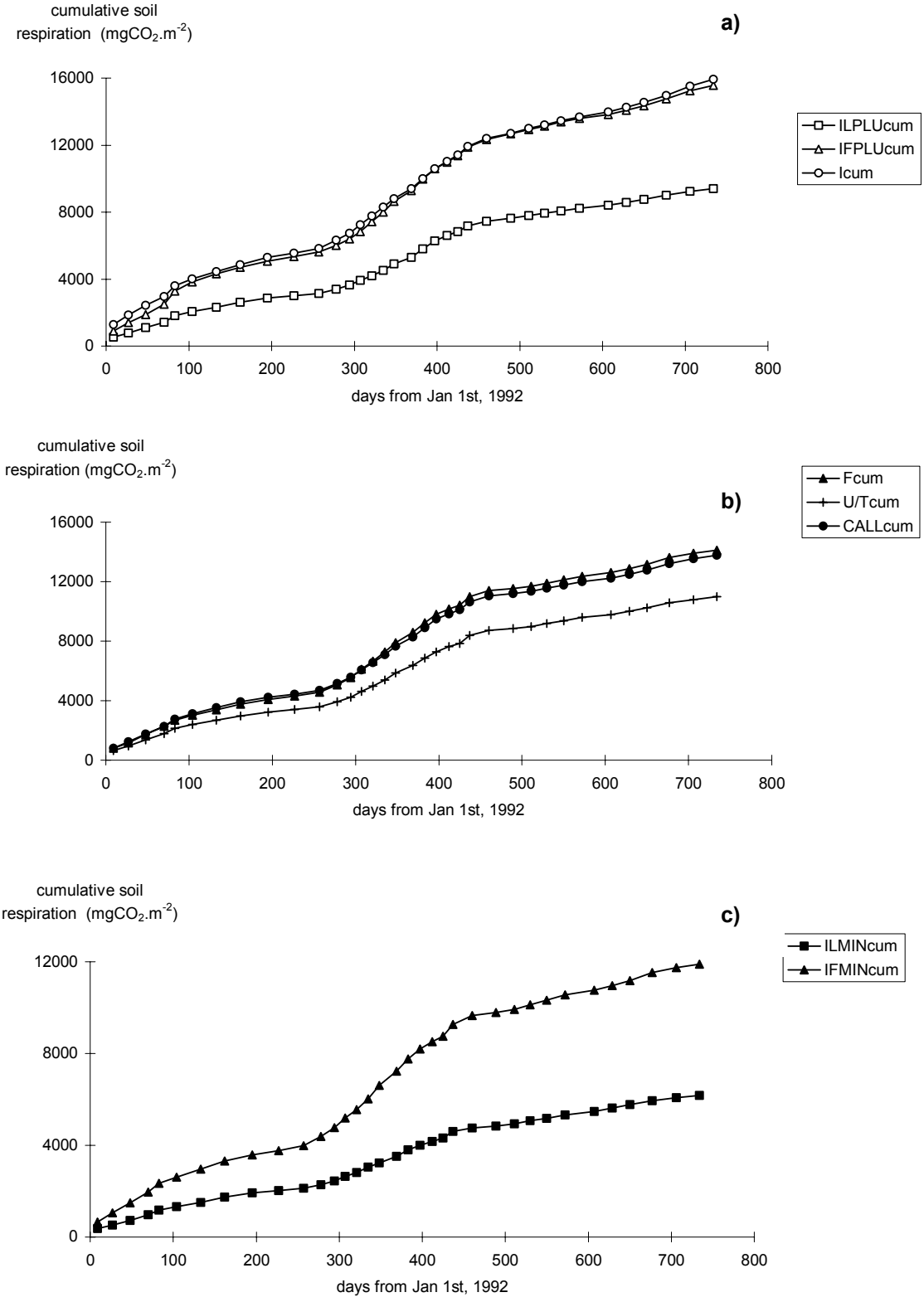


Figure 6.7: Cumulative soil respiration curves from treatments over 1992 and 1993. Each point is the mean soil respiration from each period added to the previous cumulative soil respiration. Figure 6.7(a) represents the irrigated treatments, 6.7(b) the non-irrigated treatments and 6.7(c) represents the treatments that were irrigated until 1988. Note that the scale in figure 6.7(c) is only 12,000, rather than 16,000 as in 6.7(a) and 6.7(b).

The I and IF+ treatment had the greatest cumulative soil respiration, followed closely by the C-ALL and F treatments. The lowest cumulative soil respiration occurred in the IL- and IL+ treatments, with the U/T and IF- treatments having intermediate soil respiration. Cumulative soil respiration over 1992 and 1993 ranged by almost 3-fold, from a low of 6,175 $mgCO_2.m^{-2}$ in the IL- treatment to 15,937 $mgCO_2.m^{-2}$ in the I treatment.

6.4.5 Influence of water and temperature on soil respiration rates

6.4.5.1 Simple regression

The effect of soil temperature and moisture content and litter moisture content on soil respiration rates was initially examined using simple linear regressions. Correlation coefficients are shown in Table 6.3. Exponential regressions between soil respiration and abiotic factors explained less of the variation than the simple linear regressions and are not shown.

As expected, for the irrigated treatments soil temperature had a much larger influence on soil respiration rates than did soil moisture content or litter moisture content. Soil temperature explained about 50% of the variance. In general the soil moisture and litter moisture contents were non-significant.

The non-irrigated treatments do not exhibit such clear relationships. For the IL-, C-ALL and U/T treatments soil temperature has the most significant influence on soil respiration rates explaining approximately 40% of the variation. The IF- and F treatments had soil moisture content explaining approximately 30-40% of the variation. Litter moisture content was only marginally related to soil respiration rates.

Table 6.3: r^2 values (x 100 for ease of presentation) for simple linear regressions between temperature and moisture, and estimated soil respiration rates. All regressions retained constants as these improved r^2 values. Temp 1 = soil temperature at 1 cm depth; Temp 10 = soil temperature at 10 cm depth; MC 0-5 = soil moisture content at 0-5 cm depth; MC 5-10 = soil moisture content at 5-10 cm depth; MC 10-20 = soil moisture content at 10-20 cm depth; MC-all = soil moisture content 0-20 cm and Lit MC = litter moisture content. n = 24, significance level = 0.95% (ns = non significant).

	Parameters						
Trt	**Temp 1**	**Temp 10**	**MC 0-5**	**MC 5-10**	**MC 10-20**	**MC-all**	**Lit MC**
IL+	58	51	29	22	22	24	ns
IF+	69	62	ns	ns	ns	ns	ns
I	58	57	ns	ns	ns	ns	14
IRR ALL	52	48	ns	ns	ns	ns	31
IL-	18	19	ns	ns	ns	ns	ns
IF-	34	28	32	34	39	36	ns
C1	40	60	16	19	27	23	14
C2	26	23	14	24	29	24	ns
C3	32	30	21	27	27	27	ns
C-ALL	33	49	23	28	33	28	5
F	27	23	41	46	52	49	ns
U/T	38	29	21	33	36	34	ns
NON IRR ALL	29	42	24	23	21	23	15
NON IRR NO IL-	34	50	26	34	36	34	7

For the IL- treatment, respiration rate was poorly correlated with all parameters (maximum r^2 = 19 for soil temperature at 10 cm). Thus the non-irrigated treatments were evaluated as a group, both with and without the IL- treatment. These regressions indicate that soil temperature at 10 cm depth was the most significant parameter with an r^2 of 42 with the IL- treatment included, and an r^2 of 50 without the inclusion of the IL- treatment.

6.4.5.2 Multiple Regression

The Regression Model Selection in Statgraphics Plus (Manguisitics, 1997) was used to apply multiple regression analysis to the soil respiration rates. MC-all was chosen as a measure of soil moisture following the logic and methods of Keith *et al*, (1997).

The regression model selection (RMS) method showed that in all treatments and combinations of treatments (e.g. irrigated treatments, non irrigated treatments - with and without IL-) the majority of the variation could be explained by just two parameters, although these parameters varied somewhat from treatment to treatment (Table 6.4). The correlation between soil temperature at 1cm depth and 10 cm depth was 0.80 for non-irrigated treatments and 0.94 for irrigated plots (a correlation greater than 0.5 is significant), hence the soil temperature at 1 cm and 10 cm depth were not used in the same regression.

Table 6.4: Adjusted r^2 values for multiple regressions between soil respiration rate and Temp 1, Temp 10, MC-all and Lit MC. RMS = regression model selection which provides r^2 values for linear models which account for the majority of the variation. MR = multiple regression model which actually calculates model coefficients and constants and has an associated r^2 value. ns = non significant at 95% confidence level. Bold r^2 values show the highest significance for each treatment. Empty cells indicate that simple regression explains a greater percentage of the variation.

	Temp 1 + MC-all		Temp 10 + Lit MC		Temp 10 + MC-all	
TRT	**RMS**	**MR**	**RMS**	**MR**	**RMS**	**MR**
IL+			65	ns	48	ns
IF+			63	ns	68	ns
I			50	ns	59	ns
IRR ALL			53	**53**	40	ns
IL-			24	ns	22	ns
IF-			44	ns	63	**63**
C1	68	**68**	42	ns	51	51
C2	48	48	41	ns	49	**49**
C3	62	**62**	43	ns	62	**62**
C-ALL	60	**61**	39	ns	51	51
F	57	ns	35	ns	61	**65**
U/T	64	64	53	ns	68	**69**
NON IRR ALL	46	**47**	33	ns	44	40
NON IRR NO IL-	61	**61**	41	ns	55	53

Once the most appropriate models were selected using RMS, these were run through the multiple regression model and an adjusted r^2 determined for each relationship. Table 6.4 shows that although some models were selected as appropriate in the RMS procedure, the regression analysis indicated that the second parameter was not significant for some treatments. Where soil

temperature, at either 1cm depth or 10cm depth, was used in conjunction with MC-ALL (soil moisture content 0-20cm depth) the regressions were significant for the non-irrigated treatments. The combination of soil temperature and litter moisture content did not result in any significant multiple regressions for non-irrigated treatments (Table 6.4).

For irrigated treatments the best overall descriptor of soil respiration rate was:

$$\text{soil respiration} = f(\text{Temp 10, Lit MC}) \qquad r^2 = 53.$$

(Equation 6.4)

For non-irrigated treatments (excluding IL-) the best overall descriptor of soil respiration rate was:

$$\text{soil respiration} = f(\text{Temp 1, MC-all}) \qquad r^2 = 61.$$

(Equation 6.5)

6.4.6 Influence of litter layer on soil respiration rates

The mass of litter removed from the chambers across different treatments varied threefold between maximum and minimum mass removed (range 6.41 to 18.45 tC ha^{-1} - Table 6.5). However, the influence of the litter removal on soil respiration estimates was not obvious during the final 10 measurements of soil respiration in 1993 (Table 6.6).

Table 6.5: Mean mass of litter removed from soil respiration chambers across all treatments. Litter was assumed to be 45% C (McMurtrie *et al*, 1992).

Treatment	Mass litter (tC/ha)	Standard deviation (n=6)
IL+	18.45	2.5
IF+	16.82	8.1
I	8.16	3.4
C1	6.14	3.0
C2	8.51	1.5
C3	7.28	2.2
F	6.41	2.2
U/T	8.99	4.0
IL-	13.48	1.2
IF-	9.21	1.7

Table 6.6 shows the effect of litter removal on the soil respiration rate between the chambers with litter and the chambers with litter removed. The effect of litter removal on soil respiration was rarely significant, and where it was significant the effect was not consistent across treatments, nor across irrigated and non-irrigated treatments. Figure 6.8 shows the ratio of soil respiration rates in chambers with litter to soil respiration rates in chambers without litter. The tight scatter around 1.0 indicates that litter contributes little to the measured soil respiration rates, as is also evidenced by the statistical tests in Table 6.6.

Table 6.6: Percentage difference in soil respiration rates for chambers with litter removed compared to chambers with litter retained across treatments. Differences were significant at 95%, - = not significant. There were 6 chambers with litter and 6 chambers with litter removed in each treatment.

Date	Treatment (% difference in soil respiration rates without litter)									
	IL+	IF+	IRR	C1	C2	C3	F	U/T	IL-	IF-
27/28-5-93	-	-	-	-	-	-	-32	-	47	-
15/16-1-93	-	-	-	-	-	-	-	-	-	-
5/6-7-93	93	-	-	-	-	30	-	-	-	-
27/28-7-93	-	-	-	-	-	-	-	-	-	-
31/8/1/9-93	-	-	-	-	-	-	-26	-	-	-
22/23-9-93	-	-	-	-	-	-	-	-	-	-
13/14-10-93	-	-	-	-	-	-	-	-	-	-
9/10-11-93	-	-69	-	-	-	-	-	-	-	-
8/9-11-93	-	-70	-	-	-	-	-	-	-	-
356/7-1-94	-	-58	-	-	-	-	37	-	-	-

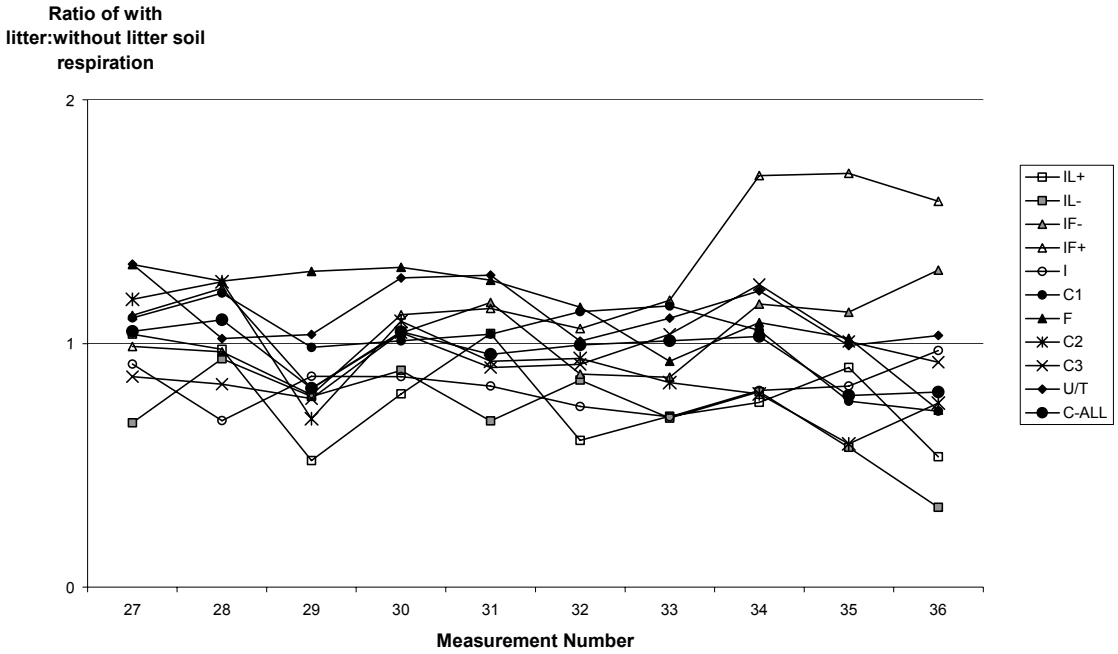


Figure 6.8: Ratio of with litter : without litter soil respiration rates for all 10 treatment plots and the C-ALL estimate. The scatter around 1.0 indicates little contribution of litter to the measured soil respiration rate.

In order to capture any short term effects of chamber litter removal on soil respiration, the measurement immediately post litter manipulation was investigated closely. This measurement occurred one week post replacing the litter with inert beads, allowing the chambers to "settle" post disturbance. Regressing the ratio of soil respiration estimates of litter removed chambers to litter retained chambers against the amount of litter removed from each of the chambers again produced inconclusive results with the regression being weakly correlated for non-irrigated treatments (r^2 = 0.25), but not for irrigated treatments (non significant - Table 6.7). The weak correlation also supports the lack of trend in Figure 6.8, which indicates that litter contributes little to measured soil respiration.

Table 6.7: Significance of regression of ratio of soil respiration estimates of litter removed chambers to litter retained chambers, and amount of litter removed from those chambers at first measurement post litter manipulation (Measurement 27 - 27/27-5-1993 one week post manipulation).

Treatments	No. of chambers	significance	r^2x100
all	59	P<0.05	7.6
irrigated	18	ns	0.2
non irrigated	42	P<0.05	24.8
non irrigated without IL-	36	P<0.05	27.4

The overall outcome of the litter manipulation experiment is that the litter layer contributes little to the overall soil respiration estimate. This is shown by the lack of response in soil respiration estimates post litter removal, and by the variation of the ratio of soil respiration in chamber with litter retained, and chambers without litter retained. Due to this lack of response of litter removal, all 12 chambers were used to estimate the average treatment soil respiration rate for the full 36 measurements undertaken over two years.

6.4.7 Influence of fine roots on soil respiration estimates

Fine root biomass estimates were described in Chapter 4, Section 4.5. To investigate the influence of fine roots on soil respiration estimates obtained, fine root biomass, fine root nitrogen concentration [N] and root N (calculated by multiplying fine root [N] by root biomass) were compared with soil respiration measurements taken in August 1992 and March 1993. This coincided with the spot biomass estimates of fine roots taken during periods of low soil respiration (August 1992) and high soil respiration (March 1993).

There was no significant relationship between soil respiration rates and fine root biomass in the <0.5mm and <2.0mm diameter classes for either 1992, 1993 or 1992 and 1993 combined (data not shown). There was also no significant relationship between soil respiration rates and root tissue [N], which contrasts with Ryan *et al* (1996a) who showed a strong correlation between root tissue respiration and root [N]. However soil respiration combines root, symbiont and decomposed respiration and the lack of a strong relationship with root tissue [N] is not unexpected. However there was a statistically significant relationship between soil respiration and total root N (Figure 6.9) which showed that soil respiration decreases as total root N increases.

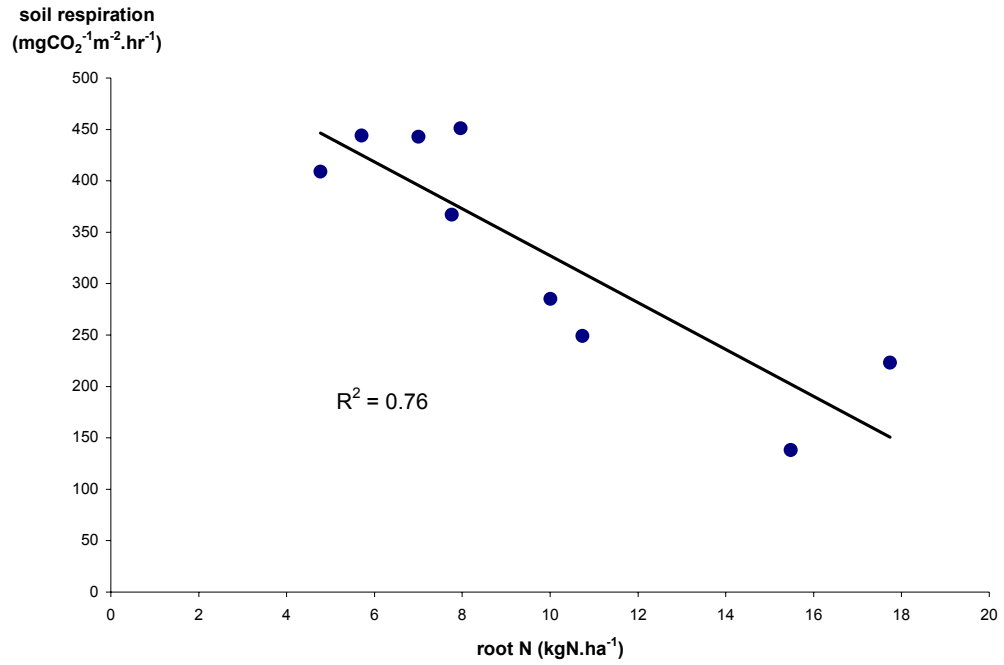


Figure 6.9: Monthly soil respiration estimates for August 1992 and March 1993 correlated with total root N of white, dead and brown roots(<2mm diameter)to 10cm depth at the same periods.

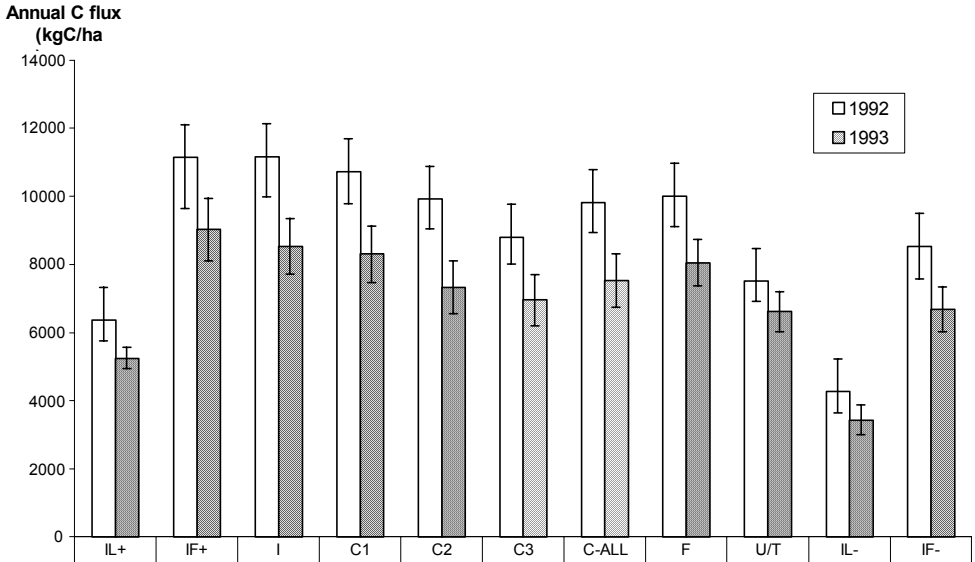
Ryan *et al* (1996a) indicated that soil respiration at BFG was likely to be dominated by root respiration, which accounted for up to 60% of total soil respiration estimates in their study. However, Ryan *et al* (1996a) also pointed out that root respiration rates estimated in their study may be falsely elevated due to the lower CO_2 concentration in the respiration cuvette compared to the normal soil CO_2 atmosphere in which the roots exist. Hence the root respiration described by Ryan *et al* (1996a) may not be truly representative of actual root tissue respiration. A strong relationship between fine root data (live biomass < 2mm diameter) and soil respiration could not be shown with the limited fine root data sampled at BFG in 1992 and 1993, although total root N did appear to have a significant, negative influence on soil respiration.

6.4.8 Annual soil C flux

The annual soil C flux was calculated by multiplying the average (start and end of period) soil respiration by the number of days between successive soil respiration measurements. This was undertaken in preference to predicting soil

respiration from soil temperature and soil or litter moisture because regression equations did not explain more than 53 or 61% of the variation in the soil respiration measurements. In addition there was no comprehensive data to drive the models in greater detail between the spot measures.

Figure 6.10 shows the annual soil C flux for each of the treatments for 1992 and 1993. Average soil C flux across all treatments was 20% lower for 1993 compared with 1992, although IL-, IF+ and U/T did not exhibit a statistically significant difference between the years. The average annual rainfall for 1992 was 1008 mm, and 808 mm for 1993, compared to the long term average of 790 mm. Soil C fluxes for 1992 may have been higher because of the 28% greater than average rainfall, and consequent stimulation of biologically mediated C cycling in the forest although a relationship between soil C flux and soil moisture or litter moisture could not be defined for the measurements taken in this study.



	IL+	IF+	I	C1	C2	C3	C-ALL	F	U/T	IL-	IF-
1992	6367.62	11144.65	11164.46	10730.39	9924.52	8802.50	9819.14	10010.71	7502.05	4256.49	8536.32
1993	5247.26	9028.99	8534.01	8302.24	7331.87	6952.07	7528.73	8050.61	6612.19	3425.91	6679.96

Figure 6.10: Annual C flux by treatment for 1992 and 1993.

Figure 6.11 shows the same data as Figure 6.10 with the 1992 annual soil C flux plotted against the 1993 annual soil C flux. The reduction in soil respiration in 1993 can be clearly seen, and as expected the relationship between the two years is strongly correlated with an r^2 of 0.97 ($P<0.01$).

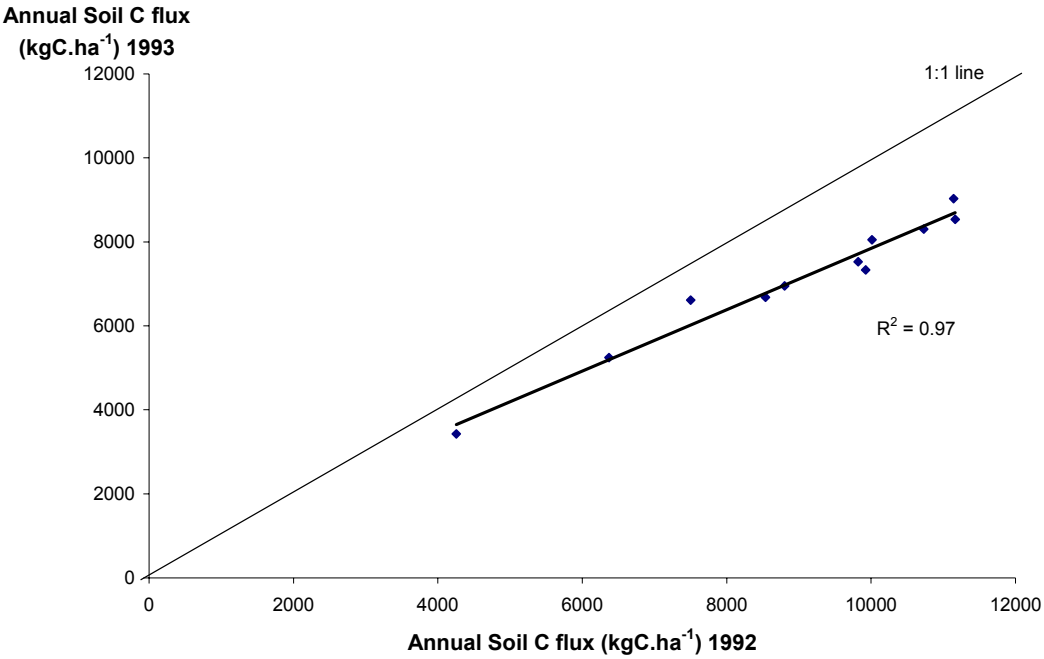


Figure 6.11: Annual soil C flux for 1992 plotted against annual soil C flux for 1993 for all 10 treatment plots and the C-ALL estimate.

Raison and Myers (1992) derived a relationship to predict aboveground net primary production from basal area increment using the data from the intensive aboveground study period between 1983 and 1988:

$$NPP = 3.5 + 1.77\ BAI \quad (r^2 = 0.76)$$

where NPP is in tC ha^{-1} and BAI is basal area increment in $m^2.ha^{-1}$. Figure 6.12 shows the total annual soil C flux compared to calculated aboveground NPP for combined 1992 and 1993 data. The upper linear relationship is derived for high nutrition treatments, IL+ and IL-, and shows a strong relationship between aboveground NPP and annual soil C flux ($r^2 = 0.78$). The lower linear relationship combines all other treatments for 1992 and 1993 and indicates a weaker, but significant correlation ($r^2 = 0.30$, $P<0.05$) between annual soil C flux and estimated NPP. Separating the data into 1992 only, and 1993 only, does not indicate a significant relationship between aboveground NPP (or basal area

increment) and annual soil C flux. The general trend shown by the combined years data is that aboveground NPP is generally increased with increasing soil C flux.

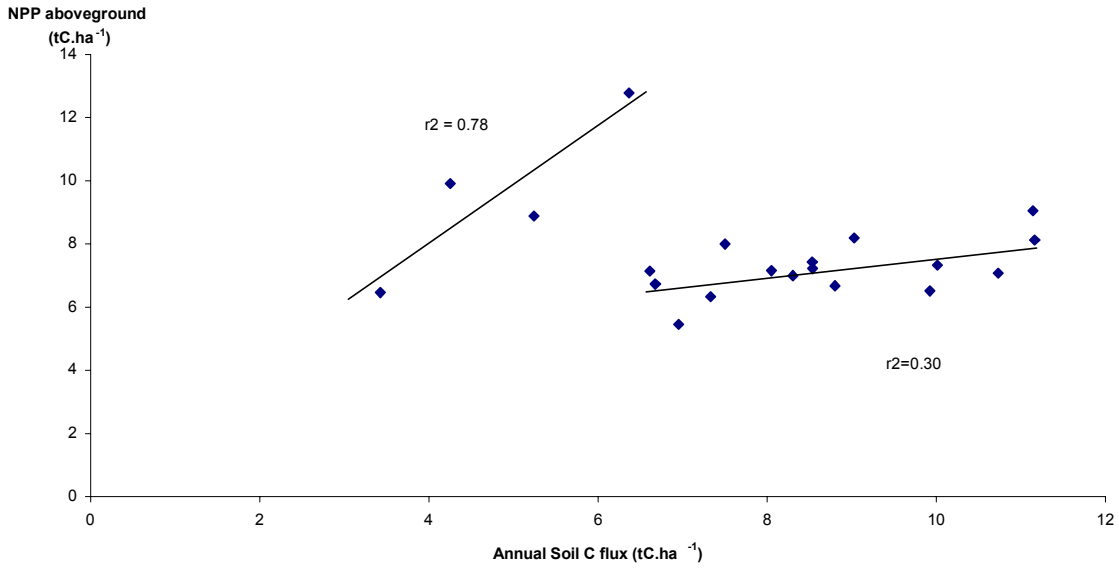


Figure 6.12: Annual soil C flux for 1992 and 1993 compared to estimated NPP for 1992 and 1993 after Raison and Myers (1992). The upper linear relationship is derived for treatments with high nutrition (IL+ and IL-), while the lower linear relationship is for all other treatments. 1992 and 1993 data were used to derive the relationship.

6.6 Integrative Discussion

Treatment soil respiration estimates at BFG varied between a minimum of 137 $mgCO_2.m^{-2}.h^{-1}$ and a maximum of 785 $mgCO_2.m^{-2}.h^{-1}$. Mean annual rates for treatments varied from 261 – 443 $mgCO_2.m^{-2}.h^{-1}$. Raich and Nadelhoffer (1989) collated soil respiration estimates in a variety of forest ecosystems, measured with a variety of techniques, which ranged from 76 to 632 $mgCO_2.m^{-2}.h^{-1}$. The highest soil respiration measurement at BFG was 24% higher than those reported by Raich and Nadelhoffer (1989), while the lower soil respiration estimates at BFG fell within the reported levels. BFG estimates higher than 632 $mgCO_2.m^{-2}.h^{-1}$ occurred only twice in 1992 and six times in 1993 during the summer in the high efflux treatments I, C1 and F.

Soil respiration estimates for *Pinus* systems quoted in Raich and Nadelhoffer's (1989) collation were 108 $mgCO_2.m^{-2}.h^{-1}$ for a low productivity *Pinus banksiana* forest and 133 to 525 $mgCO_2.m^{-2}.h^{-1}$ for a *Pinus densiflora* forest. Soil respiration measurements undertaken in natural trembling aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) forests using the soda lime technique in 1994 ranged from 80 to 685 $mgCO_2.m^{-2}.h^{-1}$ (Pongracic *et al*, 1997), showing that soil CO_2 efflux rates achieved in the manipulated system at BFG were not extreme. Similarly Haynes and Gower (1995) reported soil respiration values of 80 to 450 $mgCO_2.m^{-2}.h^{-1}$ in a red pine (*Pinus resinosa*) plantation. Ewel *et al* (1987b) estimated mean annual soil respiration in a 29-year-old slash pine (*Pinus elliotti*) plantation as 493 $mgCO_2.m^{-2}.h^{-1}$ and Raich *et al* (1990) estimated soil respiration at 58 to 746 $mgCO_2.m^{-2}.h^{-1}$ for a variety of mixed hardwood, *Pinus* and tropical forests. Keith *et al* (1997) recorded average daily soil respiration estimates from 124 to 574 $mgCO_2.m^{-2}.h^{-1}$ in an open sub-alpine *Eucalyptus pauciflora* forest situated approximately 50km from the BFG site. Carlyle and Ba Than (1988) measured a soil respiration range range between 230-890 $mgCO_2.m^{-2}.h^{-1}$ beneath a *Pinus radiata* plantation on a similar soil type to BFG.

The soil respiration estimates measured at BFG varied throughout the year with the highest rates occurring during periods of high temperature and high moisture availability. For the measurement period at BFG this translated to summer highs and winter lows with the difference within treatments over the season extremes varying 2 to 3 fold. This pattern was also described by Ellis (1969), Ewel *et al* (1987a), Carlyle and Ba Than (1988), Cropper *et al* (1985), Haynes and Gower (1995) and Keith *et al* (1997).

Haynes and Gower (1995) found the soil respiration was 72% lower for recently nitrogen-fertilized compared with unfertilized red pine plantations. Keith *et al* (1997) found that phosphorus fertilization reduced soil respiration rates by 9% in an *Eucalyptus pauciflora* forest. At BFG the soil respiration rate in 1992 and 1993 on the F treatment was not different to the control treatments (C-ALL). This was not surprising as the fertilizer was applied 8 years prior to commencing soil respiration measurements and the fertilizer effect on

aboveground growth appeared to have ceased. However the highly fertilized IL+ treatment had soil respiration rates which were significantly lower than C-ALL soil respiration rates, which follows trends reported by other workers.

Treatments with significantly lower soil respiration rates than the control treatments (C-ALL) were the high fertility, irrigated and previously liquid fertilized and irrigated treatments (IL+ and IL-). These high nitrogen treatments had lower soil respiration rates, but still had quite high basal area increment (Table 3.2, Section 3.5.1). The soil CO_2 efflux in the U/T treatment was also significantly lower than the C-ALL at BFG, possibly due to lower water availability. Irrigation alone did not appear to significantly influence soil respiration rates, although the irrigation only treatment (I) and the irrigation plus solid fertilizer (IF+) did tend to have higher soil respiration rates than C-ALL. Treatment differences in soil respiration rates reflect the integrated effects of litter decomposition, root respiration and root turn-over.

BFG data showed simple linear relationships between soil respiration and soil temperature explained 48 to 50% of the variation. When both soil temperature and litter moisture content were included for irrigated plots, 53% of variation was explained, and soil temperature and soil moisture content (0-20cm) explained 61% of variation in soil temperature in the non irrigated plots. In general soil temperature has a stronger influence on soil respiration measurements than did either soil or litter moisture content (Ewel *et al*, 1987a; Carlyle and Ba Than, 1988; Keith *et al*, 1997; Davidson *et al*, 1998) and this was supported by the measurements at BFG. Exponential regression relationships did not improve the amount of variation explained by the abiotic factors of soil temperature or soil and litter moisture content at BFG. Soil temperature at BFG was measured as a spot measurement each time soil respiration was measured and may have been insufficiently detailed to capture differences experienced over a 24 h period within the soil respiration chamber. This lack of detailed measurement may explain why only 53% of the variability in soil respiration rates was explained by the soil temperature measurements.

Ewel *et al* (1987a) derived a relationship between the natural logarithm of soil respiration and soil temperature at 5cm below the surface that explained between 75 and 89% of the variation found in soil respiration estimates. Carlyle and Ba Than (1988) described a relationship between soil respiration and soil temperature at the soil surface level that was dependent on the soil moisture content (0-10cm), where soil respiration was correlated with soil temperature when the soil moisture was higher than 12.5% (r^2=0.85). Where soil moisture was less than 12.5%, soil respiration was significantly correlated with soil moisture (r^2=0.91, Carlyle and Ba Than, 1988). Haynes and Gower (1995) found an exponential relationship between soil respiration and soil temperature at 10cm explained 54% of the variation occurring in soil respiration measurements. This is similar to Toland and Zak's (1994) findings where an exponential relationship between soil respiration and soil temperature at 10cm depth explained 43% of the variation in soil respiration measurements in northern hardwood forests. Keith *et al,* (1997) found a relationship between soil respiration and soil and litter moisture depended on the temperature range with measurements at <10^{o}C or > 10^{o}C. When all data was analysed in Keith *et al*'s (1997) study there was no significant relationship between CO_2 flux and moisture (soil and litter) variables. However separating the soil respiration values into greater than, and less than, 10^{o}C resulted in combinations of soil temperature, soil moisture and litter moisture explaining 83% of the variance in soil respiration values. Keith *et al* (1997) did not utilise Carlyle and Ba Than's (1988) 12.5% soil moisture content separation as the soil moisture did not decrease below 17% at the *Eucalyptus pauciflora* site. Davidson et al (1998) findings support Keith et al (1997) where 80% of the variation in soil respiration was explained by temperature relationships, but there appeared to be a mechanistic effect of drought stress on soil respiration rates during significantly dry periods.

Litter manipulation experiments at BFG suggested that litter respiration contributed little to measured soil respiration. Bowden *et al* (1993) estimated forest floor litter to contribute 37% to total soil respiration in a mixed hardwood forest, while Ewel *et al* (1987b) estimated 32% of soil respiration being contributed by the litter layer in a *Pinus elliottii* stand. The treatments at BFG

could not show this significant contribution. The mean annual litter fall input across the treatments over 1992/93 was 1.13 tC ha^{-1}. As the litter layer did not increase between 1991 and 1993 it could be assumed that this mass of litter was decomposed. The equivalent soil respiration rate for this 1.13 tC ha^{-1} of litter would be 48 $mgCO_2.m^{-2}.h^{-1}$. This rate of soil CO_2 efflux may be too low to be effectively captured by the soil respiration measurements.

Annual soil C flux ranged from 4.3 to 11.2 tC ha^{-1} in 1992 and from 3.4 to 9.0 tC ha^{-1} in 1993, with soil respiration rates consistently lower in 1993 compared with 1992. The almost 3-fold difference in soil flux within any one year reflects the different irrigation and fertilization regimes, with the higher rates achieved on the irrigated but poor nutrition sites (I in 1992 and IF+ in 1993), and the lower rates achieved on the non irrigated but high nutrition sites (IL- in 1992 and 1993). The high nutrition treatments, IL+ and IL-, showed a relatively strong relationship between annual soil C flux and estimated aboveground NPP (r^2 = 0.78), whereas the lower nutrition treatments showed a relatively weak, but significant positive relationship between annual soil C flux and estimated NPP (r^2=0.30, $P<0.05$). This indicates that aboveground activity is positively linked to soil activity.

6.7 Conclusions

Reliable estimates of soil respiration at the BFG site were obtained that ranged from 3.4 to 11.2 tC $ha^{-1}.y^{-1}$. Soil respiration rates varied from a minimum of 137 $mgCO_2.m^{-1}.h^{-1}$ to a maximum of 785 $mgCO_2.m^{-1}.h^{-1}$ and showed seasonal variation with winter lows and summer highs. The soil respiration estimates at BFG fall within the range and patterns of soil respiration estimates in similar forest systems available in the literature. The irrigated treatments, other than IL+, tended to have slightly higher soil respiration estimates than did non irrigated control treatments but they were not significantly greater. The soil respiration estimates from the U/T treatment were significantly lower than the control treatments. The highly fertilized treatments IL+ and IL- both had significantly lower respiration rates than the control treatments, with IL- (without continuous irrigation) having the lowest rate.

The dominant variable contributing to soil respiration among all treatments was soil temperature. A linear relationship was established between soil respiration and soil temperature at 10cm depth and litter moisture content for irrigated plots, which explained 53% of the variation. A similar relationship between soil temperature at 1 cm depth and soil moisture content was derived for soil respiration on the non–irrigated plots which explained 61% of the variation observed.

The litter layer could not be shown to be greatly influencing the soil respiration estimates, nor was there a strong relationship between soil respiration and fine root estimates. Limited fine root biomass data collected in August 1992 and March 1993 did not indicate that fine roots (<0.5mm and <2mm diameter) greatly influenced soil respiration estimates. However total root N (root [N] multiplied by root biomass) did show a significant negative relationship with soil respiration rate. Ryan *et al* (1996a) indicated that root respiration might dominate soil respiration at BFG, but the limited data collected in this study does not support this theory. Ryan *et al* (1996a) discussed that the root respiration data collected at BFG may be falsely elevated due to the CO_2 conditions in the respiration cuvette being lower than the CO_2 conditions in soil.

Annual soil C flux ranged from 4.3 to 11.2 tC ha^{-1} in 1992 and from 3.4 to 9.0 tC ha^{-1} in 1993, with soil respiration rates approximately 20% lower in 1993 compared with 1992. In Chapter 7 this treatment induced difference in annual soil C flux will be used to estimate total belowground C allocation for the different treatments at the BFG site, in combination with other C flux and C pool estimates described in Chapter 4.

CHAPTER 7: INFLUENCE OF IRRIGATION AND FERTILIZATION ON BELOWGROUND CARBON ALLOCATION

7.1 Introduction

Various workers (Grier *et al*, 1981; Comeau and Kimmins, 1989) have estimated that greater than 50% of photosynthate produced is allocated to the belowground system. The proportion of C allocated belowground varies with the forest type, forest age and with the quality of the site (Gower *et al*, 1995). The wide range of water and nutrient treatments at BFG provided the opportunity to determine the effects of growing conditions on belowground carbon allocation for a single species at a single site.

The aboveground C budget at BFG was thoroughly quantified during the period of intensive study (1984-1988) but little work was undertaken on the belowground system (Chapter 3). The aboveground biomass response to irrigation and fertilization was still evident in 1992 and 1993 with the basal area increase in the IL+ treatment being 35% greater than in the control (C1) treatment in 1993. The other two irrigated treatments (IF+ and I) had a 6% greater increase in basal area than the C1 treatment, and the solid fertilization treatment (F) basal area increase was the same as in the C1 treatment (Chapter 3, Table 3.2). These aboveground differences in stem productivity were expected to reflect differences in belowground C allocation.

Soil respiration was measured for two full years during 1992 and 1993 across 8 variants of irrigation and fertilization treatments at BFG (Chapter 6). Litterfall from each of the 8 treatments was also collected monthly during this period (described in Chapter 4). Soil C change was quantified for the decade 1983 – 1993 (Chapter 4) and forest floor litter was quantified between 1991 and 1993 (also Chapter 4). This data was used to estimate belowground C allocation using the method of Raich and Nadelhoffer (1989) described in Chapter 3, Section 3.7.

Estimates of fine root biomass for two periods during 1992 and 1993 were undertaken to provide insight into the drivers of soil respiration and belowground C allocation. Coarse root production was also estimated to assist in the compilation of a picture of belowground carbon allocation at BFG. These data were discussed in Chapter 4 and will be further examined in this chapter.

7.2 Materials and Methods

To calculate belowground carbon allocation using the method proposed by Raich and Nadelhoffer (1989) it is necessary to have estimates of:

1. soil respiration;
2. aboveground litterfall; and
3. change in the mass of C in the forest floor and soil.

These estimates were described earlier in Chapters 4 and 6.

Annual belowground carbon allocation for 1992 and 1993 was determined by:

$$\text{Belowground C} = C_{soilresp} - C_{litterfall} + C_{coarseroot} + \Delta C_{forest\ floor} + \Delta C_{soil}$$

(Equation 7.1)

Treatments that were sampled for soil C in 1984 and 1994 showed no increase in soil C (Chapter 4, Section 4.6.3). As these treatments included the high productivity (IL+) and control (C1) treatments it was assumed that soil C had not changed in any of the treatments used in the soil respiration studies during 1992 and 1993 (i.e. $\Delta C_{soil} = 0$ for all treatments). For most plots the change in forest floor carbon ($\Delta C_{forest\ floor}$) was zero (Chapter 4, Section 4.3.3.1). However the two replicate control plots established in 1991, C2 and C3, showed an increase in forest floor carbon. Belowground C allocation was estimated for these replicate control plots in two ways: firstly assuming no increase in forest floor C, and secondly assuming an increase in forest floor C ($C2_{adj}$ and $C3_{adj}$). The increase in forest floor C for C2 and C3 was adjusted by the mass of litterfall C in each year as this parameter was measured accurately, and is the upper limit to the theoretical increase in forest floor C (see Chapter 4, Section 4.7).

Belowground C allocation was calculated for all of the treatment plots at BFG for each year using Equation 7.1. This belowground C estimate consisted of coarse root biomass increase and C allocation to fine roots, root respiration, mycorrhizae and exudates for 1992 and 1993.

7.3 Results and Discussion

7.3.1 Belowground C allocation

Tables 7.1 and 7.2 show the parameters used to calculate belowground C allocation in 1992 and 1993 respectively.

Table 7.1: Parameters used to calculate belowground C allocation in 1992. All values are in tC ha^{-1}.

Treatment	Soil C flux	Litterfall C	Increase in coarse root C	Change in forest floor (standing litter) C	Change in soil C	Belowground C allocation (Equation 7.1)
IL+	6.37	1.42	5.39	0.00	0.00	*10.34*
IF+	11.15	0.83	3.00	0.00	0.00	*13.32*
I	11.16	0.68	2.42	0.00	0.00	*12.91*
C1	10.73	0.57	1.79	0.00	0.00	*11.95*
C2	9.93	0.75	1.18	0.00	0.00	*10.36*
$C2_{adj}$	9.93	0.75	1.18	0.75	0.00	*9.61*
C3	8.80	0.70	1.67	0.00	0.00	*9.77*
$C3_{adj}$	8.80	0.70	1.67	0.70	0.00	*9.07*
C-ALL	9.82	0.67	1.55	0.00	0.00	*10.69*
C-ALL_{adj}	9.82	0.67	1.55	0.67	0.00	*10.03*
F	10.01	0.55	1.95	0.00	0.00	*11.41*
U/T	7.50	0.83	2.03	0.00	0.00	*8.71*
IL-	4.26	1.27	3.68	0.00	0.00	*6.67*
IF-	8.54	1.03	1.94	0.00	0.00	*9.44*

* C-ALL is the mean of the 3 control plots (C1, C2 and C3), $C2_{adj}$, $C3_{adj}$ and C-ALL_{adj} indicate the estimate where forest floor litter increased between 1992 and 1993.

Table 7.2: Parameters used to calculate belowground C allocation in 1993. All values are in tC ha^{-1}.

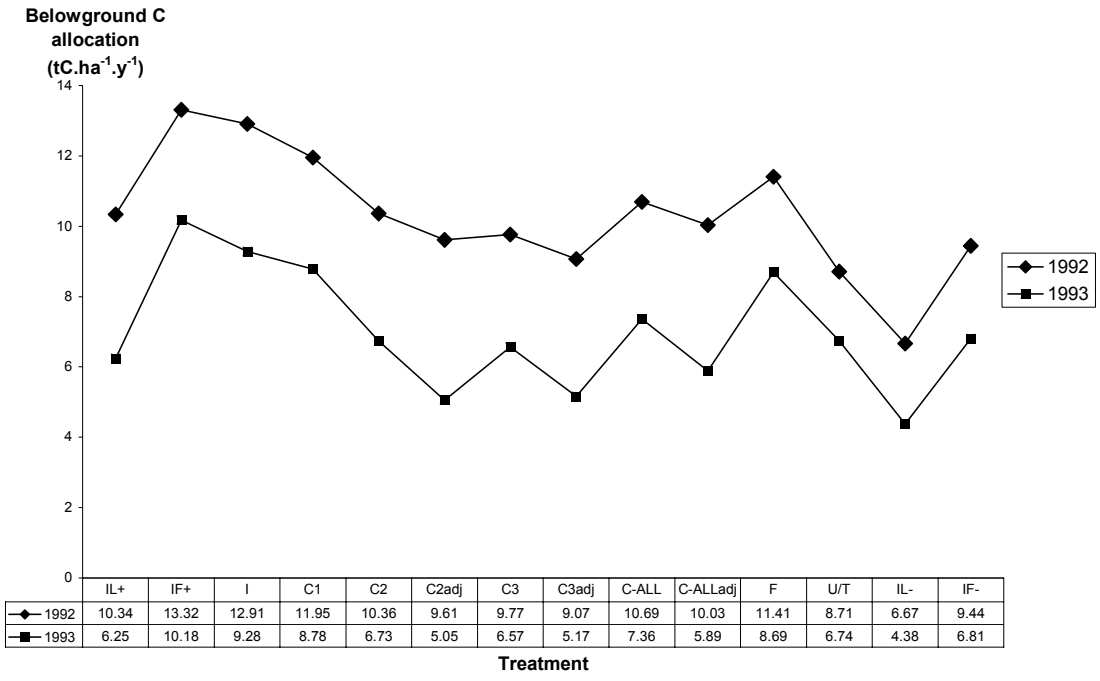
Treatment	Soil C flux	Litterfall C	Increase in coarse root C	Change in forest floor (standing litter) C	Change in soil C	Belowground C allocation (Equation 7.1)
IL+	5.25	2.24	3.24	0.00	0.00	*6.25*
IF+	9.03	1.44	2.59	0.00	0.00	*10.18*
I	8.53	1.37	2.12	0.00	0.00	*9.28*
C1	8.30	1.33	1.81	0.00	0.00	*8.78*
C2	7.33	1.68	1.08	0.00	0.00	*6.73*
$C2_{adj}$	7.33	1.68	1.08	1.68	0.00	*5.05*
C3	6.95	1.39	1.00	0.00	0.00	*6.57*
$C3_{adj}$	6.95	1.39	1.00	1.39	0.00	*5.17*
C-ALL	7.53	1.47	1.30	0.00	0.00	*7.36*
$C\text{-}ALL_{adj}$	7.53	1.47	1.30	1.47	0.00	*5.89*
F	8.05	1.29	1.93	0.00	0.00	*8.69*
U/T	6.61	1.56	1.69	0.00	0.00	*6.74*
IL-	3.43	1.74	2.69	0.00	0.00	*4.38*
IF-	6.68	1.57	1.70	0.00	0.00	*6.81*

* C-ALL is the mean of the 3 control plots (C1, C2 and C3), $C2_{adj}$, $C3_{adj}$ and $C\text{-}ALL_{adj}$ indicate the estimate where forest floor litter increased between 1992 and 1993.

As discussed in Chapter 6 (Section 6.4.7, Figure 6.7) the annual soil C flux was approximately 20% lower in 1993 compared with 1992, although there was not a statistically significant difference for the IL-, IF+ and U/T treatment plots between the years. The maximum difference in soil C flux between treatments within any one year was 62% between I and IL- in 1992, and 62% between IF+ and IL- in 1993. An ANOVA to determine differences between treatments within each of the years could not be undertaken on annual estimates of soil C flux, as each annual soil C flux is the extrapolation of 16 measurements. Annual litterfall across the treatment plots was approximately 93% greater in 1993 compared with 1992, with the F treatment showing the greatest increase of 135% and the IL- treatment showing the least increase of 37% (Chapter 4, Section 4.2.3).

Coarse root production was generally lower in 1993 compared with 1992 across all treatments. Statistical differences in coarse root production between years could not be determined as only a single annual value was available for each treatment. There was approximately a three-fold difference in the coarse root C allocation between the treatments within either year, and these differences reflected differences in basal area increment (Chapter 4, Section 4.4.3).

Belowground C allocation was calculated according to Equation 7.1 and was approximately 30% lower in 1993 compared to 1992 (Figures 7.1 and 7.2). Belowground C allocation varied from a high of 13.3 tC ha^{-1} in the IF+ treatment in 1992 to a low of 4.4 tC ha^{-1} in the IL- treatment in 1993. The treatments generally maintained their ranking of belowground C allocation within each of the years, with the IF+ treatment having the greatest absolute C allocation belowground in both 1992 and 1993, and the IL- treatment the lowest. The high correlation (r^2 =0.82) between the 1992 belowground C values and the 1993 belowground C values (Figure 7.2) indicate similar processes were affecting the change between the years.



	IL+	IF+	I	C1	C2	C2adj	C3	C3adj	C-ALL	C-ALLadj	F	U/T	IL-	IF-
1992	10.34	13.32	12.91	11.95	10.36	9.61	9.77	9.07	10.69	10.03	11.41	8.71	6.67	9.44
1993	6.25	10.18	9.28	8.78	6.73	5.05	6.57	5.17	7.36	5.89	8.69	6.74	4.38	6.81

Figure 7.1: Estimated belowground C allocation for the 10 treatments at BFG for 1992 and 1993 using Equation 7.1.

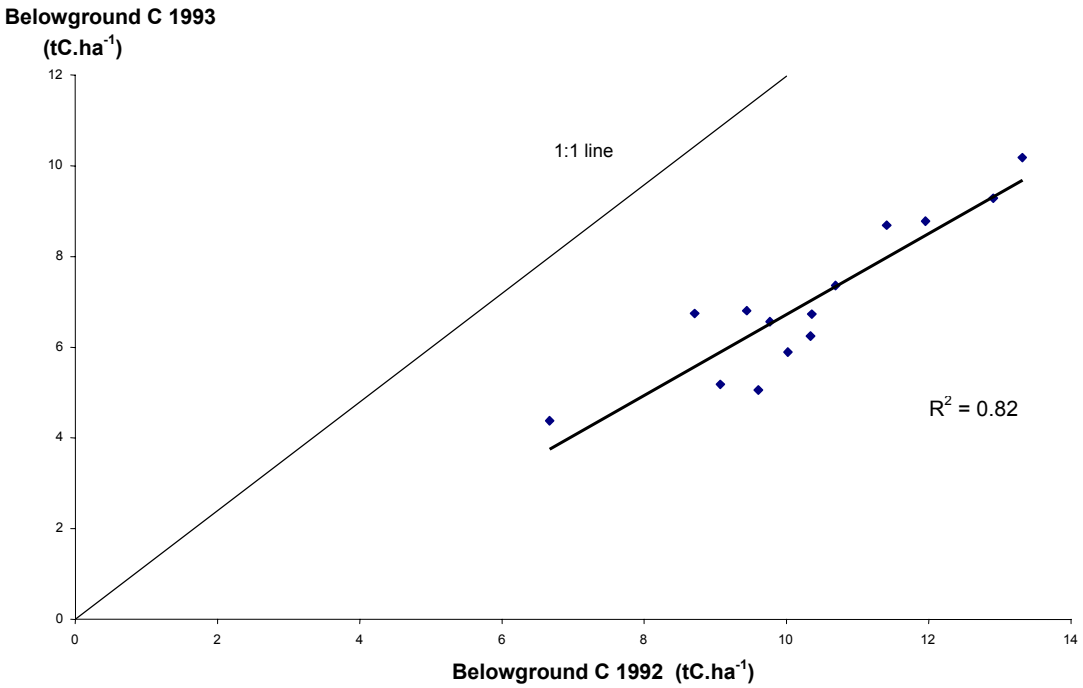


Figure 7.2: 1992 and 1993 estimated belowground C allocation for the 10 treatments plotted against each other. The high r^2 value (r^2=0.82, P<0.01) indicates similar processes are affecting the change between the years.

Table 7.3 summarises the differences in carbon pools and fluxes used to calculate belowground C allocation, between 1992 and 1993. The data is expressed as percentage change between 1992 and 1993 and is presented across all treatments, across irrigated only treatments, across non-irrigated treatments and across the "other" treatments, in order to determine whether a direct irrigation influence on belowground C allocation is obvious.

The reduction in belowground C allocation of approximately 30% between 1993 and 1992 is consistent across all treatments, as is the 20% reduction in soil C flux (soil respiration). Across all treatments the litterfall is significantly higher for 1993, with the greatest increase in litterfall C experienced in the non-irrigated treatments (an increase in litterfall C of 115%). The coarse root C allocation was reduced for all treatments in 1993, but coarse root C allocation was most reduced in the irrigated treatments. As the magnitude of the fluxes is not equal, with soil C flux being approximately three to four-fold greater than either the litterfall C or coarse root C change, it is the reduction in soil C flux between 1992 and 1993 that is exerting the most influence on the total belowground C

allocation. However, this reduction in soil C flux is aided by the increase in litterfall in 1993, which reduces belowground C allocation overall between 1993 and 1992.

Table 7.3: Percentage decrease between 1992 and 1993 in each of the annual carbon fluxes used to calculate belowground C allocation. Negative values indicate an increase between 1992 and 1993.

	All Treatments	Irrigated Treatments (IL+, IF+, I)	Non-irrigated Treatments (F, U/T, C1, C2, C3, C-ALL)	Other Treatments (IL-, IF-)
Soil C flux (soil respiration)	23	20	25	21
Litterfall C	-97	-78	-115	-45
Coarse Root C	18	22	16	20
Total Belowground C	30	30	34	31

7.3.2 Drivers of belowground C allocation

The correlation between the weighted annual mean litterfall N concentration ([N], previously shown to be strong driver of aboveground productivity, Raison *et al* (1990)) and various components of the belowground system is shown in Table 7.4. Where 1992 and 1993 data are combined, the only significant relationship is between coarse root C allocation and litterfall [N] (r^2=0.59, P<0.01). None of the other parameters are significantly related to the litterfall [N] with combined year data.

Separating the data into discrete years produces quite a different perspective. Litterfall [N] is strongly correlated with litterfall C and coarse root C allocation for both 1992 and 1993 (Table 7.4, Figures 7.3a) and 7.3b)). Belowground C allocation excluding coarse roots and soil C flux are also significantly correlated with litterfall [N], particularly in 1992 (Table 7.4, Figures 7.3c) and 7.3d)). There is no significant relationship between litterfall [N] and belowground C allocation including coarse roots in either 1992 or 1993 (Table 7.4).

Table 7.4: r^2 values and significance level (99% or 95% level) for linear correlations between annual weighted mean litterfall [N] and components used to calculate the total belowground carbon allocation. Ns = no significant relationship, N=22 for both year calculations and N=11 for 1992 or 1993 calculations respectively.

	1992 and 1993 combined	1992	1993
Belowground C allocation including Coarse Roots	ns	ns	ns
Belowground C allocation excluding Coarse Roots (soil C – litterfall C)	ns	0.78 (P<0.01)	0.53 (P<0.05)
Coarse Root C	0.59 (P<0.01)	0.74 (P<0.01)	0.55 (P<0.01)
Soil C	ns	0.73 (P<0.01)	0.47 (P<0.05)
Litterfall C	ns	0.92 (P<0.01)	0.61 (P<0.01)

Figures 7.3 a), b) c) and d) graphically show the significant correlations between litterfall [N] and the components which make up the belowground carbon estimates. As N availability increases belowground allocation excluding coarse roots (Figure 7.3a)) and soil C decrease (Figure 7.3b)). The negative correlation between belowground C allocation and litterfall [N] may be explained by a higher N availability reducing the need for fine root biomass and thereby requiring less C belowground.

An increase in N availability indicates an increase in coarse root biomass (Figure 7.3c)) and an increase in litterfall C (Figure 7.3d)). This supports the higher N treatments having a greater aboveground productivity (as coarse root biomass is proportional to basal area increase) and also producing more litterfall.

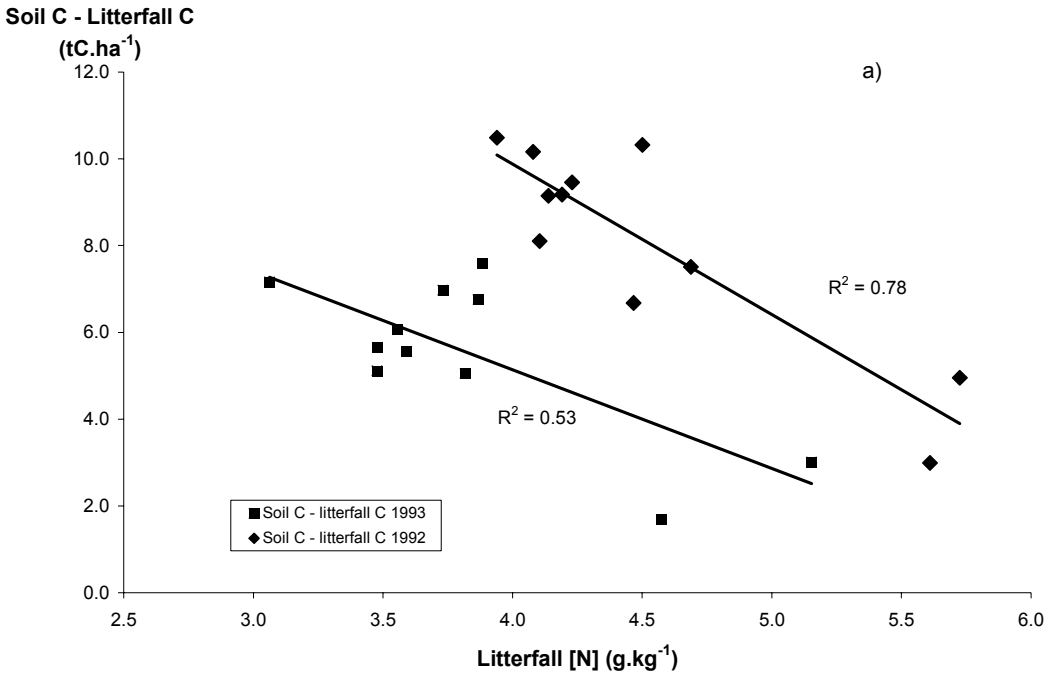


Figure 7.3 a): Annual weighted mean litterfall [N] concentration and belowground carbon allocation excluding coarse roots. N = 11 for all correlations, P<0.05.

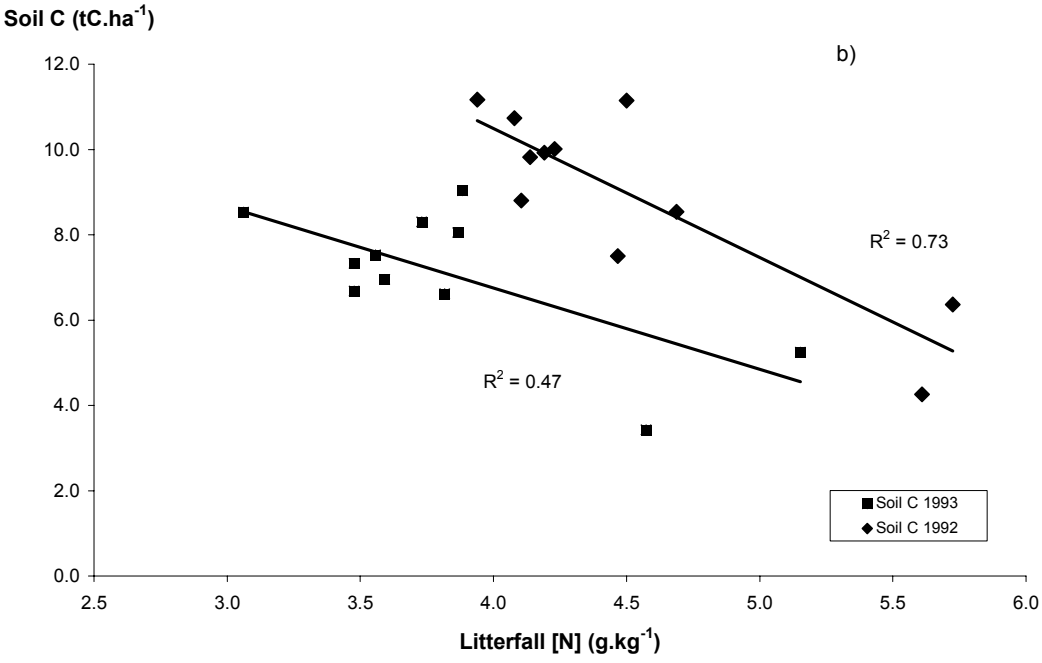


Figure 7.3 b): Annual weighted mean litterfall [N] concentration and soil C estimates. N = 11 for all correlations, P<0.05.

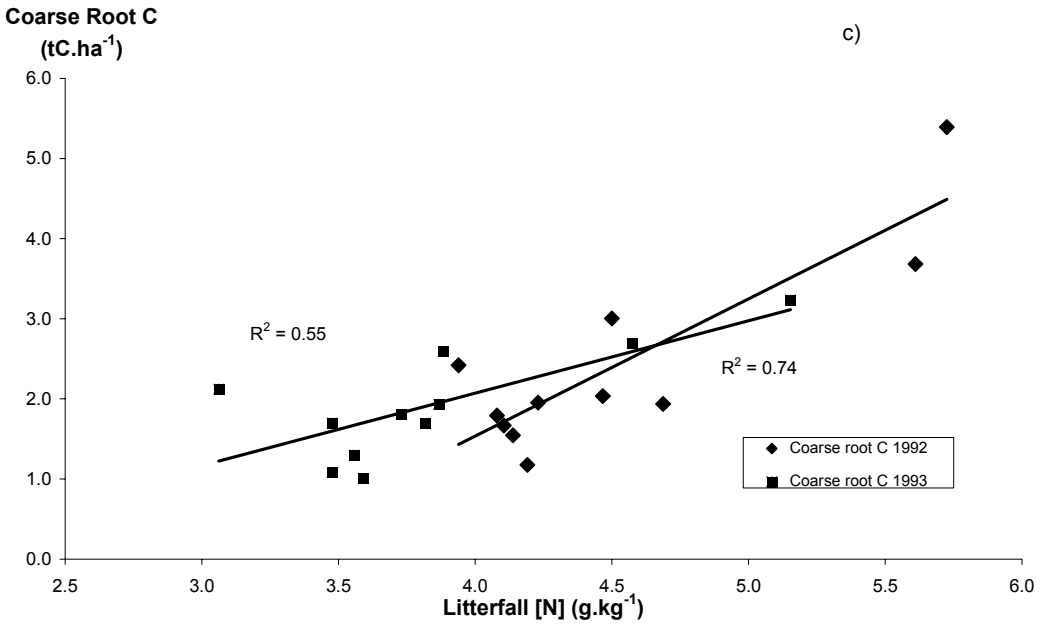


Figure 7.3 c): Annual weighted mean litterfall [N] concentration and coarse root C allocation. N = 11 for all correlations, P<0.05.

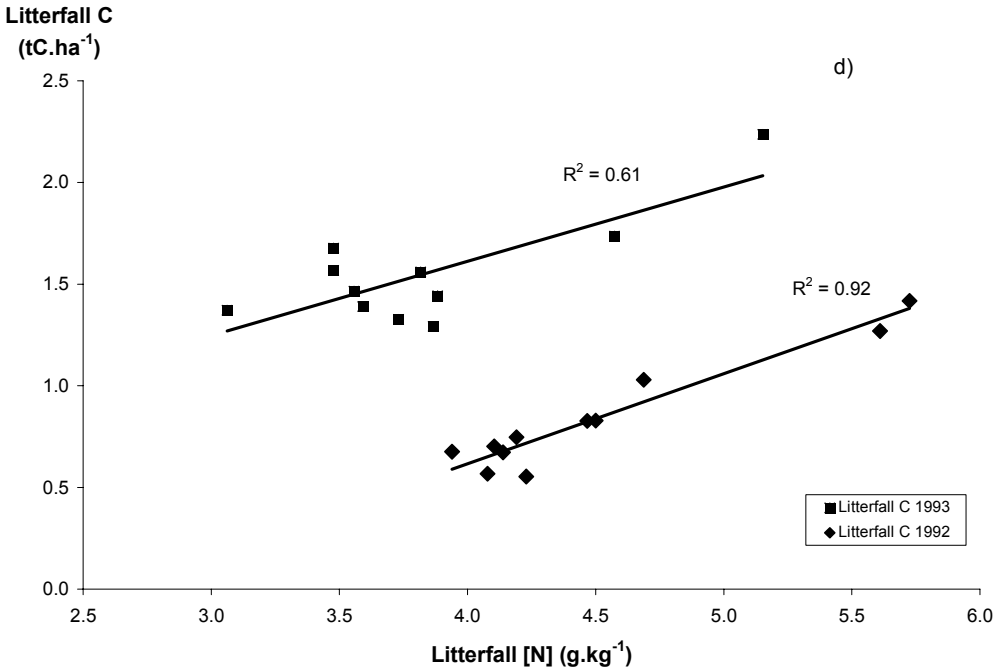
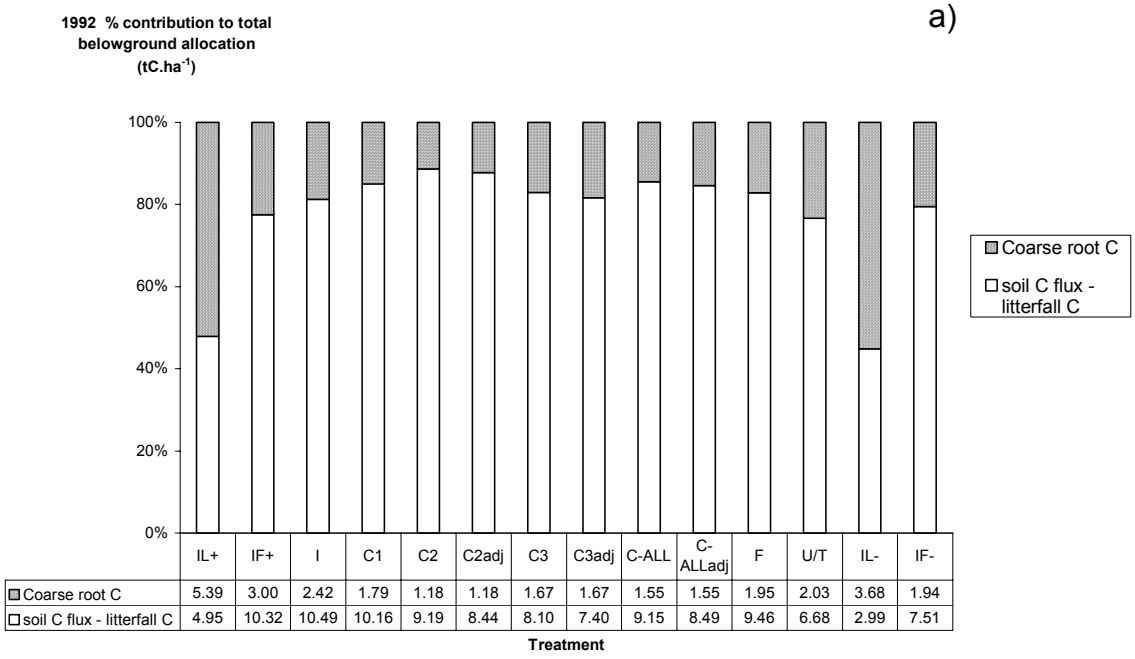


Figure 7.3 d): Annual weighted mean litterfall [N] concentration and litterfall C. N = 11 for all correlations, P<0.05.

7.3.3 Coarse root versus "other" belowground C allocation

The proportions of coarse root production to "other" belowground C allocation (calculated by subtracting litterfall C from soil C flux) are shown in Figures 7.4 a) and b). In 1992, for all treatments other than IL+ and IL-, the soil C flux minus litterfall C contributed approximately 80% of the belowground C allocation. In 1993 in these treatments, soil C flux minus litterfall C accounted for approximately 76% of the belowground allocation. This indicates that the relative proportions of coarse root to other belowground carbon remained similar at approximately 80% across both years, for the nutrient stressed treatments. The nutrient rich treatments, IL+ and IL- with a weighted annual litterfall [N] approximately 25% greater than C1 (Chapter 4, Section 4.2.3), had approximately 50% contribution by coarse root to the total belowground C allocation in both years (Figures 7.4 a) and b)).

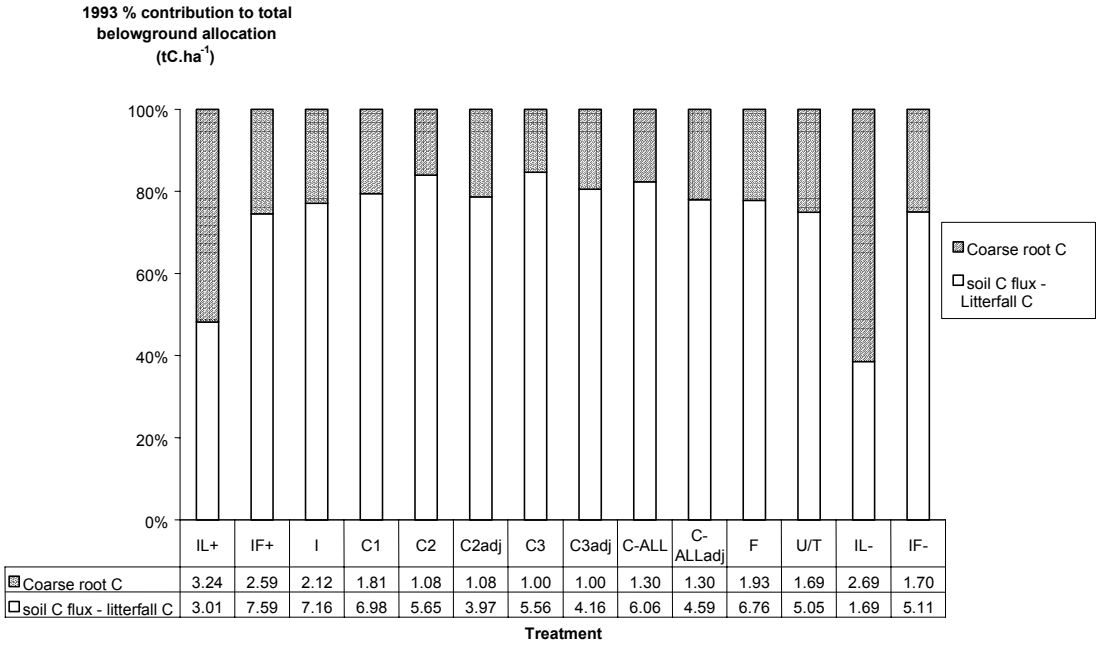
a)



	IL+	IF+	I	C1	C2	C2adj	C3	C3adj	C-ALL	C-ALLadj	F	U/T	IL-	IF-
Coarse root C	5.39	3.00	2.42	1.79	1.18	1.18	1.67	1.67	1.55	1.55	1.95	2.03	3.68	1.94
soil C flux - litterfall C	4.95	10.32	10.49	10.16	9.19	8.44	8.10	7.40	9.15	8.49	9.46	6.68	2.99	7.51

Figure 7.4a): Proportions of coarse root allocation and other belowground C allocation (calculated as soil C flux minus litterfall C) for all treatments for 1992 (a) and 1993 (b).

b)



	IL+	IF+	I	C1	C2	C2adj	C3	C3adj	C-ALL	C-ALLadj	F	U/T	IL-	IF-
Coarse root C	3.24	2.59	2.12	1.81	1.08	1.08	1.00	1.00	1.30	1.30	1.93	1.69	2.69	1.70
soil C flux - litterfall C	3.01	7.59	7.16	6.98	5.65	3.97	5.56	4.16	6.06	4.59	6.76	5.05	1.69	5.11

Treatment

Figure 7.4b): Proportions of coarse root allocation and other belowground C allocation (calculated as soil C flux minus litterfall C) for all treatments for 1992 (a) and 1993 (b).

7.3.4 Belowground C allocation versus litterfall

The relationship between belowground carbon allocation and litterfall C, shown in Figure 7.5, is opposite to the relationship derived by Raich and Nadelhoffer (1989) from global data covering a variety of forest types. The BFG data indicates a strong inverse relationship between belowground C allocation and litterfall C (r^2=0.70, P<0.01) whereas Raich and Nadelhoffer (1989) had a positive relationship between belowground C allocation and litterfall (r^2=0.52). Gower *et al* (1996a) convincingly argued that the Raich and Nadelhoffer (1989) relationship between litterfall C and belowground C allocation is not appropriate at a local scale for a single species, although it may be valid as a global trend.

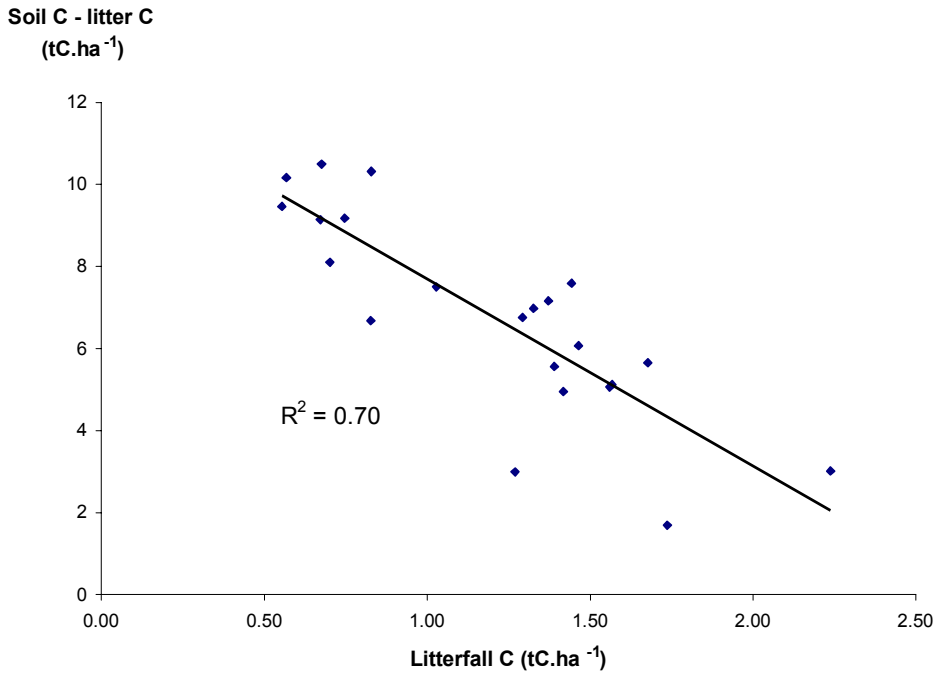


Figure 7.5: Relationship with belowground C allocation (soil C – litterfall C) and litterfall C (similar to the relationship derived by Raich and Nadelhoffer (1989)) but with an opposite orientation, (r^2=0.70, P<0.01).

7.4 Integrative Discussion

7.4.1 Annual soil C flux – 1992, 1993

As discussed in Chapter 6 the soil respiration measurements obtained from BFG were within the range and patterns of similar studies elsewhere (Section 6.7). The annual estimates of soil C flux at BFG range from 5.2 tC ha^{-1} to 11.2 tC ha^{-1} across all treatments and both years. The soil C flux was approximately 20% lower across all treatments in 1993 compared with 1992, with a maximum difference of approximately 62% between treatments within any one year.

Similarly, annual soil C flux between the years described in Haynes and Gower, (1995) varied by an average of 15% between unfertilized plots and 26% in the fertilized plots. The annual soil C flux for this red pine (*Pinus resinosa*) forest type ranged from 4.4 tC ha^{-1} to 9.04 tC ha^{-1} which was slightly lower than the

estimates of soil C flux obtained from BFG. This is reduction in annual soil respiration is not surprising given the harsher winter conditions experienced by the red pine stand in Wisconsin, USA, and the close link between temperature and respiration (Kirschbaum, 1995).

Estimates of annual soil C flux across different forest types are summarised in Raich and Nadelhoffer (1989) and range from 2.5 tC ha^{-1} to 14.5 tC ha^{-1}. The measured annual soil C flux from BFG falls within these global estimates.

7.4.2 Annual litterfall – 1992, 1993

As discussed in Chapter 4, Section 4.2.3, the annual litterfall estimates at BFG for 1992 and 1993 fall within the 10 year range of litterfall measured at BFG. The 1992 and 1993 litterfall estimates also fall within the annual litterfall estimates quoted in the literature for a variety of forest types. This provided confidence in the estimates obtained for all BFG treatments in 1992 and 1993.

The weighted annual litterfall [N] ranged from a low of 3.0 to a high of 5.7 $g.kg^{-1}$ between 1992 and 1993 for different treatments (Chapter 4, Section 4.2.3), which are slightly lower than the annual litterfall [N] quoted in Rasion *et al* (1992a), which ranged from 4.5 to 8.5 $g.kg^{-1}$. However the Raison *et al* (1992a) estimates were measured up to 3 years after the commencement of the irrigation and fertilization treatments, when N availability was at its highest for solid fertilizer application. Litterfall [N] is an indicator of site N availability (Rasion *et al*, 1990), and was significantly correlated with belowground C allocation when coarse root production was excluded.

7.4.3 Belowground C allocation – 1992, 1993

The belowground C allocation including coarse roots at BFG ranged from 13.32 tC $ha^{-1}.y^{-1}$ in the IF+ treatment in 1992 to 4.38 tC $ha^{-1}.y^{-1}$ in IL- in 1993 (Figure 7.1). The greatest difference in 1992 was between the IF+ and IL- treatments, with the IF+ treatment allocating approximately twice as much C belowground as IL-. The next greatest difference in C allocation in 1992 was between the

IF+ and the U/T treatment, with the IF+ treatment allocating approximately 53% more C belowground. In 1993 the IF+ treatment again allocated the greatest C belowground with 10.18 tC $ha^{-1}.y^{-1}$ and this was 132% greater than IL- and 51% greater than U/T in absolute terms.

The irrigated treatments did not exhibit a simple relationship between N availability and belowground C allocation. Litterfall [N] ranking was IL+ > IF+ > I, and this order remained consistent between 1992 and 1993 (Figure 4.4). However, the ranking of belowground C allocation was IF+ > I >IL+, which indicates that a water-nutrient interaction could be influencing belowground C allocation.

Litterfall [N] was significantly correlated with belowground C allocation excluding coarse roots, and with soil C, where an increase in N availability reduced belowground C allocation and soil C (Figures 7.3 a) and b)). Litterfall [N] was also significantly correlated with coarse root C and litterfall, where an increase in N availability appeared to increase site productivity and therefore coarse root allocation and litterfall production.

The contribution of coarse root C to total belowground C allocation varied with the N availability of the site. IL+ and IL-, which had approximately 25% greater weighted annual litterfall [N] compared with C1, had a coarse root C allocation of approximately 50% of total belowground C allocation (Figure 7.4 a) and b)). For all other treatments the contribution of coarse root C to total belowground C was approximately 20% in both years (Figure 7.4 a) and b)).

Table 7.5 summarises other investigations into belowground C allocation in a variety of forest types. There are 5 studies in listed in Table 7.5, including this study, which estimate belowground C allocation by C balance (Raich and Nadelhoffer, 1989; Haynes and Gower, 1995; Beets and Whitehead, 1996; Malhi *et al*, 1999; and this study). The belowground C allocation calculated for the treatments at BFG in 1992 and 1993 falls within the range quoted in these studies (Table 7.5). Both Raich and Nadelhoffer (1989) and Malhi *et al* (1999)

include tropical forests in their estimates, which have a high belowground C allocation and could represent the upper limit of belowground C allocation.

Estimates of belowground C allocation which use fine root biomass and turnover as their basis (highlighted by italics in Table 7.5) generally indicate a lower belowground C allocation than that found at BFG. This is probably due to the respiratory costs of the root system and mycorrhizae, and the C costs of exudates being ignored. Several studies have reported that the mycorrhizae and soil respiration can contribute from 30 to 62% of total soil respiration costs (Ewel *et al*, 1987b; Bowden *et al*, 1993; Haynes and Gower, 1995; Gower *et al*, 1996a), which would not have been considered in studies highlighted by italics in Table 7.5.

Raich and Nadelhoffer's (1989) model of belowground carbon allocation is a unique and innovative approach to estimating total belowground carbon allocation. Their negative correlation relating belowground C allocation to litterfall C was based on global data from a variety of biomes. Data presented in this chapter, and also in Gower *et al* (1996a), indicates that this relationship is not valid on a local scale, as the local scale correlation has a positive relationship between belowground C allocation and litterfall (Figure 7.5). It is inaccurate to use the relationship between litterfall C and belowground C allocation described by Raich and Nadelhoffer (1989) to estimate belowground C allocation within a stand.

Table 7.5: Comparison of belowground C estimates in other forest types. Italics indicate that fine root biomass and turnover were used to estimate belowground C production (fine roots assumed to be 50% C).

Belowground C allocation ($tC\ ha^{-1}.y^{-1}$)	Forest Type	Reference
4.38 –13.32	20 year old radiata pine, Canberra, Australia	This study
1.88 – 3.95	31 year old red pine, Wisconsin, USA	Haynes and Gower (1995)
2.6 – 11.0	Various global estimates	Raich and Nadelhoffer (1989)
4.99	Black spruce, Saskatchewan, Canada	Malhi *et al* (1999)
8.28	Temperate hardwood forest, Tennessee, USA	Malhi *et al* (1999)
13.70	Tropical rainforest, Amazonas, Brazil	Malhi *et al* (1999)
2.45 – 8.85	11-17 year old radiata pine, New Zealand	Beets and Whitehead (1996)
2.05 – 4.05	*40 year old Douglas fir*	*Grier et al (1981)*
2.25 –2.75	*70-78 year old lodgepole pine*	*Comeau* and *Kimmins (1989)*
0.25 – 8.20	*Various global estimates*	*Nadelhoffer and Raich (1992)*

As with soil respiration estimates (Chapter 6), there is a significant difference in belowground C allocation between 1992 and 1993. The implies that seasonal/annual differences experienced by a forest play a significant role, in addition to treatment differences, to the allocation of C belowground.

7.4 Conclusions

Belowground C allocation was calculated for eight variants of irrigation and fertilizer treatment at BFG in 1992 and 1993, using annual soil respiration estimates, annual litterfall estimates, coarse root productivity and reliable measurements of the change in soil C and the change in forest floor C. Belowground C allocation at BFG varied from 4.38 tC $ha^{-1}.y^{-1}$ to 13.32 tC $ha^{-1}.y^{-1}$, which falls within the belowground C allocation estimates in other studies covering a variety of forest types.

Total belowground C allocation varied between the treatments at BFG with a maximum difference of 98% between the IF+ and IL- in 1992, and a maximum difference of 131% between the IF+ and IL- treatments in 1993. There was also considerable variation between the years with an approximate 30% reduction in carbon allocated belowground in 1993 compared with 1992. This 30% reduction in belowground C allocation was caused by an approximately 23% decrease in soil C flux, an approximate 97% increase in litterfall C and an approximate 18% decrease in coarse root allocation between 1993 and 1992 across all treatments.

As with soil C flux (Chapter 6), differences between 1992 and 1993 were significant and resulted in the data being analysed separately for 1992 and 1993. Where data were combined, there were few significant correlations between parameters used to calculate belowground C allocation and N availability. Weighted annual litterfall [N], as an indicator of site N availability, was significantly, negatively correlated with belowground C allocation excluding coarse roots, with an r^2 of 0.78 in 1992 and an r^2 of 0.53 in 1993. Litterfall [N] was also significantly negatively correlated with soil C, with an r^2 of 0.73 and 0.47 in 1992 and 1993, respectively. This indicates that as N availability increases, belowground C allocation and soil C decrease.

Litterfall [N] was significantly positively correlated with coarse root allocation and annual litterfall with r^2s of 0.74 and 0.55 for coarse root allocation in 1992 and 1993, respectively, and r^2s of 0.92 and 0.61 for litterfall C in 1992 and

1993, respectively. This indicates that as N availability increases, site productivity is likely to be enhanced in the N limited system at BFG, resulting in greater C allocation to the bole, and therefore to coarse roots, and also increased foliar, and therefore, litterfall production.

The contribution of coarse roots to total belowground C allocation varies with N availability. Coarse roots contributed approximately 50% in the high N treatments (IL+ and IL-), but contributed only approximately 20% of belowground C allocation for all other treatments.

The relationship between belowground C allocation and litterfall production described by Raich and Nadelhoffer (1989) could not be replicated using the BFG data. BFG data indicated a decreasing belowground C allocation with increased litterfall. The relationship described by Raich and Nadelhoffer (1989) may be valid at a global scale, but should not be used to estimate belowground C allocation at a local level.

A thorough examination of whole tree/site carbon budgets at BFG will be developed in Chapter 8. Further discussion relating to the contribution of the root system to the whole tree carbon budgets will be discussed and the results obtained from this Chapter analysed in a whole stand context.

CHAPTER 8. WHOLE STAND CARBON BUDGETS

8.1 Introduction

The quantification of belowground carbon (C) allocation in forest systems is most useful where it can be combined with estimates of whole stand productivity. Experimental estimates of various forest carbon pools and fluxes involve extensive measurements, which may be unrealistic to undertake over a number of sites. A theoretical understanding of tree productivity, described by a mathematical model, can provide a useful tool to investigate stand growth and productivity.

The BIOMASS model (McMurtrie *et al*, 1990a; McMurtrie and Landsberg, 1992), developed in 1989 from BFG data, was used to provide stand scale estimates of Gross Primary Productivity (GPP) for 1992 and 1993. The results of the BIOMASS model will be compared with the annual estimates of belowground C allocation measured at the BFG study site during this period. BIOMASS does not posses a robust belowground production model and currently estimates the allocation of belowground C as a simple proportion of total productivity. This will be compared with the measurements undertaken in 1992 and 1993, which were described in Chapters 3-7 of this thesis.

8.2 The BIOMASS model

8.2.1 Introduction

BIOMASS is a mechanistic model that simulates the carbon and water balance of forest canopies (McMurtrie *et al*, 1990a). The model works on a daily time step, requiring daily inputs of meteorological data (photosynthetically active radiation, maximum and minimum temperature and precipitation) and a description of the canopy. The canopy description includes foliar nitrogen status, which must be input, and the leaf area index (LAI), which can be input or the leaf area development may be simulated by BIOMASS. The canopy is divided into three horizontal layers with foliar nitrogen (N) declining towards the base of the tree. It is assumed that the maximum photosynthetic rate and foliar nitrogen concentration are linearly related. Assimilate produced is converted to

dry matter equivalent and allocated to tree components such as stem, branches, roots and foliage. The model allows for litterfall and maintenance respiration of tissue (McMurtrie and Landsberg, 1992).

The model is described in detail in McMurtrie (1989) and McMurtrie (1993), and a summary of the key processes is given below in Table 8.1. In the following analysis only Gross Primary Production (GPP) and to some extent Net Primary Production (NPP) as outputs from the BIOMASS model will be compared with the 1992 and 1993 measurements of belowground C allocation.

Table 8.1: Summary of processes and their description in BIOMASS. Full details are given in McMurtrie (1989) and McMurtrie (1993).

Process	Description in BIOMASS model
Light interception	Beer's law with separation into sunlit and shaded foliage
Foliar photosynthesis	Sum of daily net photosynthesis by light saturated sunlit foliage, non-saturated sunlit foliage and photosynthesis from interception of diffuse radiation. Photosynthesis is dependent on temperature and foliar nitrogen concentration
Canopy architecture	Canopy is divided into 3 horizontal layers with declining N towards the base of the canopy
Gross Primary Productivity	Derived by integration across 3 foliar/light classes and 3 canopy layers
Maintenance respiration	Related to temperature and nitrogen status of foliage, branch, stem and root tissue
Growth respiration	Assumed to be 30% of assimilate remaining after subtraction of maintenance respiration
Net Primary Productivity	Gross Primary Productivity less sum of maintenance respiration of foliage, branch, stem and root tissue and growth respiration
Litterfall	Either a constant fraction of daily foliage biomass or a non-linear function constraining foliage mass to stem biomass
C allocation	Partitioning coefficients linearly related to foliar nitrogen concentration for foliage, branch, stem and root tissue

Table 8.1: (cont.) Summary of processes and their description in BIOMASS. Full details are given in McMurtrie (1989) and McMurtrie (1993).

Process	Description in BIOMASS model
Stomatal conductance	Either a function of meteorological variables, vapour saturation deficit, photon flux density and soil water content or linked to photosynthesis, relative humidity and ambient CO_2 concentration
Stand water balance	Conductance from each canopy layer with transpiration calculated from Penman-Monteith equation and an allowance for rainfall interception and evaporation of intercepted water

8.2.2 Model methods

The BIOMASS model was run for 6 of the 10 treatments for which soil respiration measurements were taken (IL+, IF+, I, C1, F, and U/T). The other treatments (IL-, IF-, C2 and C3) were omitted because reliable LAI and foliar nitrogen information was not available for these treatments. BIOMASS was simulated for 5.5 years from July 1989 through to December 1993. This period was chosen as:

- meteorological data was available for this period;
- it followed the period of intensive field study (1984 – 1988);
- it enabled the model to commence in a winter period; and
- was taken through to the conclusion of the belowground studies.

The specific time of interest from the simulations was from 1 January 1992 to 31 December 1993, where GPP and NPP were modelled for the three irrigated and three non-irrigated treatments for the 1992 and 1993 calendar years. GPP was simulated by summing photosynthesis across the three light classes (light saturated sunlit foliage, non saturated sunlit foliage and interception of diffuse radiation) in each of the three canopy layers that are used in the BIOMASS model (Table 8.1). Respiration was calculated as maintenance respiration which is related to the nitrogen status of the tree tissue (foliage, stem, branch and root) and growth respiration was estimated as 30% of the assimilate remaining after subtraction of maintenance respiration (Table 8.1). NPP was calculated as GPP less maintenance and growth respiration.

Daily meteorological data was collected on site, LAI was measured quarterly for successive seasons up to winter 1993, and foliar nitrogen concentration [N] was estimated as a constant fraction of weighted annual litterfall nitrogen concentration as described in Crane and Banks (1992). The fractions of weighted annual litterfall [N] used for foliar [N] estimates varied between the treatments from 0.53 for C1 to 0.63 for IL+, respectively.

Figure 8.1 shows the LAI values from 1989 to 1993 for the 6 treatments used as the basis for BIOMASS simulations. BIOMASS uses an LAI that is double-sided foliar area divided by PI (3.142) to fully capture photosynthesis in a needle leaved *Pinus radiata* forest. The IL+ treatment had the highest LAI across the period simulated, with the IF+ treatment generally having the next highest LAI. The U/T treatment varied between a relatively high LAI and a lower LAI and the C1, F, and I treatments tended to lower LAIs.

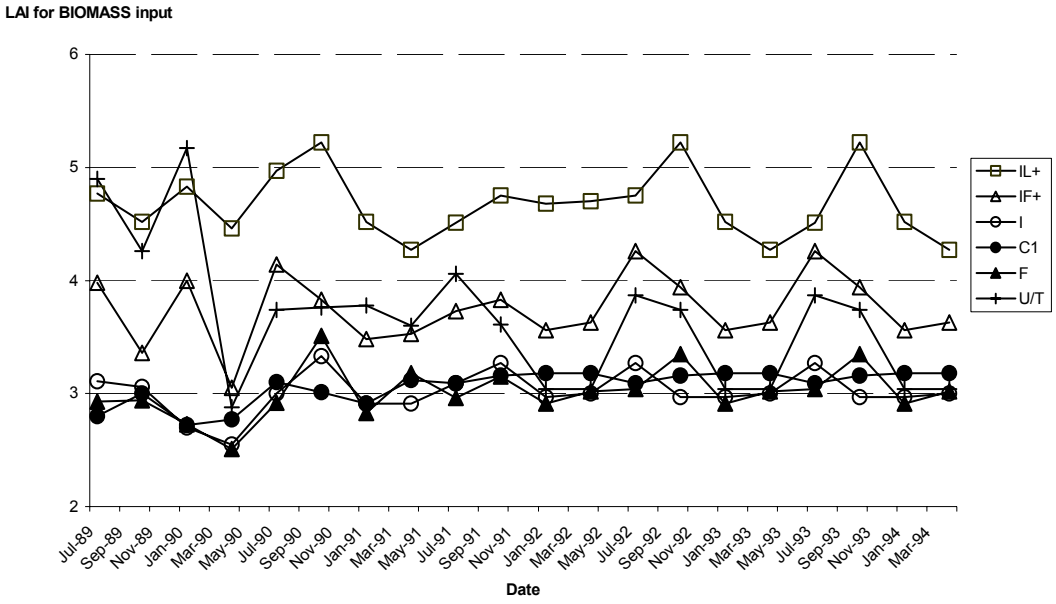


Figure 8.1: LAI used in BIOMASS to simulate GPP from 1989 to 1993. The LAI used by BIOMASS is double sided foliar area divided by PI (3.142).

Daily meteorological data, measured at the BFG site, showed that both 1992 and 1993 had higher than average (790mm) rainfall, being 1008mm and 808mm respectively, with 1992 being an extremely wet year (Table 8.2). In addition 1993 was a warmer than average year with the mean maximum

temperature being 0.5°C higher than long-term average maximum temperature, and the mean minimum temperature being 0.6°C higher than long term average minimum temperature (Table 8.2).

Table 8.2: Ten-year average and 1991,1992 and 1993 specific meteorological data for BFG field site.

	10 year average	1991	1992	1993
Rainfall (mm)	790	603	1008	808
Average Maximum Temperature (°C)	19.7	20.5	17.8	20.2
Average Minimum Temperature (°C)	7.0	7.1	6.5	7.6
Highest Maximum Temperature (°C)	42.2	41.5	40.6	39.9
Lowest Minimum Temperature (°C)	-7.4	-4.0	-5.3	-3.4

Because of the higher than average rainfall in 1992 and 1993, the soil water deficit was less extreme than in earlier years (1983 – 1989) for which the BIOMASS model had been applied. The BIOMASS model predicted that photosynthetic production was affected by water deficits in the C1, F and U/T treatments for 4, 4, and 9 months respectively, out of the 24 months spanning 1992 and 1993. This indicates that productive capacity was not markedly affected by water stress over the two years.

8.2.3 Model results

Table 8.3 shows the output of the BIOMASS model and the measured basal area increment for the 6 selected treatments over 1992 and 1993. According to BIOMASS GPP was greater for all treatments in 1993 compared to 1992, but NPP was greater for all treatments in 1992 compared to 1993. The reduced NPP in 1993 is due to higher respiratory costs in 1993 compared with 1992, due to the higher average temperature. The NPP pattern was reflected in the

measured basal area increment with basal area being greater for all treatments in 1992 compared with 1993 (Figure 8.2).

Table 8.3: BIOMASS model estimates for Gross Primary Production (GPP) and Net Primary Production (NPP) and measured basal area increment for selected treatments for 1992 and 1993.

	1992			1993		
	GPP (tC ha^{-1})	**NPP (tC ha^{-1})**	**Basal Area Increment ($m^2.ha^{-1}$)**	**GPP (tC ha^{-1})**	**NPP (tC ha^{-1})**	**Basal Area Increment ($m^2.ha^{-1}$)**
IL+	37.8	24.3	5.24	38.4	21.4	3.04
IF+	33.5	22.9	3.13	34.2	20.6	2.64
I	27.7	20.6	2.61	28.2	19.2	2.22
C1	29.4	20.8	2.02	30.5	19.2	1.97
F	29.4	20.8	2.16	30.2	19.0	2.06
U/T	28.2	19.8	2.54	29.9	18.9	2.05

Figures 8.2 a) and b) show the significant correlation ($P<0.05$) between basal area increment and GPP and NPP, respectively. The r^2 values between basal area increment and NPP are 0.77 (1992) and 0.96 (1993 – Figure 8.2b)), while the r^2 values between basal area increment and GPP was 0.82 (1992) and 0.84 (1993 – Figure 8.2a)). These strong correlations between measured and modelled parameters provide confidence in the annual estimates of the BIOMASS model, although when both years output are combined the r^2 value between basal area increment and GPP and basal area increment and NPP are 0.33 ($P<0.10$) and 0.79 ($P<0.05$), respectively (trendline for combined years not shown in Figures 8.2 a) and b)).

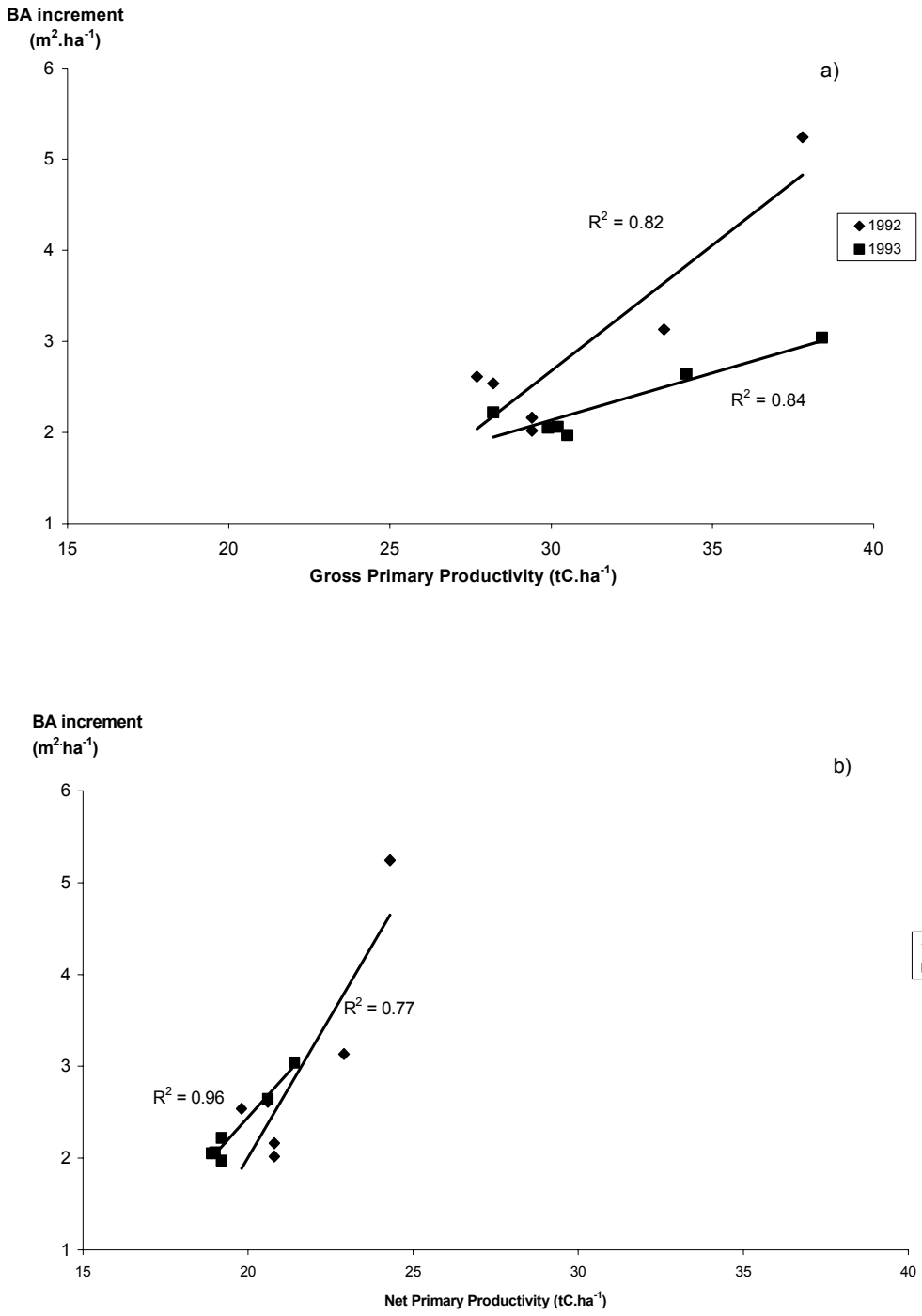


Figure 8.2: Relationship between measured basal area (BA) increment and modelled GPP (a) and NPP (b) for six treatments at BFG in 1992 and 1993. N=6 for each year, P<0.05.

8.3 Belowground productivity

8.3.1 Definition of terms

To enable the following discussion to be understood clearly, terms used are described below:

- GPP_B = gross primary productivity calculated by BIOMASS
- R_a = aboveground maintenance respiration
- R_b = belowground maintenance respiration
- Y = growth respiration factor (0.7 as 30% of assimilate after allowance for maintenance respiration is taken as growth respiration in BIOMASS)
- NPP_a = net primary productivity aboveground
- NPP_b = net primary productivity belowground
- NPP_B = net primary productivity calculated by BIOMASS
  - $NPP_B = (GPP_B – R_a – R_b) \times Y = NPP_a + NPP_b$
- GPP_b = Raich and Nadelhoffer's (1989) belowground allocation which is equivalent to gross primary productivity belowground
  - $GPP_b = NPP_b \times 1/Y + R_b$
- CR = Coarse root biomass estimated using Jackson and Chittenden (1981) – Chapter 4, Section 4.4.

8.3.2 Belowground productivity as a percentage of primary productivity

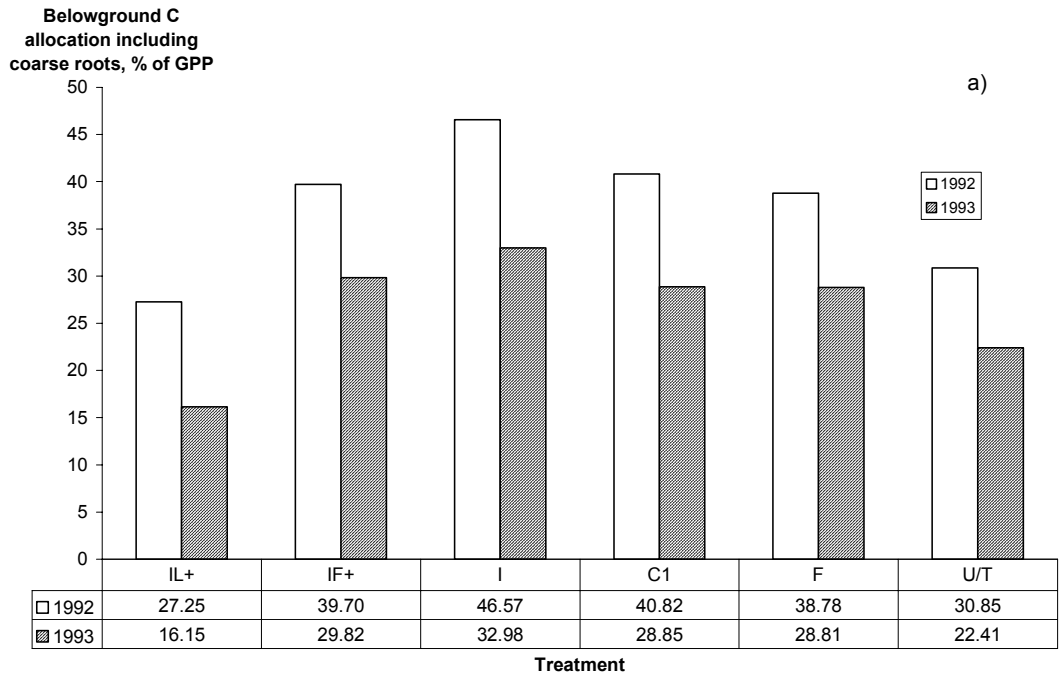
Figures 8.3a) and b) show the total belowground allocation (as estimated using the Raich and Nadelhoffer's (1989) approach (Chapter 7) and estimated coarse root biomass (Chapter4)) and belowground allocation excluding coarse roots expressed as a percentage of GPP, respectively.

The ratio used for the Y-axis in Figure 8.3a) is:

$$\frac{GPP_b + CR}{GPP_B}.$$

The ratio used for the Y-axis in Figure 8.3b) is:

$$\frac{GPP_b}{GPP_B}.$$



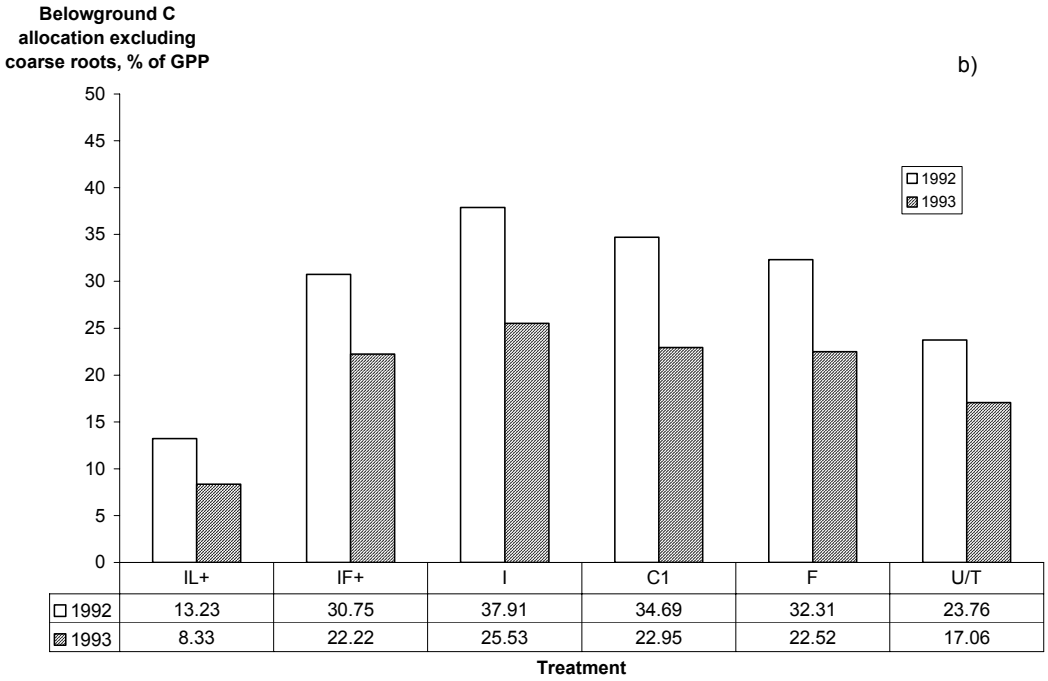


Figure 8.3a) and b): Percentage of GPP allocated belowground including (a) and excluding (b) coarse roots for selected treatments at BFG in 1992 and 1993

Total belowground allocation including coarse roots ranges from 27% of GPP for the IL+ plot in 1992 to 47% for I in 1992, and from 16% for IL+ in 1993 and 33% for I in 1993, with the treatments maintaining their rankings between the years with respect to percentage of C allocated belowground (Figure 8.3a).

Belowground C allocation excluding C allocation to coarse roots (Figure 8.3b) ranges from 13 to 38% in 1992 and from 8 to 26% in 1993 with IL+ maintaining the lowest percentage and I maintaining the highest percentage of C allocated belowground. There does not appear to be a strong water driven allocation of C belowground as two of the irrigated treatments (IF+ and I) had similar percentage C allocation to non-irrigated treatments (C1 and F).

Malhi *et al* (1999) estimated a total belowground C allocation for a single year as 45%, 48% and 52% of GPP for a tropical, temperate and boreal forest, respectively. The BFG treatments showed a slightly lower belowground C allocation for 1992 for the C1 and I (nutrient stressed) treatments, at 47% and 41% respectively, but this proportion was lower in 1993 with only 29% and 33% of GPP being allocated belowground for C1 and I, respectively. Malhi *et al* (1999) used eddy covariance data to constrain C fluxes, and the different methodologies, in conjunction with extrapolated data from a variety of studies, may not be as accurate as estimates taken on a variety of treatments in a similar forest type at a single site such as the BFG experiment.

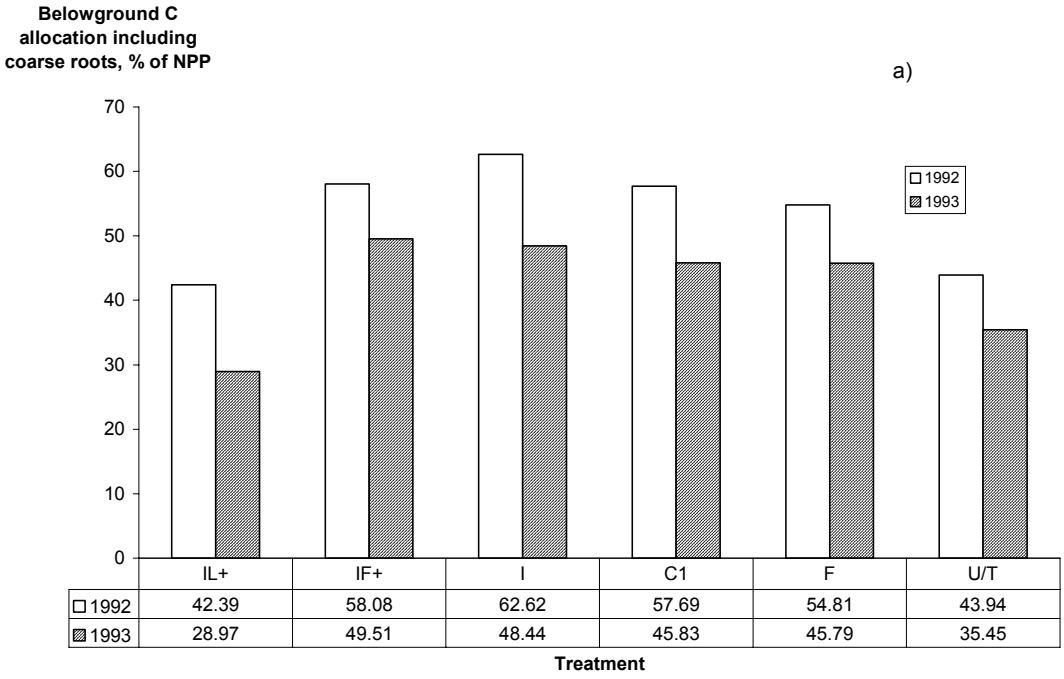
Figures 8.4a) and b) show the total C allocated belowground (using Raich and Nadelhoffer's (1989) approach and estimated coarse root biomass – GPP_b) and belowground C excluding coarse roots expressed as a percentage of NPP, respectively.

The ratio represented in Figure 8.4 a) is:

$$\frac{GPP_b + CR}{NPP_B}.$$

The ratio represented in Figure 8.4b) is:

$$\frac{GPP_b}{NPP_B}.$$



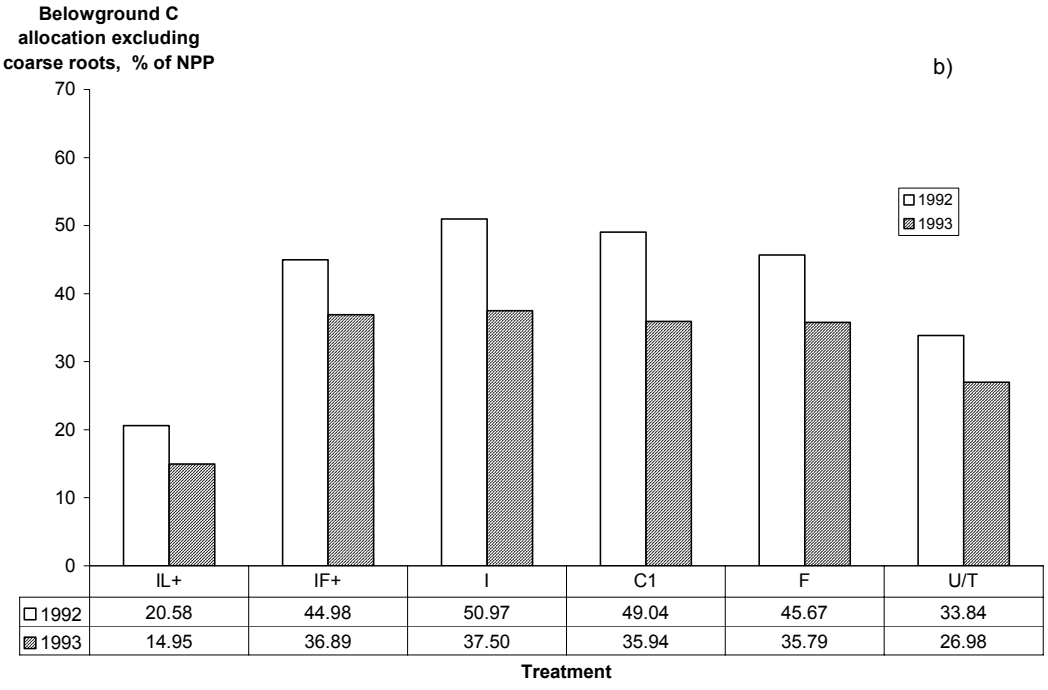


Figure 8.4a) and b): Percentage of NPP allocated belowground including (a) and excluding (b) coarse roots for selected treatments at BFG in 1992 and 1993

The percentage of NPP of total C allocated belowground ranges from 29% for IL+ in 1993 to 63% for I in 1992. The percentage of C allocated belowground excluding coarse roots ranges from 51% for I in 1992 to 15% for IL+ in 1993. Again the treatments maintain their rankings with respect to belowground C allocation with or without coarse root biomass included.

The analysis of proportional belowground allocation estimated using Raich and Nadelhoffer's (1989) method and NPP must be treated with caution. As shown in the ratios plotted in Figures 8.3 and 8.4, the Raich and Nadelhoffer (1989) belowground allocation is GPP_b, and contains a root respiratory component. The NPP calculated by BIOMASS (NPP_B) excludes the respiratory component of the belowground system, and, as it is not possible to identify that portion of GPP_b that is R_b, it is more appropriate to quote Raich and Nadelhoffer's (1989) method of belowground C allocation (GPP_b) as a percentage of GPP. However much of the data quoted in the literature is based on belowground C allocation as a percentage of the more easily measured NPP. For this reason some comparisons with NPP are discussed.

8.3.3 Drivers of proportional belowground productivity

The proportion of assimilate allocated belowground is likely to be related to the water and nutrient status of the stands. For this reason BFG was the ideal experimental site for investigating the drivers of belowground C allocation.

Water availability did not appear to have a large influence on the proportion of belowground C allocation as shown by the Figure 8.3a) and b) where there was little difference between similar N status treatments irrespective of whether they were irrigated (e.g. I and C1).

To determine the influence of N availability on belowground C allocation, litter N concentration, which was previously shown to be a good indicator of N availability at the BFG site (Rasion *et al*, 1990), was regressed against proportional belowground C allocation calculated with, and without, the inclusion of coarse roots.

Table 8.4 shows the significance and r^2 values for regressions between litter N concentration and proportional belowground C allocation. As with absolute belowground C allocation (Chapter 7), the difference between the years 1992 and 1993 is marked. The relationships are significant for all ratios and litter N concentration in 1992, but are only significant in 1993 where GPP proportional belowground allocation is utilised (Table 8.4). For the combined year data there is a significant relationship only where coarse root biomass (CR) is excluded from the belowground C allocation ratios. The strongest correlations were found for the percentage of belowground C allocation excluding coarse roots regressed against BIOMASS simulated GPP and NPP, with an r^2 of 0.87 and 0.84 respectively for 1992 only. Other strong correlations include GPP with and without coarse roots with an r^2 of 0.86 and 0.89 respectively for 1993 only, and an r^2 of 0.46 and 0.49 for both years combined for GPP and NPP, respectively. The influence of N availability on proportional GPP belowground allocation excluding coarse roots is shown in Figure 8.5. N availability appears to strongly influence proportional belowground allocation, but the relationship varies between years, although there is one extreme point driving the strength of these relationships.

Table 8.4: r^2 values for regressions between litter N concentration and the ratios shown in the header row of the table, for 1992, 1993 and 1992 and 1993 combined.

	$\frac{GPP_b + CR}{GPP_B}$	$\frac{GPP_b}{GPP_B}$	$\frac{GPP_b + CR}{NPP_B}$	$\frac{GPP_b}{NPP_B}$
1992	0.66 (P<0.05)	0.87 (P<0.05)	0.54 (P<0.1)	0.84 (P<0.05)
1993	0.86 (P<0.05)	0.89 (P<0.05)	ns	ns
1992 & 1993 combined	ns	0.46 (P<0.05)	ns	0.49 (P<0.05)

*ns = not significant at 90 or 95% confidence level, P<0.05 significant at 95% confidence level, P<0.1 significant at 90% confidence level. Symbols explained in Section 8.3.1.

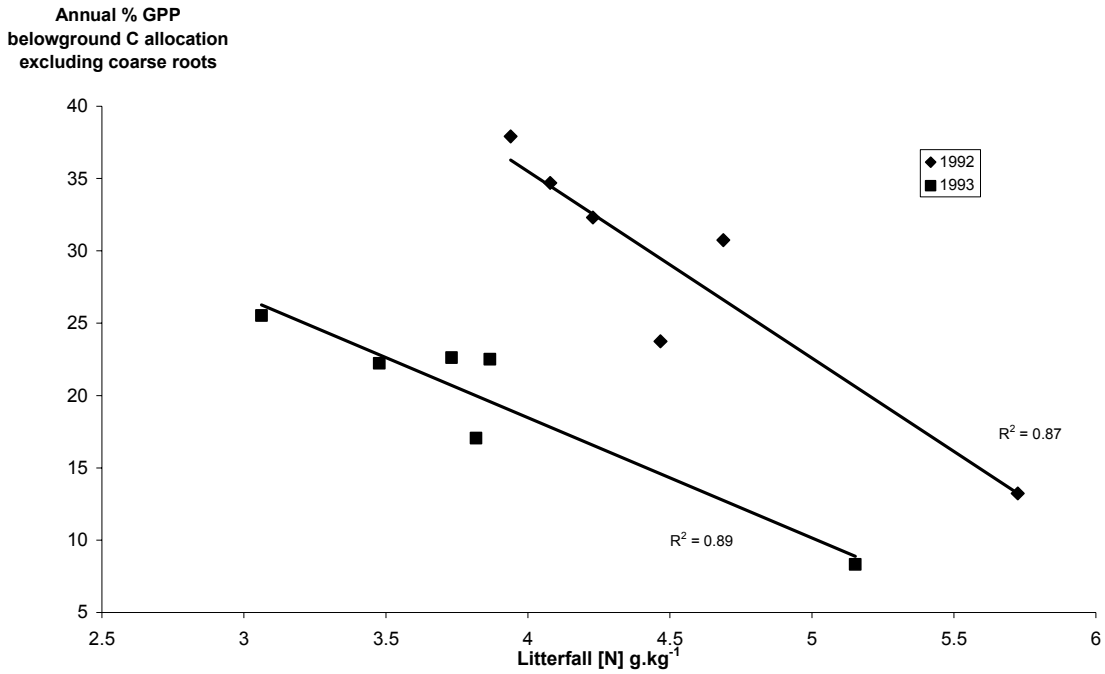


Figure 8.5: Proportional belowground C allocation plotted against litterfall [N].

8.3.4 Whole stand productivity

In order to place the measured belowground C allocation in context it is desirable to determine the C allocation to other tree tissues. BIOMASS provides an estimate of GPP, but the C allocation algorithms within the model are not well developed. It was possible to derive estimates of aboveground stem productivity from allometric relationships previously developed at BFG, but not estimates of foliage or branch production.

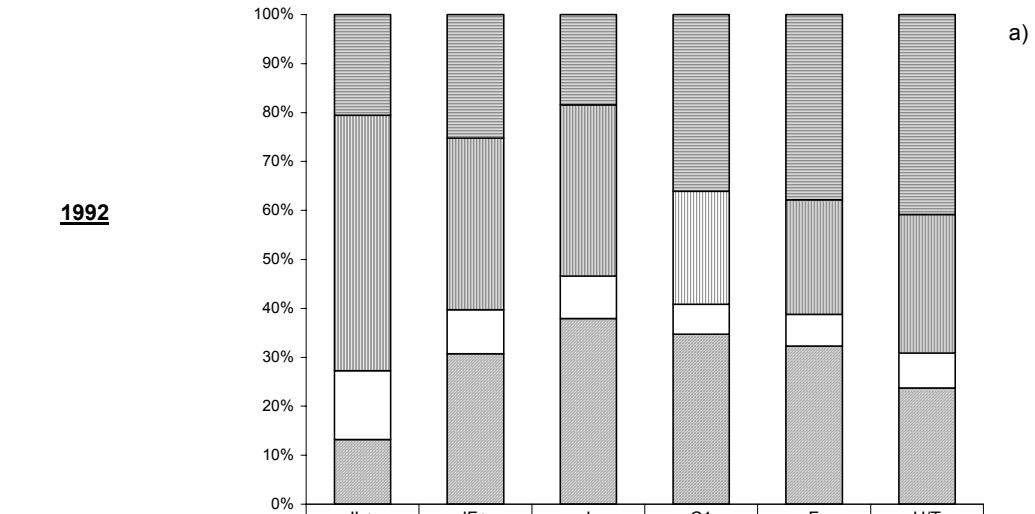
Stem productivities for 1992 and 1993 were estimated from relationships derived by Snowdon and Benson (1992) relating stem C to inventory data. Other aboveground allocation to foliage, branches and respiration of the aboveground component were estimated by subtracting belowground C allocation and stem C production from BIOMASS estimated GPP.

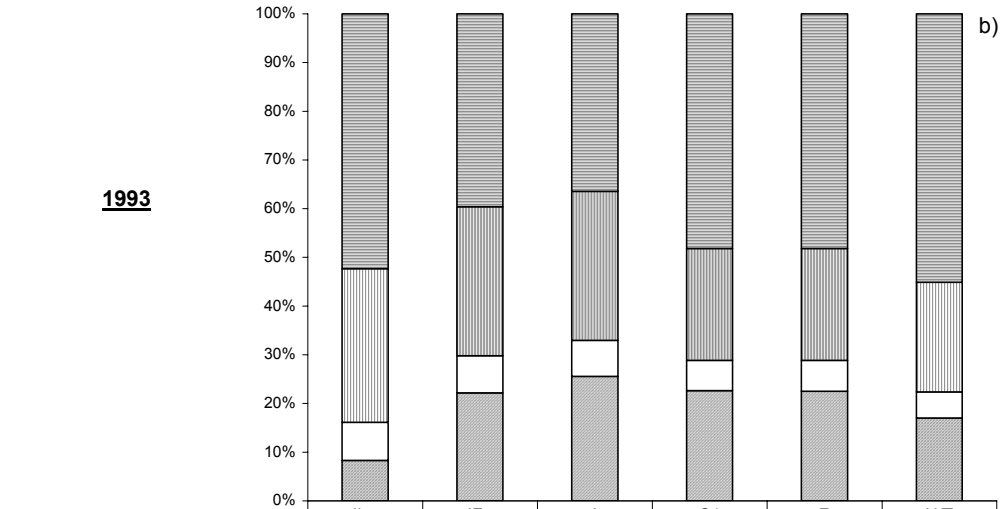
Figures 8.6 a) and b) show the percentage C allocation for the 6 selected treatments for 1992 and 1993, respectively. It can be seen that for the irrigated plots belowground allocation increases as N becomes more limiting in the order

IL+, IF+, I, with the litter [N] being 5.7, 4.6 and 3.9 $gN.kg^{-1}$ respectively for 1992. The magnitude of the percentage allocation belowground for the irrigated treatments varies quite markedly between 1992 (28 –45%) and 1993 (16-32%).

The pattern of belowground allocation is not as clear on the non-irrigated sites, where both C1 and F allocate approximately the same proportion belowground, whilst U/T allocates slightly less C belowground. This is supported by the litter [N] values which are 4.01, 4.19 and 4.41% for C1, F and U/T in 1992, respectively. The slightly lower allocation of C belowground in the U/T treatments may be because the U/T treatment has greater aboveground competition due to the larger number of stems, indicating that extra resources are allocated aboveground to gain competitive advantage for individual stems (King, 1993). Again the proportions allocated belowground vary between 1992 (35-42%) and 1993 (24-28%).

The harvest index based on GPP (stem production as a proportion of total production) for irrigated treatments ranged from 35 – 50% and 30 –32% in 1992 and 1993 respectively. For non-irrigated treatments the harvest index based on GPP was 23 – 28% and 23% for 1992 and 1993, respectively.





	IL+	IF+	I	C1	F	U/T
other aboveground (tC/ha)	20.1	13.6	10.3	14.7	14.6	16.5
Stem C production (tC/ha)	12.1	10.4	8.6	7.0	6.9	6.7
coarse root (tC/ha)	3	2.6	2.1	1.9	1.9	1.6
b/g C excluding coarse roots (tC/ha)	3.2	7.6	7.2	6.9	6.8	5.1

Treatment

Figure 8.6a) and b): Proportional allocation to belowground and aboveground components for 6 selected treatments at BFG for 1992 (a) and 1993 (b) respectively. Belowground C, coarse roots and stem C production estimated from measurements or allometric relationships, other aboveground estimated from subtracting previous estimates from BIOMASS estimated GPP.

8.3.5 Trade off between stem C and fine root C

Santantonio (1989) suggested a trade off exists between bole growth and fine root production in order to ensure that allocation to foliage remained fairly constant irrespective of the productive capacity of the site. The existence of this trade off was investigated in the treatments at BFG by regressing absolute stem C allocation versus absolute belowground C allocation excluding coarse roots, and proportional stem C allocation versus proportional belowground C allocation excluding coarse roots (Figures 8.7 a) and b)). These parameters were either measured (belowground C allocation) or estimated from allometric relationships (stem C production). The regression was undertaken separately for 1992 and 1993 as combined year data had previously shown few significant relationships. The regressions between absolute and proportional belowground C allocation excluding coarse roots were non significant for either relationship for either year, where irrigated and non-irrigated treatments were combined.

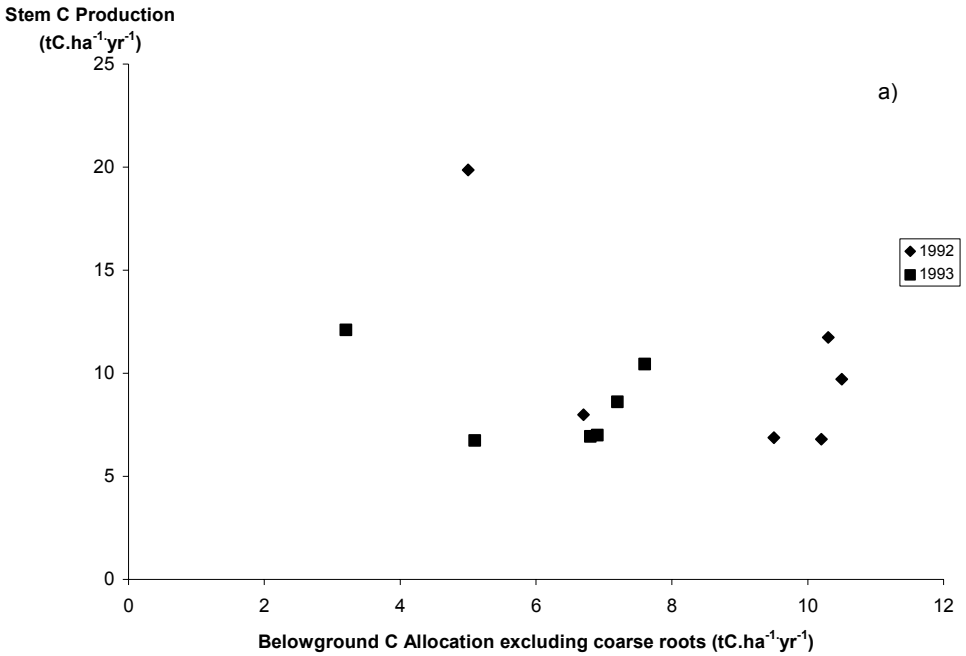


Figure 8.7a) and b): Absolute (a) and proportional (b) C allocation between stem and belowground C allocation excluding coarse roots for 6 treatments at BFG for 1992 and 1993.

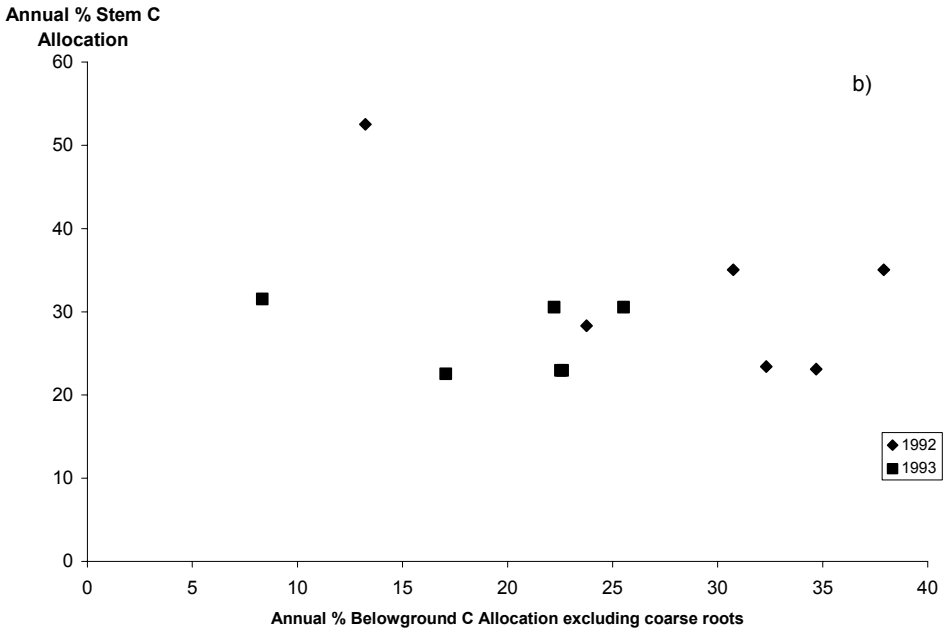


Figure 8.7a) and b): Absolute (a) and proportional (b) C allocation between stem and belowground C allocation excluding coarse roots for 6 treatments at BFG for 1992 and 1993.

Where irrigated and non-irrigated treatments were separated in each of 1992 and 1993 the results were quite different (Figure 8.8a) and b)). Figure 8.8a) shows the relationship between proportional stem C allocation and belowground C allocation excluding coarse roots. A strong negative relationship between stem and fine root C allocation for the non-irrigated plots in both 1992 and 1993, and for the irrigated plots in 1993. The irrigated plots in 1992 did not show a significant negative correlation between stem and fine root C allocation. The strong correlations for these relationships may be over-inflated, as there are only 3 points in each correlation, and these must be interpreted with caution. However, if the treatments are separated into irrigated and non-irrigated and separated into different years, it does appear that a trade-off between stem C and belowground C allocation exists. Figure 8.8b shows similar negative relationships between proportional stem C allocation and total proportional belowground C allocation.

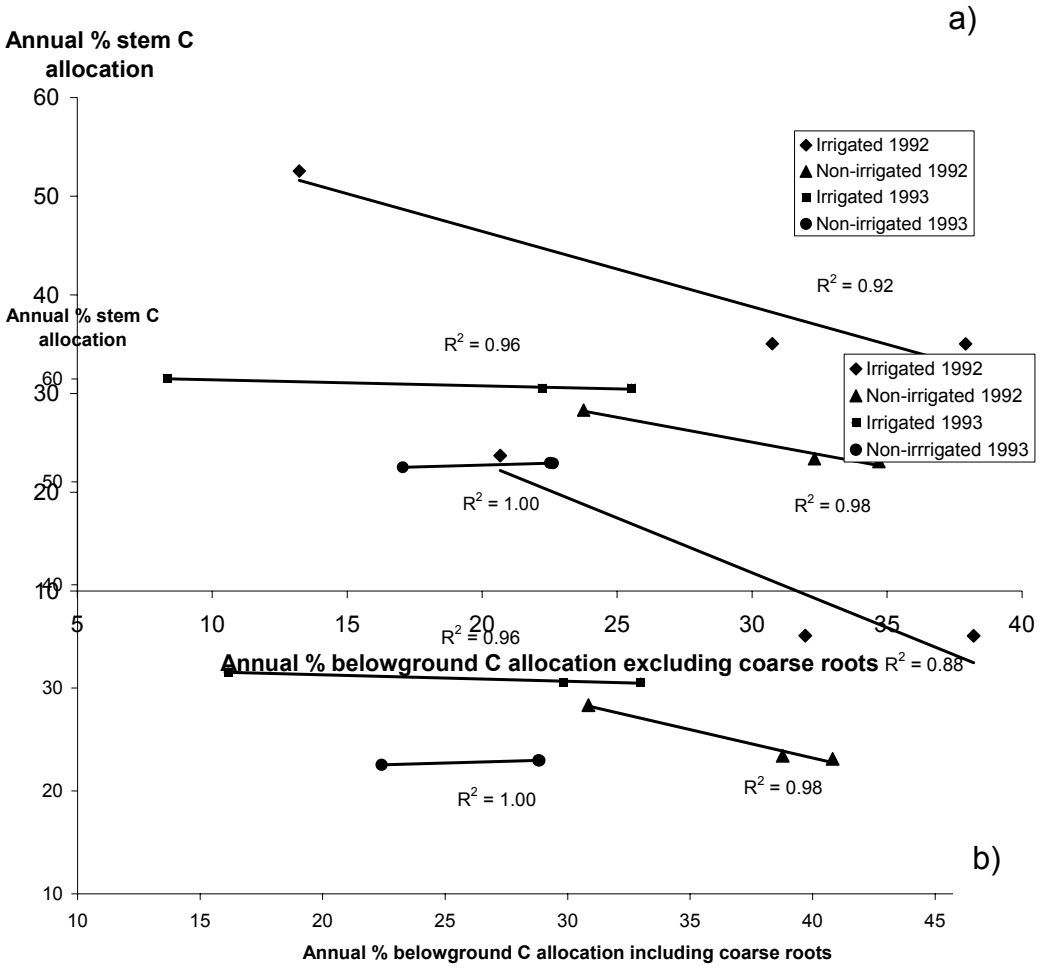


Figure 8.8a) and b): Relationship between proportional stem C allocation and proportional belowground C allocation excluding coarse roots (a) and total proportional belowground C allocation (b).

8.4 Discussion

8.4.1 BIOMASS estimates

Table 8.5 shows several GPP estimates obtained with BIOMASS for a limited number of treatments at the BFG field site over a number of years. The productivity differences between the simulations are due to the age of the stand, and therefore varying growth stage, and to the climatic conditions in the year for which BIOMASS was simulated.

Table 8.5: Annual GPP estimates simulated by the BIOMASS model at BFG used by various workers since the development of BIOMASS

Reference	Year simulated	IL+ (tC ha^{-1})	I (tC ha^{-1})	C1 (tC ha^{-1})
McMurtrie *et al*, 1990a	1984/1985 1985/1986 July – June	38	35	18.5
McMurtrie *et al*, 1992	1984/1985 1985/1986 1986/1987 July - June	45	30	17.5
Ryan *et al*, 1996a	1992/1993 July - June	36.9	26.9	29.5
this study	1992 1993 January - December	38	28	30

It can be seen that the IL+ treatment consistently has the greatest GPP. The I treatment exhibited a similar productivity to the IL+ treatment at the beginning of the intensive study period (1984 – 1988), but this is reduced over time, possibly due to N limitation in the I treatment reducing productivity. GPP estimates have

increased quite significantly for the C1 treatment from the mid 1980s to the early 1990s, possibly due to crown closure and therefore better site occupation in the early 1990s. Simulated GPP correlated well with basal area increment (Figure 8.2a), which indicates that a greater GPP results in greater stem growth. As BFG was the site used to calibrate the BIOMASS model in the mid 1980s, it was expected that model outputs would fairly well represent productivity at the site during 1992 and 1993.

8.4.2 Proportion of C allocated belowground

NPP is the estimate most often quoted by scientists in the literature, as this is the most easily measurable component of forest systems. As described earlier the estimates of belowground C allocation estimated in this study actually represent GPP_b, or the belowground gross primary productivity, and therefore cannot truly be represented as a proportion of NPP. However for gross comparisons with work undertaken elsewhere, the total belowground C allocation at BFG was estimated as between 16 – 47 % of GPP and 29 – 63 % of NPP.

Comeau and Kimmins (1989) estimated that up to 60% of NPP could be allocated belowground on a dry site, which coincides with the upper bounds of the estimates obtained from the BFG site for N stressed treatments. Linder and Rook (1984) found approximately 40% of GPP was allocated belowground in fertilized stands which also coincides with the upper bounds of belowground C allocation for some treatments at BFG. Grier *et al* (1981) found that 69% of NPP was allocated belowground in a mature fir stand. It may be expected that the amount of C allocated belowground would decrease as the stand became more mature, as available N would be derived from retranslocation and nutrient cycling rather than soil mineralisation. The proportion of C allocated belowground is likely to be species, site and time specific and the proportions of belowground allocations quoted above are only indicative of the range possible.

8.4.3 Drivers of belowground C allocation

N stress appeared to be a strong driver of belowground C allocation at BFG. This observation is supported by the strong negative correlation between proportional GPP belowground C allocation excluding coarse roots and litterfall [N] with r^2s of 0.87 and 0.89, for 1992 and 1993 (Table 8.4). The most N stressed irrigated treatment, I, showed a proportional belowground C allocation to be 33 and 47% of GPP for 1992 and 1993 respectively (Figure 8.3a)) which may indicate the upper bound of a well-watered forest stand in any given year. In the irrigated treatments, where water was non-limiting, the change in belowground allocation appeared to be linked to N limitation, and this is shown by the significant correlations between proportional belowground allocations and litterfall [N], which reflects N availability (Table 8.4). The non-irrigated treatments (C1 and F) had similar belowground C proportions and this could provide an indication of the upper limit of belowground allocation (approximately 22 –41% of GPP, Figure 8.3a)) for a typical (non-irrigated) forest in any given year. The non-irrigated treatments (C1 and F) were probably under a similar level of N stress (litterfall [N] values of 4.0 and 4.2 $gN.kg^{-1}$, and 3.7 and 3.8 $gN.kg^{-1}$, for the C1 and F treatments for 1992 and 1993, respectively) which accounts fro the very similar proportional belowground allocation in these treatments. Because of the confounding effects of water and nitrogen stress within these treatments, it is not possible to distinguish an N-driven belowground C allocation on the non-irrigated treatments.

8.4.4 Trade-off between stem C and belowground C allocation

The trade off between bole growth and fine root allocation suggested by Santantonio (1989) was not reflected in the treatments at BFG where 1992 and 1993 data were examined together. Where data were separated into years and into irrigated and non-irrigated treatments the allocation belowground did appear to decrease as stem C allocation increased. However these relationships were based on only 3 data points, for any single combination, and must be interpreted with caution.

8.5 Conclusions

The BIOMASS model estimated annual GPP values of approximately 30 tC ha^{-1} for water and N stressed treatments to 38 tC ha^{-1} for irrigated and fertilized treatments. Belowground C allocation accounted for 16 –27% of GPP for the irrigated and fertilized treatment, and approximately 22-41% of GPP for the water and N stressed treatments.

The stem C allocation based on GPP ranged from 30 – 50% for irrigated treatments over both years with the greater bole allocation going to the non N-stressed treatment. The non-irrigated treatments showed a more conservative stem C allocation range of 23-28% of GPP. The trade off between bole growth and fine root allocation was not evident in the treatments at BFG except where data was separated between years and between irrigated and non-irrigated plots.

For irrigated treatments there appears to be a strong influence of N-stress on belowground allocation, with IL+ allocating a much lower proportion belowground compared to I and IF+ treatments. Differences in N status were not strong between the non-irrigated treatments (C1 and F) and the influence of water stress confounded direct relationships. However a strong negative correlation was found between N availability and proportional fine root allocation across all treatments. The U/T treatment allocated a slightly lower proportion of C belowground compared to the other non-irrigated treatments, possible due to a greater degree of aboveground competition for light as suggested by King (1993).

The analysis undertaken in this chapter emphasises the importance of understanding whole stand dynamics when investigating belowground C allocation. Where whole tree carbon budgets are estimated in elevated CO_2 conditions, and stands may be more N stressed due to having a greater assimilative capacity, the allocation of C to the belowground system is likely to take on greater significance. Based on the proportion of GPP allocated belowground in the I treatment, which received adequate water but was N stressed, and the C1, F, and U/T treatments which all suffered a degree of N stress, the approximate belowground C allocation of GPP is 25%. This is a significant C flux in whole stand carbon budgets.

CHAPTER 9: THE INFLUENCE OF FERTILIZATION AND IRRIGATION ON BELOWGROUND CARBON ALLOCATION IN A PINE PLANTATION: A SYNTHESIS

9.1 Belowground allocation of carbon in forests

Forest systems consist of foliage, branches and stems aboveground, and the belowground components of coarse and fine roots and associated symbionts. Trees vary the allocation of carbon (C) and nutrients across the above- and belowground components in response to growing conditions. For forest managers maximising C in the stem is important as this relates directly to the economic return from timber.

The allocation of C belowground is intimately linked with whole tree or stand C allocation dynamics. Forest growth and the allocation of C belowground are influenced by a variety of environmental and plant related factors (e.g. genetics, age). The mechanistic understanding of fine root systems has not yet developed to a stage where fine root biomass and turnover can be accurately estimated, or modelled, in forest systems. Generally, allocation of C to fine roots is greater on drier or nutritionally poor sites, and live root mass may be shorter lived in water or nutrient stressed systems (Chapter 1). However, insufficient data exists to allow confident generalisations.

Allocation of C to root systems needs to be understood in the context of the C balance of the whole stand. The overall productive capacity of a system is a key driver of root activity, and productivity is influenced by species, site fertility and climate. The enhanced greenhouse effect is predicted to cause climatic changes estimated to be an increase of 0.6 – 3.8^{o}C across the Australian continent by 2070, and a decrease in winter rainfall (IPCC, 1996). The net effect of climate change on forest productivity needs to be better understood so that adaptive management can be adopted. However the impact of the enhanced greenhouse effect on forest systems is not easily investigated, and the feedback mechanisms relating to belowground productivity need to be better understood.

9.2 Potential effects of elevated CO_2 on forest productivity

The National Greenhouse Advisory Committee Dedicated Grants Scheme, who were interested in the effect of elevated CO_2 on forest productivity, partially supported this study. Because of this support the influence of elevated CO_2 on forest productivity is discussed.

CO_2 is one of the greenhouse gases present in increasing concentrations in the atmosphere. CO_2 is also the carbon source for photosynthesis. The effect of elevated CO_2 on forest productivity is a result of complex feedbacks and interactions between various processes that occur at a range of scales (Wolfe, 1994). For example an increase in atmospheric CO_2 is predicted to increase photosynthesis, and therefore influence whole plant productivity at an individual tree level. However this increase in photosynthesis may result in a greater requirement for nutrients, particularly nitrogen (N). In order to acquire this extra N, trees may respond by increasing their proportional allocation of C belowground.

Recent experimental work, investigating the influence of doubling CO_2 on tree productivity, has predicted increased photosynthesis. However the overall impact of feedbacks on forest growth is likely to reduce the predicted impact of the photosynthetic boost obtained from a doubling of CO_2 (Idso and Idso, 1994). These feedbacks work at an individual tree, stand and ecosystem level, and trees/stands are likely to respond in a manner that ensures their survival. Atmospheric CO_2 has increased gradually over since the mid 1800s and in 1998, was 32% higher than the atmospheric CO_2 levels in 1850. Yet there is little evidence in long-lived trees of an increase in the rate of stem biomass growth based on tree ring analysis. This may be due to photosynthetic and other systems gradually adjusting to the changing environment and preventing any sharp increases in productivity.

Understanding the belowground system responses to elevated CO_2 requires an understanding of belowground systems in ambient CO_2 conditions. This study investigated the influence of differing levels of fertilization and irrigation on

belowground C allocation in a mature forest stand in ambient CO_2 conditions. The hypothesis tested was whether trees responded to increased nitrogen and water limitation, by allocating a greater proportion of C belowground. These estimates of belowground productivity were investigated between 1991 and 1993 in a mature forest ecosystem of an established *Pinus radiata* field experiment near Canberra, Australia.

9.3 Field site description and summary of previous work at the site

The Biology of Field Growth (BFG) field experiment, a multi-disciplinary project established in 1983 to study the effects of irrigation and nutrition on the productivity of a radiata pine plantation (Benson *et al*, 1992), was used to test the hypothesis. The BFG stands were limited by N and water availability and there was a marked positive interaction between these factors affecting stand growth. Intensive investigation of aboveground growth responses was undertaken between 1984 and 1988. Further work, framing the basis of this thesis, and including belowground investigations, was conducted between 1991 and 1993.

Several methods exist to quantify belowground carbon or root biomass in forests, but many of these techniques involve some form of system disturbance and none easily takes into account root respiration or turnover rates. In addition the large spatial variation found in soil systems requires extensive sampling to ensure that the measurements actually represent the wider soil system. Some of these problems were overcome using the approach of Raich and Nadelhoffer (1989).

Raich and Nadelhoffer (1989) suggested that the annual amount of carbon (C) allocated belowground could be indirectly estimated by quantifying the C released from the soil (soil respiration) and subtracting the measured amount of C entering the system as aboveground litter fall. This theory is based on the premise that the system is in steady state with respect to soil and litter C, so that on an annual time scale the C flux into this unchanging C pool must equal

the C flux out of it. A schematic representation of this model (Figure 5.1) is reproduced below.

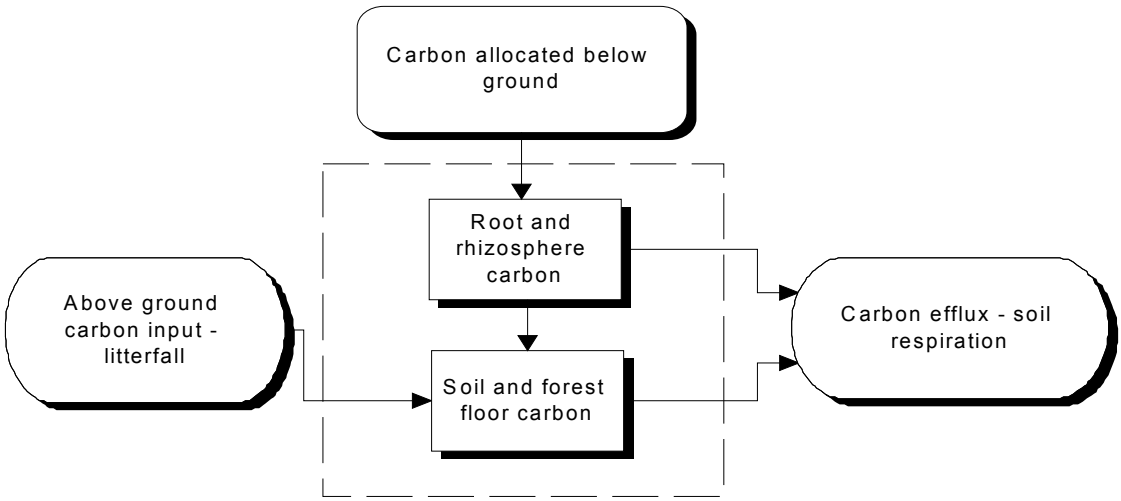


Figure 9.1 (same as Figure 5.1): Schematic showing Raich and Nadelhoffer's (1989) principle of using soil respiration and litterfall measurements to estimate belowground carbon allocation. Carbon pools within dashed line box are assumed to be in steady state, therefore flows into must equal flows from it. The principle can still be applied if change within the pools in the box are known and can be adjusted accordingly.

Using this approach C allocated belowground includes: C incremented in root biomass; C exudates from roots; and any C respired by the roots or symbionts. Root turnover contributes to this C flux as live roots respire C and dead roots decompose. The appropriate time scale for applying the principle is 1 year, as this enables root turnover to be estimated as CO_2 release after decomposition. This approach does not provide quantitative estimates of root biomass, as the C allocated belowground is to increment C in standing root biomass, and root, rhizosphere and mycorrhizal respiration.

The Raich and Nadelhoffer (1989) approach requires the accurate measurement of soil respiration and litterfall, and the testing of the assumptions of steady state for soil and forest floor systems.

9.4 Estimates of litterfall, forest floor litter, root and soil C pools in contrasting BFG stands

C pools and/or fluxes that affect the belowground dynamics include litterfall C, forest floor C, fine and coarse root C and soil C. At BFG each of these pools was measured:

- litterfall C was measured monthly for 10 years (1983 – 1993):
- forest floor standing litter C was measured 5 times - 1983, 1986, 1988, 1991 and 1993;
- coarse root C was estimated from an allometric relationship with diameter at breast height (dbh) for 1992 and 1993 (Jackson and Chittenden, 1981);
- fine root biomass was estimated directly by core sampling in a selection of treatments in August 1992 and March 1993; and
- soil C was estimated in 1983, 1984 and 1994.

During the period of belowground study (1992 and 1993) litterfall values ranged from 0.55 to 2.24 tC ha^{-1}, which is within the 10 year values of annual litterfall at BFG (0.47 – 2.28 tC ha^{-1}). The litterfall was approximately double in 1993 compared with 1992 across all treatments, possibly because 1992 was a wet year that stimulated foliage growth that was released as litterfall in 1993.

Forest floor standing litter had accumulated significantly in all plots over ten years between 1983 and 1993, with an initial litter layer of just over 1 $t.ha^{-1}$ in 1983 across all treatments to a litter layer of 27.5 $t.ha^{-1}$ and 13.5 $t.ha^{-1}$ in the IL+ and C1 treatments respectively in 1993. However, during 1991 and 1993 treatments IL+, IL-, IF-, IF+, I, C1, F and U/T showed no change in the mass of standing litter. Thus no adjustments from the impact of a changing standing litter carbon pool are required in these treatments when applying the Raich and Nadelhoffer (1989) approach to estimating belowground C allocation. The C2 and C3 treatments showed a measured mean increase in mass of standing litter of 1.60 and 1.33 tC $ha^{-1}.yr^{-1}$ respectively. The increment in standing litter in C2 and C3 cannot exceed the measured input in litterfall, and, since the

litterfall was accurately measured, this was taken as the upper limit for correction. This was 0.70 and 0.75 tC ha^{-1} for C2 and C3 respectively. The further scenario that no increment in forest floor standing litter C occurred (i.e. that the measurements were in error) was also explored.

The allocation of C to coarse root (>2 mm diameter) increments was calculated using Jackson and Chittenden's (1981) allometric relationship between dbh and coarse root biomass. Jackson and Chittenden (1981) developed their allometric relationship based on 247 radiata pine trees from variable sites across New Zealand and achieved an r^2 of 0.899 for the relationship between the weight of roots greater than 2 mm diameter and dbh. At BFG estimates of coarse roots ranged from 1.0 to 5.4 tC ha^{-1} in the C3 treatment in 1993 and the IL+ treatment in 1992, respectively, and C increments into coarse roots were generally 18% lower in 1993 compared with 1992. As coarse root C increment is proportional to the basal area increment of the treatments, this reduction in coarse root C increment reflected the reduction in basal area growth in 1993 compared with 1992.

Limited fine root biomass (<2 mm diameter) measurements were taken during 1992 and 1993 and ranged between 2.1 $t.ha^{-1}$ and 3.9 $t.ha^{-1}$ for IL+ and I respectively. Differences between treatments were unable to be statistically determined due to the high variability of the samples. Within the treatments fine root biomass was similar for periods of high soil respiration (March 1993) and low soil respiration (August 1992), indicating little seasonal difference in fine root biomass. There appeared to be a difference between the treatments within each sampling period, with the IL+ treatment exhibiting approximately 37% lower total fine root (<2mm) biomass compared to the I and C1 stands, indicating that both N status and water availability influence fine root biomass production.

Fine root nitrogen concentrations ranged from 12.9 and 7.9 $mgN.g^{-1}$root in the IL+ and I treatments respectively in August 1992. The fine root N concentrations did not differ within the treatments between the sampling periods. There was no difference in the root N concentrations of live/brown and

dead roots, although white fine roots had an N concentration approximately 50% lower than live/brown and dead roots.

Short term changes in forest soil C are generally difficult to detect against large background soil C values, making it necessary to investigate soil C change over periods of 10 years or more. Over the 10 year period between 1984 and 1993 there was no significant change in the soil carbon pool within the IL+, IF+, I, C1, F and U/T treatments. These treatments represent the extremes of forest growth and litter inputs at the site, and it is assumed that there was no change in the soil carbon pools in the IL-, IF-, C2 and C3 treatments which lacked the 1984 soil C data. Hence no adjustments were made to account for change in soil C when estimating belowground carbon allocation by using the C budget approach by Raich and Nadelhoffer (1989).

These estimates of C pools and fluxes are needed to use Raich and Nadelhoffer's (1989) approach to estimating belowground C allocation using soil respiration values.

9.5 Soil respiration methodology

Field measures were needed to quantify the gross flux of C from the soil and litter layer in the different treatments at BFG. Two common techniques used to measure soil respiration *in situ* employ either alkali absorbents or infra-red gas analysis (IRGA) and these techniques are generally characterized by the absence (static) and presence (dynamic) of air flow in a chamber, respectively. The IRGA can also be used in the absence of airflow by analysing air samples from chambers where CO_2 build up over time has occurred.

Several studies (see Table 5.1) have concluded that estimates of soil respiration measured by soda lime differ from those measured with an IRGA. Generally, results from field measurements showed that at high rates of CO_2 efflux, the soda lime methodology provided lower estimates of soil respiration, and that flux rates from the two methods are sometimes highly correlated

through an exponential relationship (Ewel *et al*, 1987b; Haynes and Gower, 1995).

Soil respiration measurements were taken with a specialised adapted soda lime methodology at BFG in 1992 and 1993 (Chapter 5). This approach ensured that many of the previous criticisms of the soda lime methodology were eliminated (e.g. instantaneous disturbance through non-permanent measuring collars; small collar size; CO_2 leakage around the lids to the collars; and the soda lime chemical interacting with the holding container).

A comparison of the soda lime technique and IRGA methods was undertaken. The impetus for this method comparison was unrealistically high estimates of CO_2 efflux at BFG if the soda lime-IRGA conversion described in Ewel *et al* (1987b) was applied. The converted estimates were approximately 40 tC $ha^{-1}yr^{-1}$ in the most active treatment (I - irrigated) in 1992. Such rates are clearly unrealistic for this system where the annual GPP estimates are approximately 27 tC ha^{-1}.yr for the (I – irrigated) treatment (McMurtrie *et al*, 1992; Raison and Myers, 1992; Ryan *et al*, 1996a). Ryan *et al* (1996a) developed a detailed carbon budget for the *Pinus radiata* site that indicated that for the I – irrigated treatment, coarse and fine root respiration, plus coarse and fine root production was 10.4tC $ha^{-1}.yr^{-1}$ in 1992/93.

Soda lime in the laboratory was shown to efficiently absorb all CO_2 present, provided adequate moisture was available. Field estimates of soil CO_2 efflux using an IRGA were greater than those using soda lime and the discrepancy was particularly large when the measurement period was short - 8 h compared to 24 h. The size of chamber used for IRGA and soda lime estimates of CO_2 flux was unimportant over the range of flux rates estimated. However build up within the chamber headspace was apparent in large volume chambers and soda lime estimates should be adjusted for this. The use of fans to aid air mixing in soda lime chambers may overcome some of the discrepancy between soda lime and IRGA estimates of soil respiration. Diurnal variation in CO_2 efflux rate also requires that care be taken in scaling up short-term IRGA measurements to daily values. These results are fully discussed in Chapter 5.

Recent work has shown that even a minor chamber pressure difference can have a significant influence on soil CO_2 efflux (Fang and Moncrieff, 1998; Lund *et al*, 1999). It is likely that the discrepancies between the soda lime and IRGA measurements are an artefact of pressure differences within the chamber and the lack of air mixing within the static soda lime chamber. There is no standard reference to test accuracy of soil respiration measurements and there is considerable uncertainty in all types of soil respiration measurements.

The exponential relationship between soda lime and IRGA measures of CO_2 flux described by Ewel *et al* (1987b) and Haynes and Gower (1995) could not be established in studies in a boreal forest in Canada or in the Australian radiata pine plantation. The exponential relationships between soda lime and IRGA estimates of soil CO_2 efflux published in the literature are based on limited data, and these relationships appear not to be generic and should not be applied without prior evaluation. Based on the detailed work described in Chapter 5, and recent international work on methods of measuring soil respiration, no adjustment was made to the soil respiration rates estimated using the soda lime technique at the BFG site during 1992 and 1993. There was no obvious basis for making an adjustment, and application of the published relationships would have produced unrealistically high estimates of CO_2 evolution (see Chapter 6).

9.6 Soil respiration measurements

Soil CO_2 efflux measurements were taken every 2 or 4 weeks over 2 full years from January 1991 through till December 1993 at ten treatments at BFG. In addition to soil CO_2 efflux measurements, soil temperature, and soil and litter moisture content were also estimated.

Soil respiration rates varied from a minimum of 137 $mgCO_2.m^{-2}.h^{-1}$ to a maximum of 785 $mgCO_2.m^{-2}.h^{-1}$ and showed seasonal variation with winter lows and summer highs. The dominant variable contributing to soil respiration among all treatments was soil temperature. A linear relationship was established between soil respiration and soil temperature at 10cm depth and

litter moisture content for irrigated plots, which explained 53% of the variation. A similar relationship between soil temperature at 1 cm depth and soil moisture content was derived for soil respiration on the non–irrigated plots which explained 61% of the variation observed.

The soil respiration estimates at BFG fall within the range and patterns of soil respiration estimates in similar forest systems. The irrigated, low N fertility treatments tended to have slightly higher soil respiration estimates than did non-irrigated, low N fertility control treatments. The soil respiration estimates from the U/T treatment were lower than the thinned control treatments. The highly fertilized treatments, IL+ and IL-, both had lower respiration rates than the control treatments.

The litter layer could not be shown to be greatly influencing the soil respiration estimates. In mid 1993 half of the chambers in each of the treatments had the litter within the chamber replaced with inert alkathane beads, and soil respiration was measured as normal. The replacement of the litter layer with the alkathane beads had little effect on soil respiration rates, only having a significant, but inconsistent, influence in 7 out of a possible 100 measurements. This lack of effect of the standing litter layer on measured CO_2 efflux indicates that CO_2 release from forest floor litter decay must be balanced by the litter input. The influence of the litter layer is also likely to be a small proportion of the total soil respiration.

A strong relationship between soil respiration and fine root estimates could not be identified. Limited fine root biomass data collected in August 1992 and March 1993 did not indicate that fine roots (<0.5mm and <2mm diameter) greatly influenced soil respiration estimates. However total root N (root [N] multiplied by root biomass) did show a significant negative relationship with soil respiration rate.

The annual soil C flux was calculated by multiplying the mean of the soil respiration at the start and end of the measurement period, by the number of days between successive soil respiration measurements. This was undertaken

in preference to predicting soil respiration from soil temperature and soil or litter moisture because:

- soil respiration measurements spanned the entire annual cycle; and
- regression equations did not explain more than 61% of the variation in the soil respiration measurements, so that modelling of the annual flux is likely to have led to significant errors.

Annual soil C efflux ranged from 4.3 to 11.2 tC ha^{-1} in 1992 and from 3.4 to 9.0 tC ha^{-1} in 1993, with soil respiration rates consistently lower in 1993 compared with 1992. The almost 3-fold difference in soil CO_2 efflux between the treatments reflects the different irrigation and fertilization regimes. N is the main growth-limiting factor at the BFG site (Raison and Myers, 1992) and the highest soil respiration rates were measured in the treatments that were irrigated but had poor N nutrition. Lower rates were measured on the non-irrigated but high N sites. The high N treatments, IL+ and IL-, showed a relatively strong relationship between annual soil C flux and estimated NPP (r^2 = 0.78, $P<0.05$), where NPP was estimated using the allometric relationship derived by Raison and Myers (1992) for the BFG site. The lower N treatments showed a significant but relatively weak relationship between annual soil C flux and estimated NPP (r^2=0.30, $P<0.05$).

9.7 Influence of irrigation and fertilization on belowground carbon allocation

Belowground C allocation was calculated for ten treatments having varying availability of water and N utilising information on annual soil respiration, annual litterfall, annual coarse root productivity and reliable measurements of the change in soil C and the change in forest floor C. The equation used to calculate belowground C allocation was:

Belowground C Allocation = *Soil Respiration + Coarse Root Increment + change in Forest Floor C + change in Soil C – Litterfall C*

Estimates of C allocation belowground at BFG varied from 4.38 tC $ha^{-1}.y^{-1}$ to 13.32 tC $ha^{-1}.y^{-1}$. The rankings of absolute belowground allocation, from greatest to least for 1992 was IF+, I, C1, F, C-ALL, C2, IL+, C-ALL_{adj}, C3, $C2_{adj}$, IF-, $C3_{adj}$, U/T and IL-. In 1993 the ranking of the 5 treatments with the greatest belowground allocation was the same as 1992, namely IF+>I>C1>F>C-ALL, and IL- also had the lowest amount of C allocated belowground in 1993. Within any one year there was a 2-fold difference between the treatments with the greatest and least C allocation belowground.

There was an approximate 30% reduction in carbon allocated belowground in 1993 compared with 1992. This 30% reduction in belowground C allocation was caused by an approximately 23% decrease in soil C flux, an approximate 97% increase in litterfall C and an approximate 18% decrease in coarse root allocation between 1993 and 1992 across all treatments.

As with soil C flux, belowground C allocation showed significant differences between 1992 and 1993, which resulted in the data being analysed separately for 1992 and 1993. The capacity to explain variation in belowground C allocation was increased by separating data into the two years.

Weighted annual litterfall [N], which is an indicator of site N availability (Raison *et al*, 1990), was significantly, negatively correlated with belowground C allocation excluding coarse roots, with an r^2 of 0.78 in 1992 and an r^2 of 0.53 in 1993. Litterfall [N] was also significantly negatively correlated with measured soil C within the treatments, with an r^2 of 0.73 and 0.47 in 1992 and 1993, respectively. This indicates that as N availability increases, belowground C allocation and soil C decrease.

Litterfall [N] was significantly positively correlated with coarse root allocation and annual litterfall with r^2s of 0.74 and 0.55 for coarse root allocation in 1992 and 1993, respectively, and r^2s of 0.92 and 0.61 for litterfall C in 1992 and 1993, respectively. This indicates that as N availability increases, stand productivity is enhanced, resulting in greater C allocation coarse roots and

therefore, via an allometric equation, to the bole. Litterfall production also increased as N availability increased.

The contribution of coarse roots to total belowground C allocation varied with N availability. Coarse roots contributed approximately 50% in the high N treatments (IL+ and IL-), but contributed only approximately 20% of belowground C allocation for all other treatments. This shows that the C cost of maintaining the ephemeral fine root system (i.e. fine root respiration and fine root turnover) is greater in low N stands.

The positive relationship between belowground C allocation and litterfall production described by Raich and Nadelhoffer (1989) did not hold for the BFG stands, where there was a significant negative relationship ($r^2 = 0.70$) between belowground C allocation and litterfall. The relationship described by Raich and Nadelhoffer (1989) may be valid at a global scale, but should not be used to estimate belowground C allocation in particular forest stands.

These belowground C allocation estimates are most useful where they can be combined with estimates of whole stand productivity (GPP). To enable this a process-based model was used to simulate total C fixation in the BFG stands.

9.8 Whole stand carbon budgets

BIOMASS is a mechanistic model that calculates gross primary productivity (GPP) of forest stands. The model works on a daily time step, requiring inputs of meteorological data and a description of the canopy, including the leaf area index (LAI) and foliar nitrogen status to provide an estimation of photosynthetic capacity.

The BIOMASS model estimated GPP values in 1992 and 1993 of close to 30 tC ha^{-1} for the water and N-stressed treatments, and 38 tC ha^{-1} for irrigated and fertilized treatments. The estimated belowground C allocation from soil respiration measurements accounted for 22-40% of GPP in the water and N-

stressed treatments, and approximately 16 –28% of GPP in the irrigated and fertilized treatment.

The trade off between bole growth and belowground fine root allocation was only evident in the treatments at BFG in 1992 when data for 1992 and 1993, and irrigated and non-irrigated treatments, were analysed separately. However, these relationships were only based on 3 data points for any one combination of year and irrigated versus non-irrigated treatments, and must be interpreted with caution. The C allocation to the bole, based on GPP, ranged from 30 – 50% for irrigated treatments over both years with the greater bole allocation occurring in the stand having high N availability. The non-irrigated treatments showed a more conservative stem C allocation of 23-28% of GPP.

There was a strong negative correlation between litterfall [N] and proportional belowground C allocation excluding coarse roots, with r^2s of 0.87 and 0.89 for 1992 and 1993 respectively. This indicates a strong relationship between N availability and belowground fine root allocation.

For irrigated treatments there appeared to be an influence of N stress on belowground allocation, with IL+ allocating a much lower proportion (13%) belowground compared to I (38%) and IF+ (31%) treatments. Differences in N status were minor in non-irrigated treatments (C1 and F), and so the N influences on belowground allocation in non-irrigated treatments were not as obvious, with 35% and 32% allocated to fine roots respectively. The U/T treatment allocated 24% C belowground compared to the other non-irrigated treatments, possible due to a greater degree of aboveground competition for light as suggested by King (1993).

The analysis undertaken emphasises the importance of understanding whole stand dynamics when investigating belowground C allocation. Where whole tree carbon budgets are estimated under elevated CO_2, and stands may be increasingly N stressed due to an increased assimilative capacity, and a dilution of tissue N concentration, the allocation of C to the belowground system is likely to be increased. This will have the effect of decreasing aboveground allocation

of C, and increasing the input of C to the soil, which could lead to accumulation of soil C. Based on the proportion of GPP allocated belowground in the I treatment, which received adequate water but was N stressed, and the C1, F, and U/T treatments which all suffered a degree of N stress, the approximate belowground allocation of C was about 25% of GPP. This is a significant component of the whole stand carbon budget.

9.9 Conclusions and future directions

Soil respiration can be reliably estimated using the soda lime technique provided care is taken in the application of the methodology. This requires permanent, large surface area chambers, minimum disturbance of the soil during measurement, minimum or no pressure change at time of measurement, adequate moisture to allow dry soda lime to absorb CO_2 efficiently and an adequately sealed chamber. One improvement that could be made to the current technique is to install small fans within the chamber to aid air mixing, and specifically allow CO_2 to pass over the soda lime. However extreme care must be taken with these fans to ensure no pressure change is induced within the chamber as this could provide a large source of error.

The magnitude of belowground allocation of C is influenced by both water and N stress. In the current study the main differences in N status between treatments occurred in the irrigated treatments. In these stands belowground C allocation was increased by 16 – 20% under high N limitation. There was a strong negative correlation between belowground C allocation as a proportion of simulated GPP and N availability, but this relationship differed between the years. The unthinned treatment (U/T) allocated a slightly lower proportion of C belowground compared to similar thinned treatments.

These results suggest that belowground C allocation is likely to increase with increasing N limitation. The CO_2 fertilization effect is likely to increase N stress in many forests where growth is stimulated but N uptake cannot be increased at the same rate. Under N limitation, forests must invest more C in their fine root systems, which may be in the range of 16-20% greater C allocation

belowground. This increase in C allocation belowground may directly decrease allocation to stem C, or commercial timber production, by the 16-20%.

The CO_2 fertilization effect alone is unlikely to lead to increased timber production. The CO_2 fertilization effect may increase the productivity of forest and plantation canopies, but this increased productivity may result in a greater allocation of C belowground unless there is a concomitant increase in forest nutrition and water status. Where there is sufficient moisture and N, bole growth may increase from 30% to 50% due to a reduction in the allocation of C to the root system. However this is unlikely to exist in a natural system. For Australia with 752,000 ha of radiata pine plantation, and assuming an average growth rate of 15 $m^3.ha^{-1}.y^{-1}$, a harvest of 1% of total plantation per year and a stumpage value of $\$50.m^{-3}$, this 60% increase in bole growth could be worth $9.4 million per year. However it is highly unlikely that all areas of radiata pine plantation in Australia have adequate water and N.

The inter-year variation is considerable, and care must be taken when extrapolating over a forest rotation. Other aspects of climate change, such as an increase in temperature, may also affect forest physiological processes (e.g. respiration), and these influences must also be accounted for when predicting the effect on an enhanced greenhouse environment on forest productivity.

The “difference” approach to estimating belowground C allocation proposed by Raich and Nadelhoffer (1989) appears reasonable on an annual time-step where soil and standing litter C pools are either constant or can be adjusted for. However, large differences between the years in belowground estimates (approximately 30% decrease in belowground fine root allocation between 1992 and 1993), probably due to climate variability, must be considered when applying estimates over the time-scales of a forest rotation.

Further work is required to more fully understand the dynamics of the belowground system. It is still difficult to quantify belowground C pools and fluxes and there is considerable uncertainty surrounding field obtained estimates. Understanding the impact of an elevated CO_2 environment and a

temperature increase on forestry production demands the full recognition of drivers and feedbacks within the complex forest production system. More work is required to understand belowground dynamics in different forest systems including hardwood and softwood plantations and natural forest systems. Further research should focus on mature forest systems, such as this study, to isolate the impacts of natural ontogenetic changes to perturbation effects on the forest system.

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