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SEASONAL BELOW-GROUND CARBON BALANCE
FOR *PINUS RADIATA* TREES GROWING AT
AMBIENT AND ELEVATED CO₂ CONCENTRATION

A thesis

submitted in partial fulfilment

of the requirements for the Degree of

Doctor of Philosophy

by

Stephen Mark Thomas

Lincoln University

1997

DEDICATION

*To Sonya, Bridget,
our baby in preparation,
and to my parents.*

DECLARATION OF ORIGINALITY

This thesis reports the original work of the author except where otherwise stated.

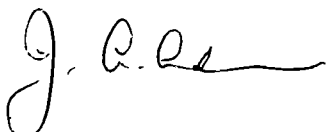
A handwritten signature in black ink, appearing to read 'S M Thomas', written in a cursive style.

S M Thomas

DEPARTMENT OF SOIL SCIENCE

CERTIFICATE OF SUPERVISION

I certify that the work described in this thesis was conducted under my supervision.

A handwritten signature in black ink, appearing to read 'J. A. Adams', with a long horizontal flourish extending to the right.

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ABSTRACT

Atmospheric CO₂ concentration is increasing at *c.* 0.5% y⁻¹, predominantly as the consequence of fossil fuel combustion and deforestation. By the end of the 21st century, based on current emission rates, the atmospheric CO₂ concentration will reach *c.* 500 μmol mol⁻¹. Many studies have shown that total plant productivity is enhanced at elevated CO₂ concentration and there is some evidence to suggest that allocation below-ground is also increased. However, the effects this may have on the below-ground carbon fluxes is poorly understood. This thesis investigated the effects of *Pinus radiata* growth at elevated CO₂ concentration on the seasonal below-ground carbon balance for young *Pinus radiata* trees in the first two years after planting.

The study was conducted at the Forest Ecosystems Elevated CO₂ Project facility at Bromley, Christchurch. Genetically identical *Pinus radiata* D. Don trees were grown at ambient (350 μmol mol⁻¹) and elevated (650 μmol mol⁻¹) CO₂ concentration in large open top chambers. Bi-weekly fine root measurements were made to investigate firstly whether tree growth at elevated CO₂ concentration increased carbon allocation below-ground, secondly to determine whether the seasonality of the rates of fine root production and loss changed, and thirdly to determine whether the fine root distribution was modified. Root measurements were made from minirhizotrons placed horizontally at four depths in the soil. A linear relationship was determined between root numbers observed from minirhizotrons and root length density and root carbon density in the soil.

Estimates of the seasonal change in carbon flux from the soil surface for tree plots were made to determine if the rate of carbon loss from the tree root systems increased at elevated CO₂ concentration, and whether this could be attributed to increases in the rate of fine root growth. A model describing the relationship between carbon flux density (*f*) at the soil surface with distance from the tree stems was used to estimate the annual carbon flux from the trees on a unit ground area basis. Carbon flux density was measured monthly using a chamber placed on the soil surface at 0.35 m from the stem which was attached to a gas analyser and, was estimated at the stem from soil CO₂ concentrations at four depths using a one-dimensional gas diffusion model.

More carbon was allocated to root production for trees growing at elevated CO₂ concentration. After two years, 36% more roots had been produced at elevated CO₂ concentration than at ambient CO₂ concentration, although the difference was not significant. In the first year, fine root (<1 mm diameter) production at a depth of 0.3 m was observed to occur six weeks earlier than for trees at elevated CO₂ concentration. However, the same difference did not recur at the beginning of the second growth season. Seasonal changes of root production

were largely explained by changes in soil temperature. Root loss only occurred after one year from when the trees were planted and total root loss after two years tended to be greater at elevated (14%) than at ambient (9%) CO₂ concentration. The life span of fine roots was significantly reduced at elevated CO₂ concentration and half-lives for roots were estimated to be 951 d at ambient and 333 d at elevated CO₂ concentration. Root longevity was also a function of the time in the season when the roots first appeared. Horizontal and vertical fine root distribution tended to differ between the two treatments. Relatively more fine roots were concentrated close to the stem for trees growing at elevated than those at ambient CO₂ concentration. In addition, relatively more fine roots occurred deeper in the soil profile for trees growing at elevated than for those at ambient CO₂ concentration.

Carbon loss from the root systems of trees growing at elevated CO₂ concentration, measured as CO₂ flux from the soil surface, tended to be higher than that for trees at ambient CO₂ concentration. For the second year of growth, the estimated annual total flux from the tree plots was 13% higher in the elevated treatment (1895 g y⁻¹) than in the ambient (1671 g y⁻¹) CO₂ treatment. The higher carbon fluxes at elevated CO₂ concentration were largely explained by increased fine root production. There were strong positive relationships between measurements of f and root production, and f and stem growth. Daily changes in f were strongly and positively related to temperature. The seasonal change of f was a function of soil temperature and changes in root biomass carbon. Both f and root production declined exponentially with distance from the stem. These results are relevant when developing sampling procedures to estimate tree or plot carbon fluxes.

This study has shown that there was an increase in below-ground carbon allocation for young *Pinus radiata* trees growing at elevated CO₂ concentration and, as a consequence of this, carbon efflux from the soil increased. However, long-term studies of trees growing at elevated CO₂ concentration are needed to determine whether these changes will affect long-term carbon balance and lead to increases in soil carbon storage.

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CHAPTER 1

INTRODUCTION

Since 1800, atmospheric carbon dioxide (CO₂) concentration has increased by c. 30%, largely due to combustion of fossil fuels and deforestation, and the concentration is presently increasing at a rate of 0.5% y⁻¹ (Houghton *et al.* 1996; Melillo *et al.* 1996). By the end of the 21st Century, the projected atmospheric CO₂ concentration will be c. 500 µmol mol⁻¹, based on the continuation of 1994 emission rates (Houghton *et al.* 1996). One response to this increase is the so-called “CO₂ fertilisation effect” on plant growth which may partly explain the global carbon imbalance or “missing sink” of 1.6×10^{15} g y⁻¹ (King *et al.* 1997; Wullschleger *et al.* 1995).

A wide range of responses have been recorded for plant species growing at elevated CO₂ concentration. In most cases total biomass was increased, both above- and below-ground, but with highly variable responses of root:shoot ratios (Ceulemans & Mousseau 1994; Idso & Idso 1994; Rogers *et al.* 1996). It has been argued that these changes in allocation pattern are often a response to other indirect environmental effects (Eamus & Jarvis 1989; Stulen & den Hertog 1993). Plant responses at elevated CO₂ concentration may be subject to a range of positive or negative environmental feedbacks. At the ecosystem level, responses are more complex because of the likelihood of multiple, potentially contrasting, interactive feedbacks on plant growth (Berntson & Bazzaz 1996b).

The major components of an ecosystem carbon balance are illustrated in Figure 1-1. Photosynthetic responses to elevated CO₂ concentration have been well studied (eg. Gunderson & Wullschleger 1994; Tissue *et al.* 1997). Increased carbon uptake from the atmosphere is likely to occur resulting from stimulation of photosynthesis at elevated CO₂ concentration. However, plants may also acclimate to the increased CO₂ concentration and a number of studies indicate that photosynthetic “down-regulation” occurs (Amthor 1995; Mooney *et al.* 1997). Approximately 50% of carbon fixed from the atmosphere by photosynthesis is respired; the remainder is available for growth, propagation, nutrient acquisition and litter production (Ryan 1991). Increased below-ground carbon allocation of plants growing at elevated CO₂ concentration is likely to stimulate carbon losses from root and heterotrophic (microbial and mycorrhizal) respiration (Lambers *et al.* 1996). Whilst there is growing recognition of the importance of below-ground responses to increasing atmospheric CO₂ concentration, there is however a lack of quantification and understanding of controls of the below-ground carbon fluxes between pools, a salient point that has been noted by a number of authors (eg. Canadell *et al.* 1996; Curtis *et al.* 1994a; Koch & Mooney 1996; Norby 1994; Tate & Ross 1997; van de Geijn & van Veen 1993; van Veen *et al.* 1991). Integrative studies that determine the changes

to carbon fluxes and pools, and the nature of feedbacks between plant and soil at changing atmospheric CO_2 concentration, are crucial to predicting ecosystem responses to elevated CO_2 concentrations (Norby 1994).

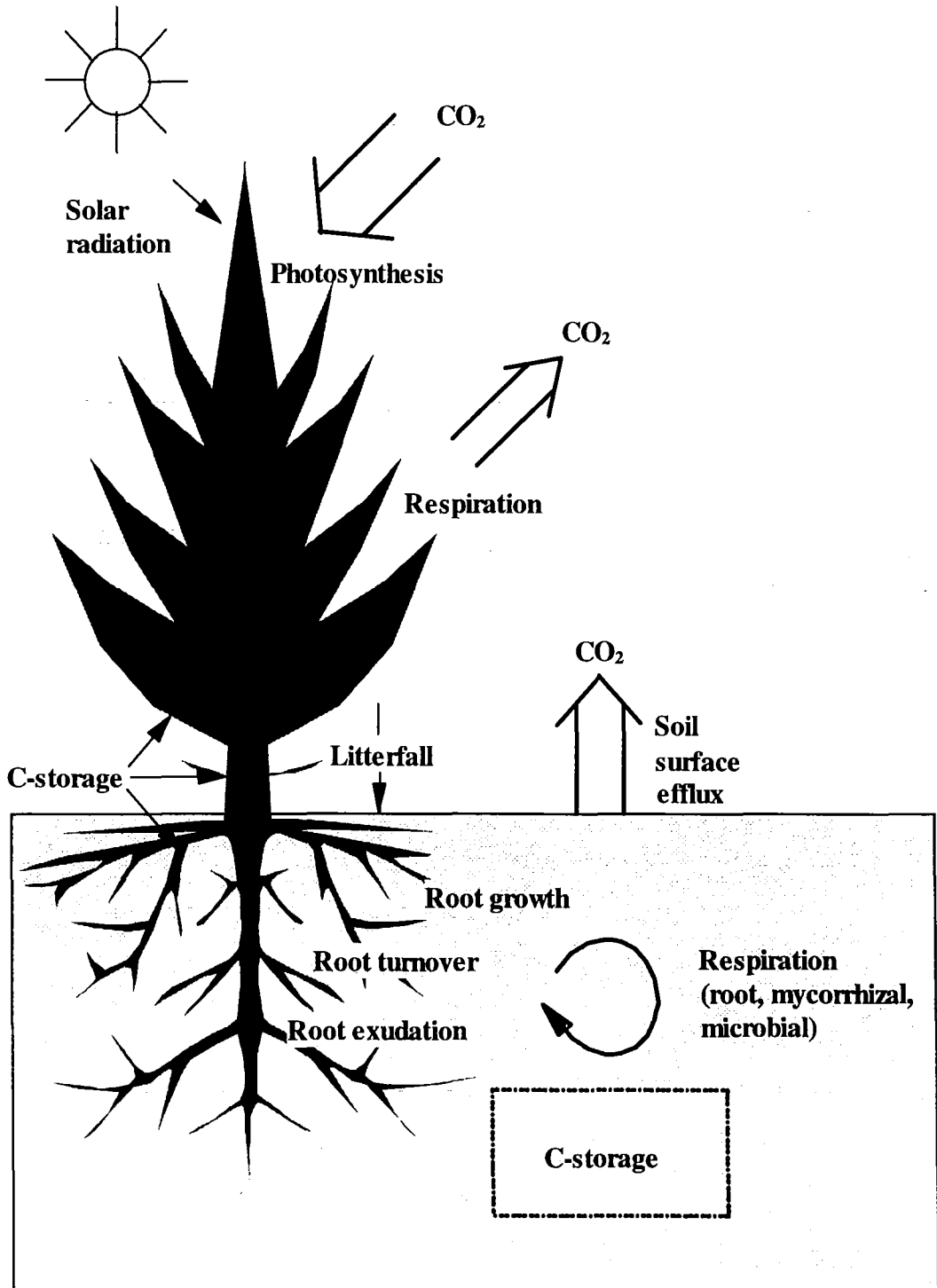


Figure 1-1 Schematic diagram of the major forest carbon balance components.

Soils are the most important terrestrial carbon sink for the storage of carbon sequestered from the atmosphere. The estimated global soil carbon pool is c. 1400 to 1500×10^{15} g and accounts for approximately three-quarters of terrestrial carbon (Schlesinger 1991; 1995). Therefore, changes to below-ground carbon allocation and cycling are likely to have significant effects on the carbon balance for terrestrial ecosystems. Improved understanding of the soil carbon fluxes will allow better model predictions of ecosystem and global carbon budgets.

Several studies at elevated CO_2 concentration have shown that carbon allocation below-ground is increased (eg. Gorissen 1996; Norby *et al.* 1987; Schapendonk *et al.* 1997). Some studies have suggested that the increased carbon allocation to the soil and reduced rates of decomposition of plant material at elevated CO_2 concentration are likely to lead to increased ecosystem carbon storage (van Ginkel *et al.* 1997). Other studies indicate that the rate of decomposition is not always reduced at elevated CO_2 concentration, and that whilst green leaves tend to have greater C:N ratios, senescent litter is often of the same quality as that for litter produced by plants growing at ambient CO_2 concentration (Franck *et al.* 1997; Hirschel *et al.* 1997). Other evidence indicates that the rate of carbon cycling of some plant components may be increased. This is likely to limit the increase in soil carbon storage (Körner & Amone 1992; Ross *et al.* 1996). Detection of changes in soil ecosystem carbon storage is only likely to occur in the long-term or with experimental designs that are statistically more powerful, as the carbon pools in most soils are much larger than likely changes due to increases in below-ground carbon allocation at elevated CO_2 concentration (Hungate *et al.* 1996).

A range of plant-mediated changes to soil carbon fluxes have been measured at elevated CO_2 concentration. These include increases in root respiration (Lambers *et al.* 1996), root turnover (Berntson & Bazzaz 1997; Fitter *et al.* 1996; Pregitzer *et al.* 1995), carbon exudation from roots (Norby *et al.* 1987; Rouhier *et al.* 1996) and mycorrhizal infection (O'Neill *et al.* 1987; Rygielwicz *et al.* 1997). Indirect effects of the increase in below-ground carbon allocation include increased microbial biomass (Runion *et al.* 1994; Zak *et al.* 1996) and soil respiration (Luo *et al.* 1996; Ross *et al.* 1995).

Prediction of ecosystem responses to enhanced CO_2 concentration will require improved mechanistic understanding of the positive and negative feedbacks that occur between soil and plants (Berntson & Bazzaz 1996b). Most ecosystem studies at elevated CO_2 concentration have been conducted with short-lived and short-statured vegetation and young trees (Mooney *et al.* 1997). Most of the experiments studying tree responses have been conducted with seedlings for one growing season or less (Ceulemans & Mousseau 1994).

Forests are a major component of the terrestrial biome. It is estimated that they account for up to 80% of the terrestrial above-ground carbon pool and c. 40% of the below-ground carbon pool (Dixon *et al.* 1994). Within the forest ecosystems higher than two-thirds of the carbon is below-ground (Dixon *et al.* 1994). Carbon in forest soils tends to have long residence times,

particularly for sites at high latitudes. Forest soil carbon sinks have the potential to increase if more carbon is allocated below-ground (Bird *et al.* 1996). In New Zealand, forests cover c. 8×10^6 ha, equivalent to 30% of the total land area. The main commercial forestry species, *Pinus radiata*, occupies c. 1.5×10^6 ha of this forest area (April 1996), accounting for 91% of the plantation forest estate (New Zealand Forest Owners Association 1997). Therefore, in addition to its commercial importance for New Zealand, this forest ecosystem is also a major carbon sink (Hollinger *et al.* 1993).

Nature and scope of the thesis

This study contributes to the Forest Ecosystems Elevated CO₂ project at Bromley, Christchurch. Large open-top chambers, the same as those described by Heagle (1989), are being used in a long-term investigation of the effects of elevated CO₂ concentration on the growth of clonal *Pinus radiata* D. Don trees (Whitehead *et al.* 1995). Tissue culture propagation techniques were used to produce clonal plantlets (Davies *et al.* 1992) to remove the effects of genetic variability in this study. Trees were propagated, and subsequently grew, at ambient ($350 \mu\text{mol mol}^{-1}$) and elevated CO₂ concentration ($650 \mu\text{mol mol}^{-1}$). The Forest Ecosystems Elevated CO₂ project (Project 1105) contributes to the Core Research Programme for the GCTE (Global Change and Terrestrial Ecosystems) component of the IGBP (International Geosphere-Biosphere Programme).

The primary objective of this thesis was to investigate the seasonal below-ground carbon fluxes from clonal *Pinus radiata* D. Don trees growing at ambient and elevated CO₂ concentrations. The carbon fluxes investigated were fine root carbon production and loss, and the CO₂-C (carbon) efflux measured at the soil surface. This flux, often referred to as soil respiration, is the sum of root and heterotrophic respiration.

To measure the carbon fluxes of individual trees growing in open-top chambers at ambient it was important to exclude soil carbon inputs from sources not related to the study trees. This was achieved by isolating the root systems of the trees to a depth of 1.2 m by sheets buried in the soil before trees were planted and by growing trees in a soil with very low carbon concentration.

Fine root production, loss and longevity were measured using video recordings made from minirhizotrons (Upchurch & Ritchie 1983) buried beneath individual trees. Minirhizotron root observations were converted to root length and root carbon densities with destructive soil-root measurements made adjacent to additional minirhizotrons. Soil surface carbon fluxes were measured with a soil respiration chamber and infrared gas analyser, and estimated using a gas-diffusion model, with soil CO₂ concentration measurements sampled from chambers buried beneath the tree.

A longer term goal, which the findings of this thesis will contribute to, is the modelling of whole-tree carbon balances growing at ambient and elevated CO₂ concentrations.

Objectives and thesis organisation

The structure of the research in the thesis is shown in Figure 1-2. The objectives of the thesis are described below with the appropriate chapters which address them.

1. Determine a suitable methodology for investigating the effects of tree growth at elevated CO₂ concentration in terms of carbon for: (i) fine root production and loss, and (ii) the soil surface carbon flux density.

Chapter 2: Seasonal root distribution and soil surface carbon fluxes for one-year-old *Pinus radiata* trees growing at ambient and elevated carbon dioxide concentration

2. To investigate the effects of tree growth at elevated CO₂ concentration on seasonal fine root carbon dynamics and distribution.

Chapter 2: As above

Chapter 3: Growth, loss, and vertical distribution of *Pinus radiata* fine roots growing at ambient and elevated CO₂ concentration

3. To determine the effects of tree growth at elevated CO₂ concentration on the seasonal changes in carbon flux from the soil, and CO₂ concentrations in the soil.

Chapter 2: As above

Chapter 4: Seasonal and radial CO₂ fluxes from root-soil systems of young *Pinus radiata* trees growing at ambient and elevated CO₂ concentration

4. To investigate the effects of fine root distribution on the carbon flux from the soil.

Chapter 4: As above

To address objectives 3 and 4 a model of CO₂ gas diffusion (Cook *et al.* 1997) was used and is included as an Appendix. **Chapter 5** is a synthesis of the results.

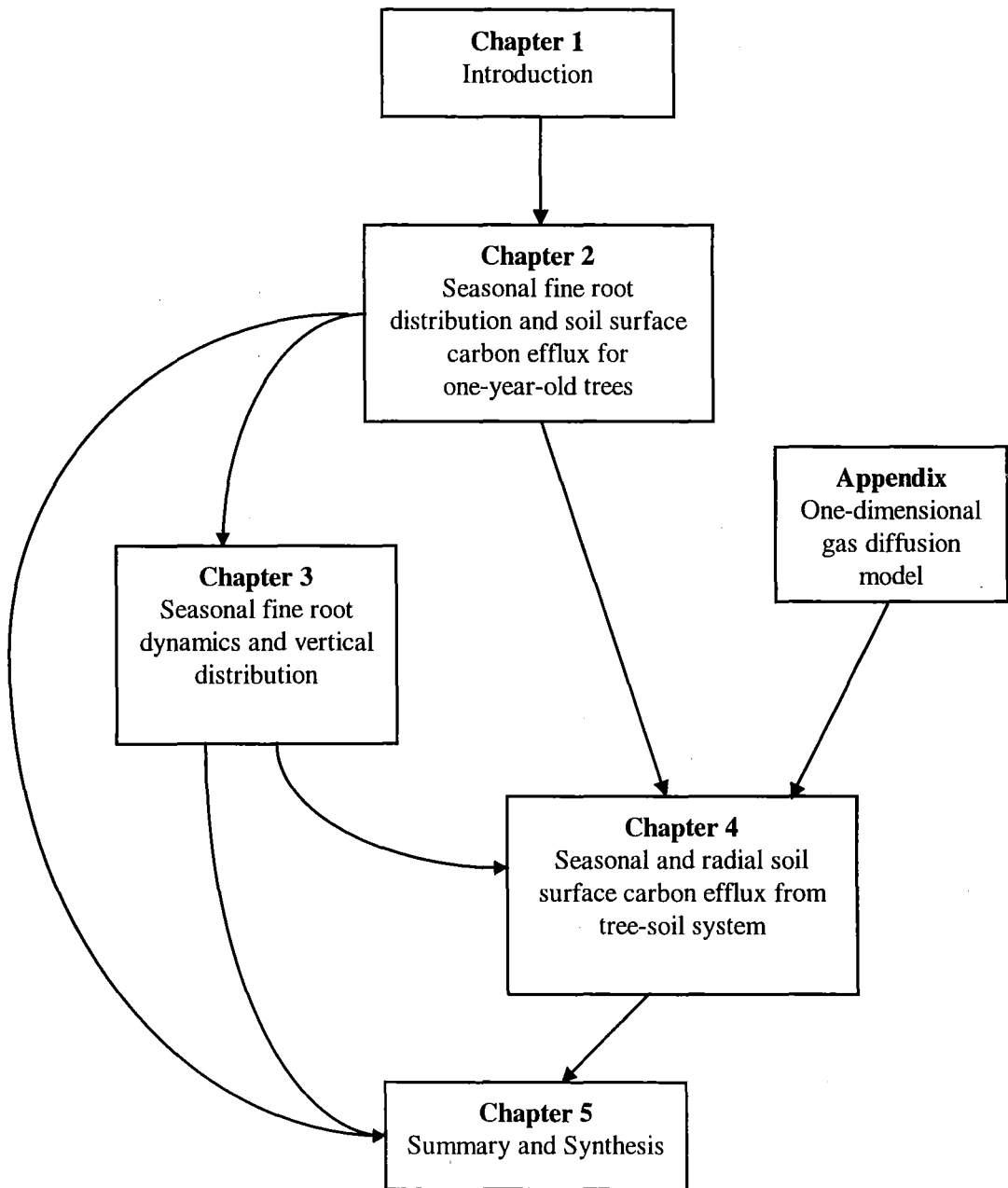


Figure 1-2 Flow diagram of thesis layout

CHAPTER 2

SEASONAL ROOT DISTRIBUTION AND SOIL SURFACE CARBON FLUXES FOR ONE-YEAR-OLD *PINUS RADIATA* TREES GROWING AT AMBIENT AND ELEVATED CARBON DIOXIDE CONCENTRATION [†]

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Summary

The increase in numbers of fine (<0.5 mm diameter) roots for one-year-old clonal *Pinus radiata* D. Don trees grown at ambient (362 $\mu\text{mol mol}^{-1}$) and elevated (654 $\mu\text{mol mol}^{-1}$) CO_2 concentrations were estimated using minirhizotron tubes placed horizontally at a depth of 0.3 m. The trees were grown in large open-top field chambers and were well supplied with water and nutrients. Destructive harvesting of roots along an additional tube showed that there was a linear relationship between root number estimated from the minirhizotron and root length density, L_v , and root carbon density, C_v in the surrounding soil.

Root distribution decreased with horizontal distance from the tree. At a depth of 0.3 m, 88 % of the total C_v was concentrated in a radius of 0.15 m from the stem of trees growing at elevated CO_2 concentration, compared with 35 % for the trees growing in ambient conditions. Mean C_v along the tubes ranged up to $5 \times 10^{-2} \mu\text{g mm}^{-3}$ and tended to be greater for trees grown at elevated CO_2 concentration, although the differences were not significant. Root growth started in spring and continued until late summer. There was no significant difference in the seasonal rates of increase in C_v between the treatments, but roots were observed four weeks earlier for trees growing at elevated CO_2 concentration. No root turnover occurred at this depth during the first year after the trees were planted.

Mean values of carbon flux density at the soil surface, f_o , increased from 0.02 to 0.13 $\text{g m}^{-2} \text{h}^{-1}$ during the year and f_o was 30 % greater for trees grown at elevated CO_2 concentration. Diurnal changes in f_o were related to air temperature. The seasonal increase in f_o continued through the summer and into early autumn, well after temperature had begun to decline, suggesting that this increase was partly attributable to the increase in C_v as the roots colonised the soil profile.

Keywords: *Pinus radiata* D. Don, root length, minirhizotron, carbon flux, elevated CO_2 concentration

[†] Published in *Tree Physiology*, 16, 1015-1021, 1996.

Introduction

Many short-term studies have shown that trees respond to a doubling of atmospheric CO₂ concentration with an increase in biomass (eg. Idso & Idso 1994), but the long-term effects of global change on carbon uptake and storage by forest ecosystems are less certain. In particular, it is difficult to predict changes in turnover and storage of carbon in the roots, and losses of below-ground carbon by respiration and leaching (Melillo *et al.* 1993). For further progress, it is important to quantify the allocation of carbon below-ground in relation to above-ground carbon assimilation and the regulation of these processes by environmental variables.

Fine root annual net primary production in conifers can exceed the values for foliage in developing stands (Gower *et al.* 1994) and there are marked seasonal changes (Santantonio & Grace 1987). The use of minirhizotron tubes offers a non-destructive technique that is used widely to estimate seasonal changes in the numbers of roots (Brown & Upchurch 1987), although there are important, unresolved issues related to scaling from images of roots observed within a small volume of soil surrounding the tube, to the distribution of roots in the bulk soil (Reid & Bowden 1995). To convert root numbers measured from minirhizotron tubes into root length density, L_v , and root carbon density, C_v , requires destructive harvesting of roots in the soil next to the tubes.

The loss of soil carbon by roots and soil organisms, or respiration, measured as the CO₂ flux density at the soil surface, f_o , is positively related to temperature (Lloyd & Taylor 1994) but also depends on the root density (Haynes & Gower 1995). Increases in f_o have been measured in response to trees grown at elevated CO₂ concentration (eg. Johnson *et al.* 1994) resulting from enhanced root activity.

The objective of this study was to determine differences in the seasonal changes in L_v , C_v and f_o for *Pinus radiata* D. Don trees growing at ambient (362 mmol mol⁻¹) and elevated (654 mmol mol⁻¹) CO₂ concentration in open-top chambers during the first year of growth.

Materials and methods

Site description

Measurements were made on trees growing in eight large open-top chambers at Christchurch, New Zealand (latitude 43°32'S, longitude 172°42'E, elevation above sea level 9 m). The flat site was on recently stabilised, weakly developed Kairaki dune sand, which was free to rapidly draining (New Zealand Soil Bureau 1974). When the trees were established the concentrations

of soil total carbon and nitrogen were 0.11 and 0.01 %, respectively. Mean annual temperature was 12.2 °C, with a mean daily range of 3.5 °C, and mean annual rainfall was 616 mm.

The design of the open-top chambers was identical to that described by Heagle *et al.* (1989). Each chamber was 4.7 m in diameter and 4.3 m in height. Air was supplied to the chambers by large fans, providing about two air exchanges per minute. This was sufficient to maintain the temperature and humidity within the chambers close to ambient conditions (Whitehead *et al.* 1995). In four of the chambers the CO₂ concentration was elevated by introducing a supply into perforated tubes situated behind the fan. Air temperature, air saturation deficit and CO₂ concentration were measured continuously in all chambers using an automatic sampling system described by Whitehead *et al.* (1995). Mean (\pm standard error) CO₂ concentrations were 362 ± 37 and $654 \pm 69 \mu\text{mol mol}^{-1}$ for the ambient and elevated treatments, respectively.

Two rigid, plastic sheets radiating from the centre to the edge of each chamber were dug into the soil to a depth of 1.2 m. This provided an area equal to one sixth of the total chamber and isolated the root systems of the measurement trees from those of other trees in the chambers. The minirhizotron tubes were installed before planting with access to the tubes provided by lined pits dug external to the chambers.

Pinus radiata was propagated by tissue culture methods (Davies *et al.* 1992) from a single bud taken from a four-year-old tree. This provided a genetically identical tree in each chamber. The tree material was propagated, rooted and grown at ambient or elevated CO₂ concentration in controlled environment facilities to ensure that it was fully acclimated to the treatment. The trees were planted in the open-top chambers in autumn (April) 1994. The roots were inoculated with mycorrhizae by including litter from an adjacent forest plantation with the roots. Irrigation was supplied each night to maintain well-watered conditions throughout the year. A balanced fertiliser (Osmocote Plus, Grace Sierra International, The Netherlands) was applied to the soil surface at three monthly intervals to supply nitrogen to the trees at a rate equivalent to $15 \text{ g m}^{-2} \text{ y}^{-1}$. Measurements were made during the year following planting. Half-hourly measurements of air temperature at 1.5 m above ground-level and solar irradiance were made continuously.

Stem basal area

Stem basal areas of the eight trees were measured every 2 weeks from winter (August) until late summer (February). A further set of measurements was made in the following autumn (April). Measurements were taken at a height of 0.01 m above the soil surface.

Numbers of roots

Before the trees were planted, a 1.8 m long acrylic minirhizotron tube with internal and external diameters of 34 and 38 mm, respectively, was installed horizontally at a depth of 0.3 m below the ground surface between the centre and the edge of each of the eight chambers. The depth was chosen because up to 90 % of the total fine roots occur within this zone in *Pinus radiata* plantations (Nambiar 1983). Two parallel transect lines 20 mm apart were etched on to the outside surface along the length of each tube and lines at 20 mm intervals were etched perpendicular to the long axis of the tube. This provided reference for distances along the tubes. The tubes were installed with the etched lines facing the soil surface. The trees were planted directly above the centre position of the tubes.

Images of the soil and roots, including the etched lines, were viewed by passing a miniature colour CCD camera and wide-angle lens (Models Panasonic WV-KS152 and GP-LM7R5TA, Matsushita Ltd., Osaka) along the tubes. Illumination was provided by four incandescent lights. Images were reflected by a mirror mounted at an angle of 45 ° in front of the camera lens and these were recorded on to high resolution video tape using a video camera recorder (Model TR705E, Sony Corporation, Tokyo).

The images were captured by a computer (Model Power PC 7100 80AV) using a built-in digitising card and up to four images from different periods at the same location were displayed on the computer monitor. This allowed subtle changes in the characteristics of individual roots to be recorded. The numbers of root intersections were counted manually directly from the video images displayed on a second monitor. For each 20 mm section, the position, numbers of roots intersecting the parallel lines along the length of the tubes, the colour and diameter size class (<0.5, 0.5-1, 1-2, 2-3 and 3-4 mm) were recorded.

Estimation of root length density and root carbon density

Measurements for conversion of numbers of roots into L_v (root length per unit volume of soil) and C_v (root carbon mass per unit volume of soil) were made using an additional minirhizotron tube placed under a tree outside the chambers. The tree was provided with the same fertiliser and irrigation treatments as the trees inside the chambers. The images of roots along this tube were recorded in early winter (May) at the end of the first year and the data were analysed as described above. The tree was cut down at the soil surface and the soil was removed to the depth of the top of the minirhizotron tube. Immediately adjacent to the tube, cores (100 mm long, 75 mm wide and 40 mm deep) were removed from either side using a metal box. The cores were positioned at 100 mm intervals along the tubes for direct comparison of L_v with data from the images. Each pair of cores from the two sides of the tube were bulked and kept frozen.

Roots from the cores were separated by hand-washing the soil on to an 0.5 mm sieve. The roots were sorted by diameter class (as above) and root lengths for each class were measured on a grid using the line-intersect method (Tennant 1975). The roots were dried at 70 °C to a constant mass, then finely ground and analysed for total carbon concentration (Model Roboprep CN analyser, Europa Scientific, Cheshire, UK). L_v and C_v were calculated for each sample. It was assumed that the mass of carbon per unit dry mass was the same for roots growing in both treatments.

Soil surface carbon flux density

The carbon flux density at the soil surface (f_o , g m⁻² h⁻¹) was measured every 4 weeks in the open-top chambers using a portable soil respiration system (Model SRC-1, PP Systems, Hitchin, UK) placed on the soil surface (Parkinson 1981). Eight measurements were made in each chamber at an approximate distance of 0.4 m from the tree stem. Diurnal flux density measurements were made in two open-top chambers in late summer (February). Half hourly measurements of soil temperature in each chamber at a depth of 0.1 m using copper-constantan thermocouples and soil matric potential using calibrated resistance sensors (Model Watermark, Irrometer Co. Inc., Riverside, USA) were made with a datalogger in combination with multiplexers (Campbell Scientific Inc. Logan, USA).

Results

During the measurement period, daily mean air temperature was 13.3 °C with a maximum and minimum hourly temperature of 36.9 and -4.0 °C on 26 January and 30 June, respectively. Air temperature was lowest in July, began to increase in August with the steepest increase occurring during October. Soil temperature at a depth of 0.1 m closely followed air temperature (Figure 2-1). Solar irradiance was minimum in late June and maximum in late December and the total irradiance for the year was 10.9 kmol m⁻². Analysis of soil matric potential data showed that the profile was maintained close to field capacity throughout the year.

Stem basal area for the trees increased from winter (July) to late summer (January), indicating that above-ground growth was continuous throughout the period (Figure 2-1). Basal area of trees growing at ambient and elevated CO₂ concentration increased from 97 to 373 mm² and from 69 to 341 mm², respectively during the period. By early autumn (April) mean basal area had increased to 642 and 649 mm² for the ambient and elevated treatments, respectively. Although the mean basal area for the trees growing at ambient CO₂ concentration was larger

initially, the rate of growth was greater for the tree growing at elevated CO_2 concentration during summer (November to January).

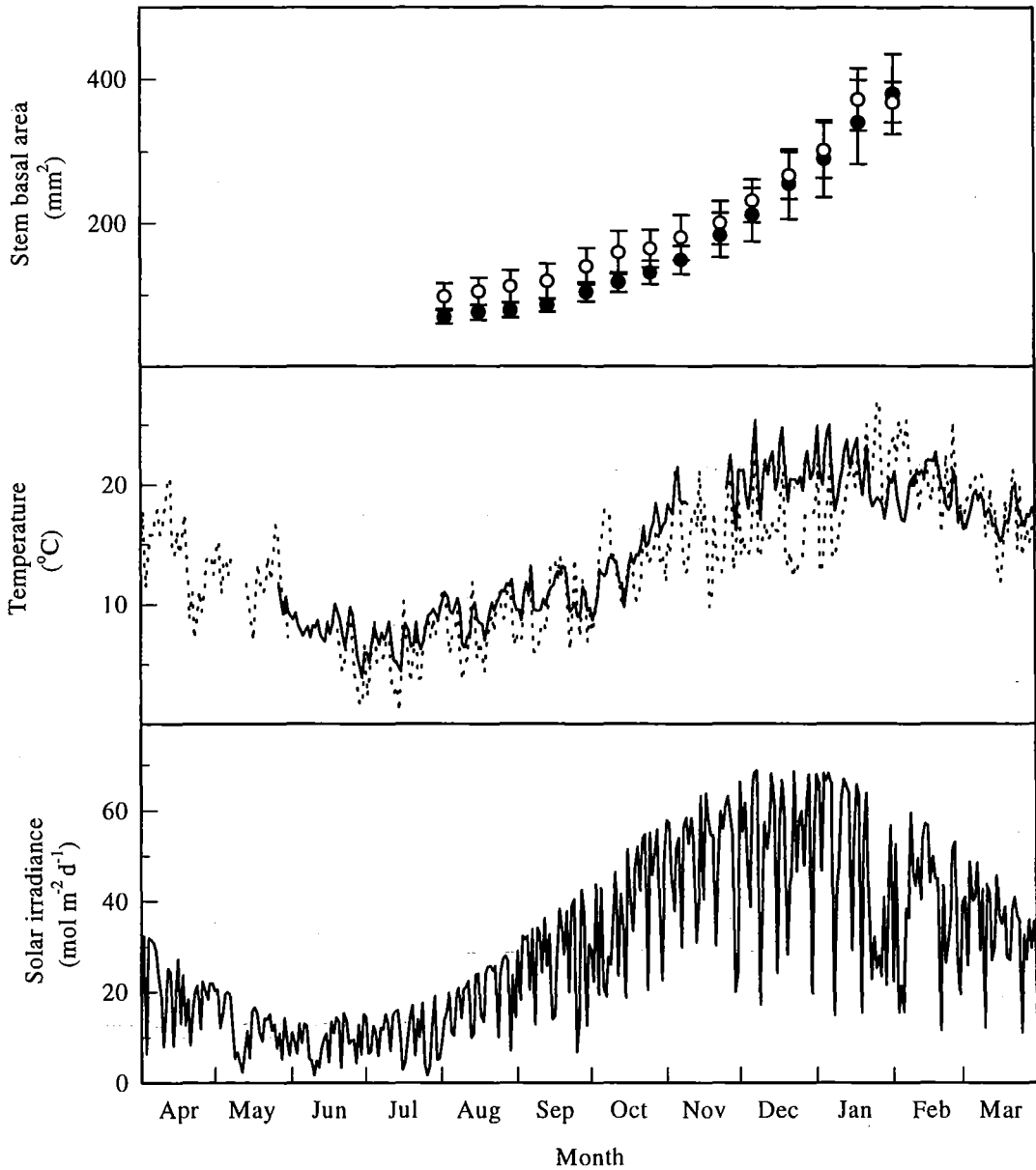


Figure 2-1 Seasonal changes in stem basal area, daily mean air (dashed line) and soil at 0.1 m (solid line) temperatures, and daily total solar irradiance, for the year beginning in April 1994. The symbols refer to the mean (\pm standard error) stem basal area of 4 trees grown in open-top chambers at ambient (\circ) and 4 trees at elevated (\bullet) CO_2 concentrations.

Root length density and root carbon density

Analysis of data for roots <4 mm in diameter from the cores located immediately adjacent to the minirhizotron tube in the plot outside the chambers showed that roots <0.5 mm in diameter accounted for 86 % of the total root length but contained only 36 % of the carbon. There was only 0.5 % of the total length in roots >2 mm but this accounted for 19 % of the total carbon, owing to the much greater carbon concentration per unit root length for larger diameter roots (Table 2-1). For roots <0.5 mm in diameter, the data yielded a range of L_v and C_v up to 0.048 mm mm^{-3} and $0.59 \text{ } \mu\text{g mm}^{-3}$, respectively. There was a linear relationship between these values and the number of root intersections counted from the images recorded by the camera along the tube (Figure 2-2). This relationship was used as a calibration to estimate L_v and C_v along the 8 tubes in the chambers from measurements of the numbers of root intersections from the video images.

Table 2-1 Total root length, dry mass of carbon and root carbon mass per unit root length for different diameter classes of roots from the cores taken immediately adjacent to the minirhizotron tube outside the open-top chambers. An average ratio for carbon to total dry mass of 0.44 g g^{-1} measured was used. The total volume of soil from which the roots were extracted was 0.01 m^3 . The values shown in parentheses are percentages.

| Diameter class (mm) | Total root length (m) | Mass of carbon (g) | Carbon mass per unit root length ($\mu\text{g mm}^{-1}$) |
|------------------------|--------------------------|-----------------------|---|
| <0.5 | 70.48 (86%) | 0.769 (36%) | 12.3 |
| 0.5-1 | 8.49 (10.5%) | 0.466 (22%) | 62.0 |
| 1-2 | 2.54 (3%) | 0.515 (23%) | 229.4 |
| 2-3 | 0.22 (0.3%) | 0.168 (7.8%) | 846.3 |
| 3-4 | 0.16 (0.2%) | 0.243 (11.2%) | 1767.5 |

Distribution of carbon root density in the chambers

There was considerable variability in the numbers of roots observed along the tubes. Near to the end of the year in March, the total number of root intersections along the whole tubes for roots in all diameter classes varied between 10 and 140. At this time, roots <1 mm in diameter accounted for 93 and 97 % of the total length for the ambient and the elevated CO_2 concentration treatments, respectively. When normalised with respect to the total length of

roots (<0.5 mm diameter) measured along the length of the tubes, the horizontal distribution of C_v for roots in all diameter classes combined along the tubes showed a maximum value directly below the tree. However, the roots for trees growing at elevated CO_2 concentration were more concentrated close to the tree than those for the ambient treatment. There were 88 % of the total roots (<0.5 mm) within a radius of 0.15 m from the tree for the elevated CO_2 concentration treatment, compared with 35 % in the same zone for trees growing in the ambient treatment (Figure 2-3).

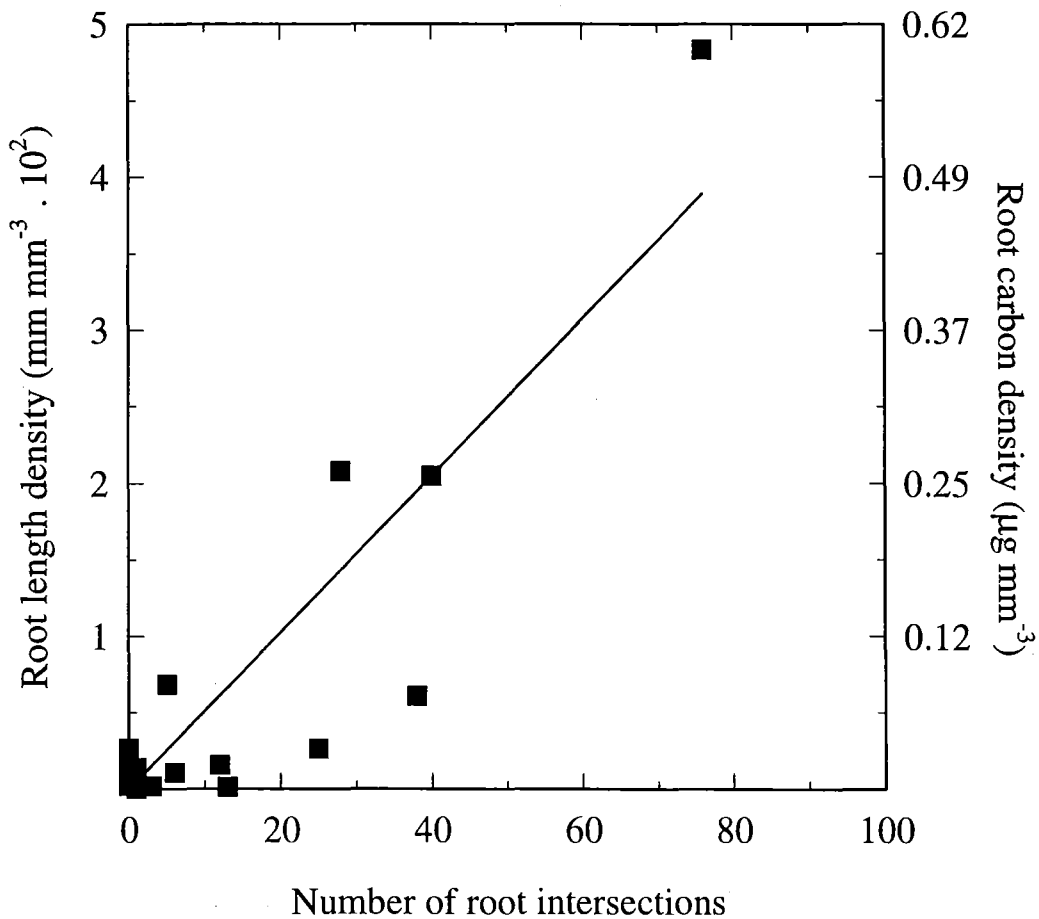


Figure 2-2 Relationships between the number of observed fine (<0.5 mm) root intersections within a 100 mm segment along a minirhizotron tube at a depth of 0.3 m and root length density, L_v , and root carbon density, C_v , measured from cores taken immediately adjacent to the same tube. The slope of the line is 0.051 and 0.0063 for L_v and C_v , respectively and $r^2=0.80$, $n=17$, $p<0.001$.

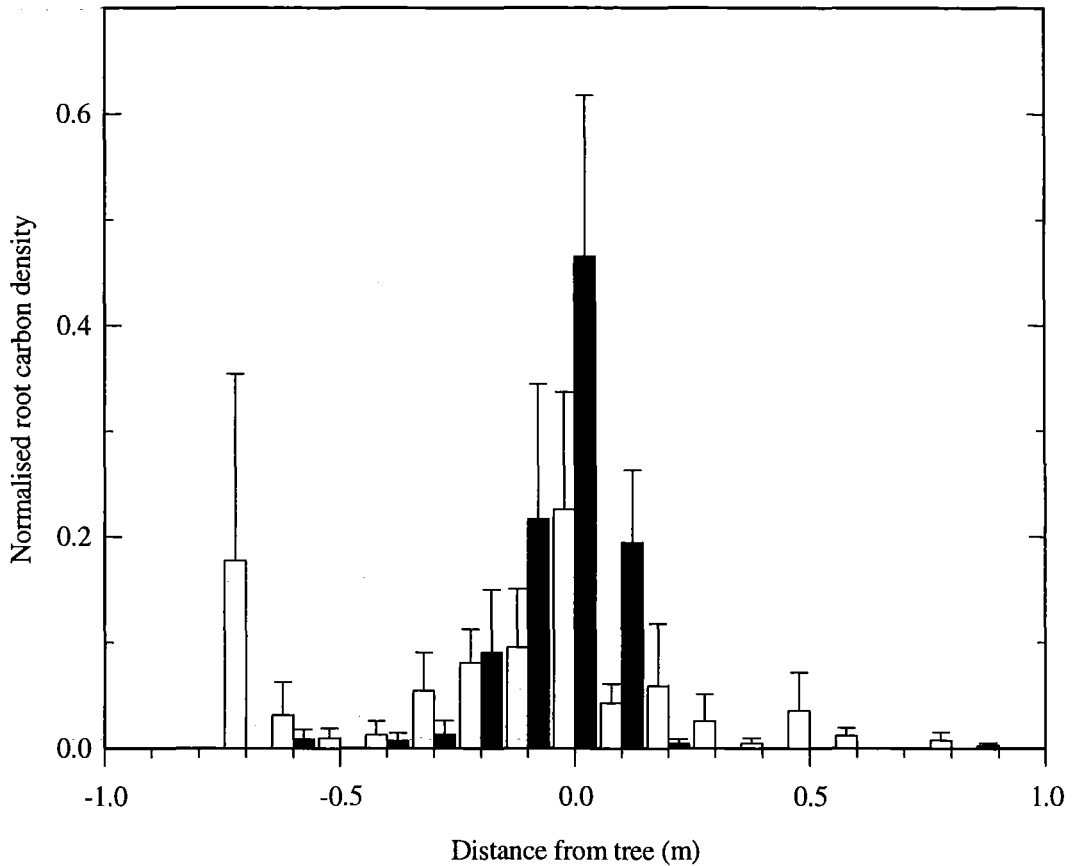


Figure 2-3 Distribution of fine (<0.5 mm diameter) root length density, L_v , along the minirhizotron tubes at a depth of 0.3 m with distance from the centre of the tree for the ambient (open) and elevated (closed) CO_2 treatments in March, one year after the trees were planted. The data have been normalised with respect to the total L_v for each tube and means (\pm standard error) for four tubes in each treatment are shown.

Seasonal changes in root carbon density

The number of roots and values for C_v were greater for trees growing at elevated CO_2 concentration than for trees at ambient CO_2 concentration but, because of variability, the differences were not significant (Table 2-2). This difference was apparent in early spring when the first roots were observed and continued throughout the year.

The increase in C_v at a depth of 0.3 m started in early spring and continued to late summer. The first roots appeared eight weeks after the trees were planted. During this early period of colonisation, the roots were relatively large (0.5-2 mm diameter). The first fine roots (<0.5 mm diameter) were observed 20 weeks after planting. Rapid growth started almost four weeks earlier for trees growing in the elevated CO_2 treatment (Figure 2-4). There then followed a rapid linear increase in C_v for all chambers until midsummer (December) followed by a slower rate of increase until late summer (February). There is some indication that the rate of increase

in C_v declined to low values earlier for trees growing at elevated CO_2 concentration

(Figure 2-4). During the linear phases, there were no significant differences in the relative increases in C_v between the treatments (Table 2-2).

Table 2-2 Mean root carbon density, C_v , and mean relative rate of increase in C_v for roots <1 mm at a depth of 0.3 m for trees growing at ambient and elevated CO_2 . Values of C_v along the 1.7 m length of the tubes are shown for three dates during the year. The relative rates of increase in C_v were calculated for the period between 12 October (t_1) and 6 December (t_2), and 6 December (t_1) and 31 January (t_2) as $(\ln C_{v2} - \ln C_{v1}) / (t_2 - t_1)$. The data shown are means \pm standard error for the four trees in each treatment.

| Date | Ambient | Elevated |
|---|-----------------|-----------------|
| $C_v (\mu\text{g mm}^{-3} \cdot 10^3)$ | | |
| 12 October | 12.5 ± 9.3 | 29.3 ± 14.7 |
| 6 December | 24.8 ± 15.7 | 36.0 ± 15.6 |
| 31 January | 32.1 ± 15.5 | 46.1 ± 17.2 |
| <i>Relative rate of increase in C_v ($d^{-1} \cdot 10^2$)</i> | | |
| 12 October - 6 December | 37.3 ± 11.4 | 25.2 ± 16.4 |
| 6 December - 31 January | 11.2 ± 5.1 | 16.6 ± 13.5 |

Soil surface carbon flux density

Diurnal measurements of f_o showed an increase during the early morning to reach a maximum around midday, followed by a decrease during the afternoon to reach minimum values just prior to dawn (Figure 2-5). In late summer (February), maximum f_o in the ambient and elevated chambers was 0.092 and $0.099 \text{ g m}^{-2} \text{ h}^{-1}$, respectively and minimum values were about half of these. Values of f_o in the chambers with elevated CO_2 concentration tended to be greater than those at ambient CO_2 concentration, although the differences were not significant. The diurnal changes were attributable to changes in air temperature following an Arrhenius relationship of the form

$$f_o = Ae^{-E_o/(T-T_o)} \quad (1)$$

where T is temperature ($^{\circ}\text{K}$), T_o is a base temperature ($=227.13 \text{ }^{\circ}\text{K}$), E_o is a constant ($=308.56 \text{ }^{\circ}\text{K}$) and A is a variable dependent on the data set (Lloyd & Taylor 1994).

During the year, mean f_o was greater for trees growing in the elevated CO_2 concentration than for trees growing in ambient conditions (Figure 2-6). There was an almost linear increase in f_o

between winter (August) and midsummer (January). This was followed by a steeper increase in f_0 during late summer and a smaller increase during autumn.

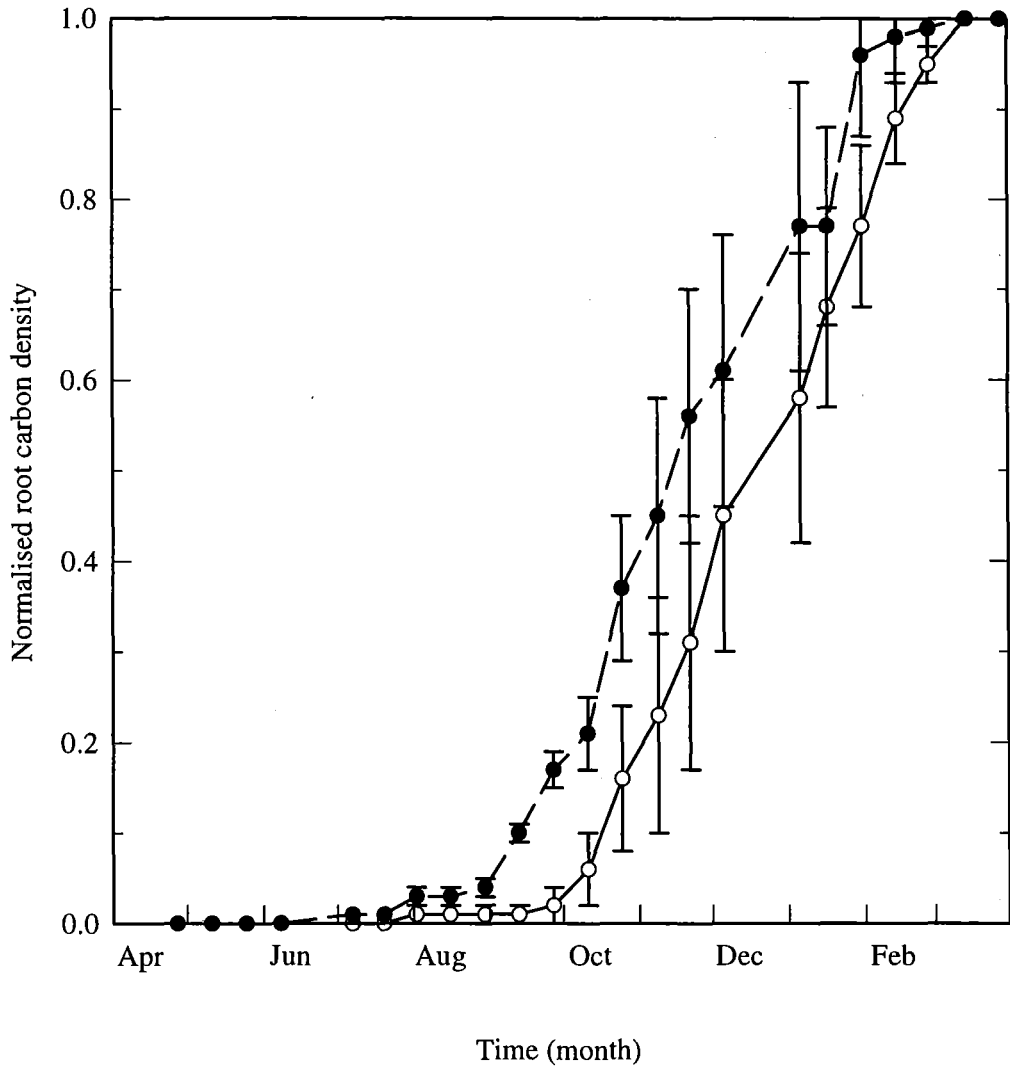


Figure 2-4 Seasonal increases in fine (<1 mm diameter) root carbon density, C_v , at a depth of 0.3 m for trees growing at ambient (O) and elevated (●) CO_2 concentration. The data have been normalised with respect to the final value (28 March) of C_v for each tube. The data shown are means (\pm standard error) for four tubes in each treatment at two-weekly intervals.

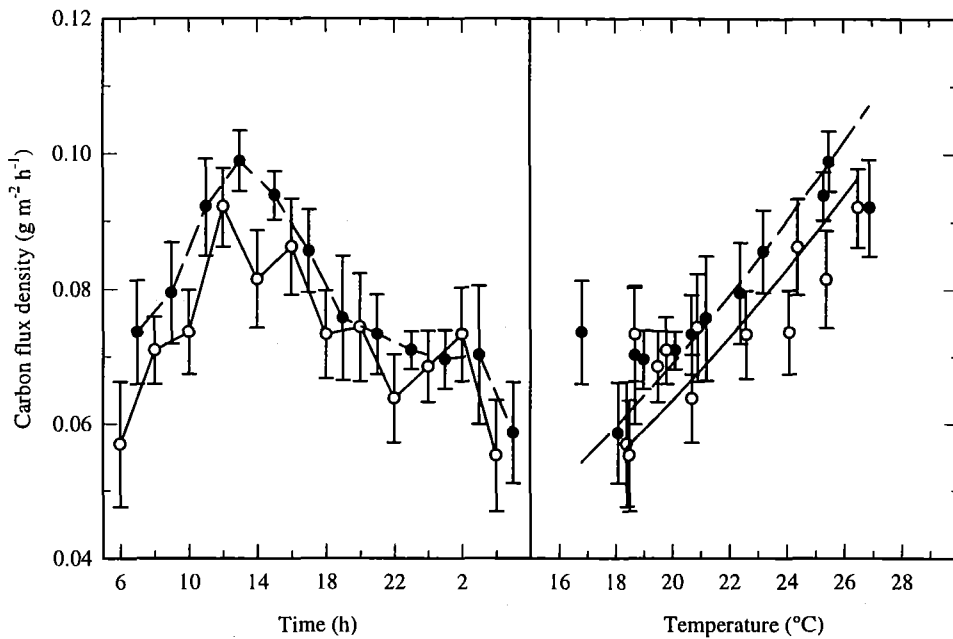


Figure 2-5 Diurnal measurements of carbon flux density, f_o , from the soil surface measured around a tree growing at ambient (O) and elevated (●) CO_2 concentration on 15 February 1995. The data shown are means (\pm standard error) of eight measurements. The relationships between f_o and air temperature were fitted using the Arrhenius function given in the text and values for A for the ambient and elevated treatments are 6.79 and 7.37, respectively. $r^2=0.52$ (ambient) and 0.54 (elevated).

Discussion

The measurements of L_v were variable, depending on the position along the minirhizotron tubes in relation to the tree. No roots were present in the soil before the planting of the trees at the start of the year, so the data represent the initial exploration of the soil profile by young, actively growing roots. There was a general concentration of roots close to the trees (Figure 2-3) where the maximum L_v recorded was almost 0.04 mm mm^{-3} . This was much greater than typically low values of L_v measured within young *Pinus radiata* plantations (Nambiar 1983), although L_v has been shown to increase to greater values approaching 0.08 mm mm^{-3} in older tree stands (Bowen 1985). Despite the low values of L_v , the rate of growth of individual roots at the site was rapid and other measurements showed that roots were present at depths up to 0.9 m within six months after the trees were planted (SM Thomas, unpublished data).

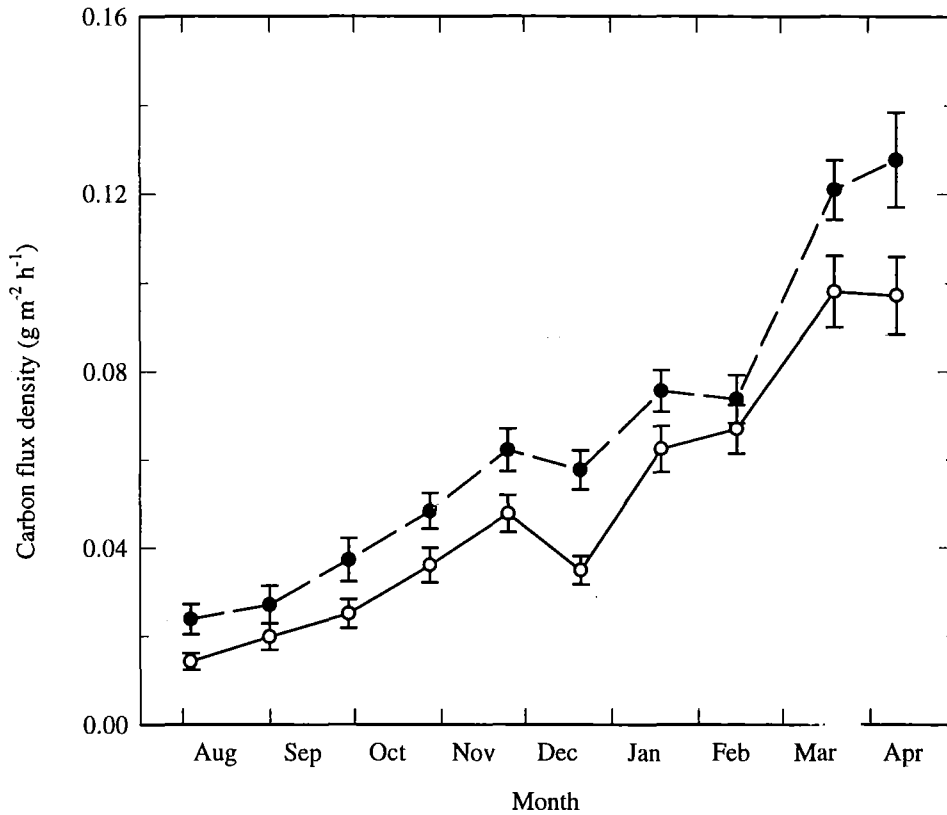


Figure 2-6 Seasonal measurements of carbon flux density, f_o , from the soil surface measured around trees growing at ambient (O) and elevated (●) CO₂ concentration at monthly intervals throughout the year. The data shown are means (\pm standard error) for four trees in each treatment.

No turnover was apparent in the root systems in the chambers. Root longevity in tree species is likely to be more than one year (Vogt & Bloomfield 1991), so it is less surprising that root turnover had not yet begun. Turnover of roots in older tree stands can account for up to half of the carbon allocated below-ground (Vogt 1991) and it is anticipated that this will be a major component of the below-ground carbon balance for the trees in the chambers in subsequent years. Roots with diameters less than 1 mm comprised 96 % of the total L_v (Table 2-1). While this is particularly important for water and nutrient uptake, in terms of carbon these roots accounted for only 58 % of the total. In the young trees the larger roots provide greater storage for carbon than fine roots but, in older stands, allocation of carbon to fine root turnover may exceed total root biomass (Vogt 1991).

Working with a range of crops, Smit *et al.* (1994) found that the relationship between root number and L_v and C_v varied with season and between species. A possible explanation was that root distribution around the tube is variable. Poor contact between soil and the tubes could lead

to variability. Despite this difficulty, the minirhizotron technique provides the most suitable non-destructive, replicated method for estimating seasonal changes in carbon storage in roots.

There was an apparent increase in the numbers of roots <0.5 mm in diameter, L_v and C_v for trees growing at elevated CO_2 concentration, although the differences between the treatments were not significant (Table 2-2). This was accompanied by an increase in tree basal area (Figure 2-1), tree height and biomass (O.J. Sun, personal communication) during the first year of growth. Increases in root biomass when trees have been grown at elevated CO_2 concentration have been reported for woody species (eg. Curtis *et al.* 1990; Idso & Kimball 1992; Norby *et al.* 1992), and this may result, at least in soybean (*Glycine max* (L.) Merr) from changes in root morphology, rather than an increase in the number of roots (Rogers *et al.* 1992a). Increases in root dry weight per unit length could be associated with increased carbohydrate concentrations (Lewis *et al.* 1994). In poplar (*Populus x euramericana* cv. Eugenei), Pregitzer *et al.* (1995) measured increases in the length of fine root and root mortality at elevated CO_2 concentration, resulting in faster turnover rates of root carbon.

There was a difference in the timing of root appearance and the increase in L_v between the treatments (Figure 2-4). The first roots were visible 8 weeks after the trees were planted and these were large (>0.5 mm) in diameter. The fine roots did not begin to appear until 20 weeks after planting. By 24 weeks L_v for the trees growing at elevated CO_2 concentration was greater and this difference remained until the end of the period of growth in late summer. Because there was no significant difference in the relative rates of increase in C_v between the treatments (Table 2-2) the increase in C_v resulted from an earlier start to the period of growth. The growth of roots continued throughout the spring and summer (Figure 2-4) and the rate of growth did not decrease until well after air temperature had reached maximum (Figure 2-1). This contrasts with the marked seasonality observed in mature *Pinus radiata* stands by Santantonio and Grace (1987) where the rate of change of fine root biomass peaked in early spring then continued to fall to reach near zero by late summer. It is likely that the continuous growth in L_v (Figure 2-4) and tree basal area (Figure 2-1) are attributable to the availability of water and nutrients throughout the year and the trees being in the early establishment growth phase.

Rates of carbon flux density from the soil surface, f_o , were approximately 30% greater for trees growing at elevated CO_2 concentration throughout the year (Figure 2-6). This is consistent with results for other coniferous species (Johnson *et al.* 1994; Pajari 1995). The change in f_o is attributed to increased photosynthate to roots resulting in increased metabolic and microbial activity, and increased growth of roots (Norby 1994). Values of f_o were low in comparison with those measured for mature plantation conifers (Haynes & Gower 1995), reflecting the low carbon concentration in the soil before the trees were planted and the low C_v values. Measurements of f_o are sensitive to changes in temperature (Figure 2-5) but, during the late summer, f_o continued to increase (Figure 2-6), well after air temperature had begun to decline

(Figure 2-1). Mean air temperature for the four months from December varied between only 20.2 and 22.9 °C, but there was a large increase in C_v (Figure 2-4) and f_o (Figure 2-6). This suggests that the increase in f_o was attributable to an increase in C_v , rather than temperature.

Acknowledgements

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CHAPTER 3

GROWTH, LOSS, AND VERTICAL DISTRIBUTION OF *PINUS RADIATA* FINE ROOTS GROWING AT AMBIENT AND ELEVATED CO₂ CONCENTRATION[‡]

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Abstract

Increased carbon allocation below-ground in forest ecosystems is a likely consequence of rising atmospheric CO₂ concentration. If this results in changes to fine root growth, turnover and distribution long-term soil carbon cycling and storage could be altered.

Bi-weekly measurements were made to determine the dynamics and distribution of fine roots (<1 mm diameter) for *Pinus radiata* trees growing at ambient (350 µmol mol⁻¹) and elevated (650 µmol mol⁻¹) CO₂ concentration in large open-top chambers. Measurements were made using minirhizotrons installed horizontally at depths of 0.1, 0.3, 0.5 and 0.9 m.

During the first year, at a depth of 0.3 m, the increase in relative growth rate of roots occurred 6 weeks earlier in the elevated CO₂ treatment and the maximum rate was reached 10 weeks earlier than for trees in the ambient treatment. After 2 years, cumulative fine root growth (P_t) was 36% greater for trees growing at elevated CO₂ than at ambient CO₂ concentration, although this difference was not significant. A model of root growth driven by daily soil temperature accounted for between 43 and 99% of root growth variability.

Total root loss (L_t) was 9% in the ambient and 14% in the elevated CO₂ treatment, although this difference was not significant. Root loss was greatest at 0.3 m. In the first year, 62% of fine roots grown between mid-summer and late-autumn disappeared within a year in the elevated CO₂ treatment, but only 18% in the ambient CO₂ treatment ($p < 0.01$). An exponential model relating L_t to time accounted for between 74 and 99% of the variability. Root cohort half-lives were 951 d for the ambient and 333 d for the elevated treatment.

Root length density decreased exponentially with depth in both treatments, but relatively more fine roots grown in the elevated CO₂ treatment tended to occur deeper in the soil profile.

Keywords: *Pinus radiata*, elevated CO₂ concentration, fine root production, fine root loss, root distribution, minirhizotron

[‡] Accepted by *Global Change Biology*.

Introduction

In forest ecosystems, fine root growth represents an important component of the carbon budget with between 3 and 60% of net primary production allocated to the roots (Vogt *et al.* 1996; Landsberg & Waring 1997). Both fine root growth and subsequent turnover represent considerable carbon inputs to the soil. In temperate forests, fine root turnover may equal or exceed carbon inputs from above-ground litter production (Vogt *et al.* 1986b).

Many studies have shown that carbon assimilation and growth are enhanced when plants are grown at elevated CO₂ concentration (Rogers *et al.* 1994). In woody plants, this is often accompanied by an increase in the ratio of below-ground to above-ground biomass (Eamus & Jarvis 1989; Ceulemans & Mousseau 1994). There is strong evidence to suggest that increased allocation of carbon to roots may lead to changes in the below-ground carbon pools (Norby *et al.* 1987; O'Neill *et al.* 1987; Norby *et al.* 1992; Zak *et al.* 1993; Rouhier *et al.* 1994; Rygielwicz *et al.* 1997), and rates of cycling between the pools may be altered. However, the integrated effects of elevated CO₂ concentration on the processes of carbon cycling in the soil are unclear (van Veen *et al.* 1991; van de Geijn & van Veen 1993; Canadell *et al.* 1996b). There is evidence to indicate that greater fine root production than turnover, and slow rates of decomposition may be responsible for recent increased carbon accumulation in some forest soils (Steele *et al.* 1997). Any long term increase in soil carbon storage is also likely to be a function of soil-type, nutrient availability and moisture status (Tate & Ross 1997).

In order to predict the effects of elevated CO₂ concentration on the dynamic processes regulating the carbon pools in the soil, it is important to estimate the input of carbon from the growth and turnover of fine roots. In many studies, these components have not been determined separately. It is likely that the rates of growth and loss are regulated by environmental and physiological variables and estimation of each component is required for inclusion in models describing soil carbon dynamics. Limited evidence suggests that changes in the rate of fine root turnover for trees growing at elevated CO₂ is variable (Eissenstat & Yanai 1997) and may be dependent on the species and soil nutrient status (Pregitzer *et al.* 1995).

Estimates of fine root growth and turnover have been made predominantly by destructive sampling using soil cores (Vogt *et al.* 1986a; Persson 1990; Vogt *et al.* 1993), but concurrent seasonal changes in growth and mortality can lead to large errors (Persson 1983; Santantonio & Grace 1987; Hendrick & Pregitzer 1993; Reid *et al.* 1993). More recently, video recording of images from minirhizotron tubes buried in the soil profile (Upchurch & Ritchie 1983) has allowed non-destructive, repetitive *in situ* measurements of individual roots. The technique is well suited to investigating the timing of root growth and loss and, by following the progress of individual roots, the data can be used to estimate root longevity and turnover (Curtis *et al.* 1994a; Hendrick & Pregitzer 1996a; Steele *et al.* 1997) and changes in the vertical distribution

of roots with depth in the soil profile (Day *et al.* 1996; Hendrick & Pregitzer 1996b; van Vuuren *et al.* 1997). There has also been a number of successful estimations of root biomass using comparisons between minirhizotron data and root cores (Hendrick & Pregitzer 1996a). The technique can be used to estimate the seasonal changes of root carbon density, the root carbon mass per unit volume of soil (Thomas *et al.* 1996).

The long-term effects of elevated CO₂ concentration on the carbon balance for trees is being measured by growing *Pinus radiata* D. Don in large, open-top chambers at ambient and elevated CO₂ concentration at a site in Christchurch, New Zealand. As a contribution to the larger project, this study was undertaken to investigate the effects of the treatment on fine roots and soil carbon dynamics for a period of two years from the time of tree establishment. The objectives of this study were to measure the seasonal growth, loss, longevity and turnover of fine roots for the trees in the two treatments, and to determine the effect of elevated CO₂ concentration on the vertical distribution of roots.

Materials and Methods

Measurements were made on six *Pinus radiata* D. Don trees, three grown at ambient (350 $\mu\text{mol mol}^{-1}$) and three at elevated (650 $\mu\text{mol mol}^{-1}$) CO₂ concentration. The trees were individually located in six identical large open-top chambers at Christchurch, New Zealand (latitude 43° 32' S, longitude 172° 42' E, elevation above sea level 9 m). Each open-top chamber was 4.7 m in diameter and 4.3 m high. Full details of the experimental facility and the performance of the open-top chambers have been described by Whitehead *et al.* (1995). The trees were propagated from a single bud from a four-year-old tree using tissue culture at ambient or elevated CO₂ concentration to allow acclimation to the treatments (Davies *et al.* 1992). This provided genetically identical trees in each chamber. The trees were planted in April (autumn) 1994.

The trees were growing freely in an Ustipsammments sandy mixed mesic soil (Soil Survey Staff 1990), described as recently stabilised, weakly developed, rapidly, freely draining Kairaki dune sand (New Zealand Soil Bureau 1974). Across the site there were small differences of up to 0.2 m in the elevation of the soil surface. Depth to the water-table was monitored weekly at a site approximately 500 m from the chambers, but at the same elevation. Inside the chambers, the root systems of the trees were confined to an area equal to one sixth of the total chamber area using rigid plastic sheets that were placed to a depth of 1.2 m. The trees were irrigated each night to ensure adequate water supply. During the first year a balanced fertiliser (Osmocote Plus, Grace Sierra International, The Netherlands) was applied to the soil surface at three monthly intervals to supply nitrogen at a rate equivalent to 15 g m⁻² y⁻¹, and during the second year at monthly intervals to supply nitrogen at a rate equivalent to 60 g m⁻² y⁻¹. The

fertiliser was in a form designed to be released slowly over a five to six month period, and had an elemental formulation of 15% N (as NH_4 and NO_3 in approximately equal proportions), 4.4% P, 10% K, 1.2% Mg and trace elements.

Prior to planting, an acrylic, minirhizotron tube was installed horizontally, beneath each tree at each of the following depths: 0.1, 0.3, 0.5 and 0.9 m, using the procedure described by Thomas *et al.* (1996). Each tube was 1.8 m long, with internal and external diameters of 34 and 38 mm, respectively. Two parallel lines were etched 20 mm apart along the outer surface of the tubes and, perpendicular to these, lines were etched at 20 mm intervals. These lines provided references for locations along the tube. Each tree was planted directly above the centre position of the tubes, except the tube at 0.1 m which was necessarily laterally offset from the tree. The minirhizotrons were also slightly offset in the horizontal plane, to minimise the chance of repeated measurements of the same roots at two or more depths.

Inside the chambers, half-hourly average air temperatures were measured at 1.5 m above the soil surface. Mean annual air temperature at the site was 12.2 °C, with a mean daily range of 3.5 °C. Average hourly soil temperatures were measured adjacent to the minirhizotron tubes at the four depths in each chamber.

Stem basal area at 0.01 m above the soil surface was measured at approximately monthly intervals from August 1994 (winter). Relative growth rates for stem basal area, R_s were calculated for each interval following Hunt (1982).

Seasonal measurement of fine roots

Over a period of two years, bi-weekly measurements of the growth and loss of fine roots (<1 mm diameter) were made by counting the roots on images captured from the minirhizotrons by passing a camera down the tubes as described by Thomas *et al.* (1996). Images taken at 20 mm intervals along the tubes were digitised and analysed using the software package RooTracker (Duke University, Durham, NC, USA). Tracings of individual roots were made and the diameter and condition were recorded.

Fine roots were recorded the first time they were observed, and re-measured until they disappeared. Fine root growth at time t (P_t) was defined as the difference between the number of new roots present at times t and $t-1$, and fine root loss (L_t) was defined as the number of roots that had disappeared during the same time interval. After disappearance of a root, the location of the image was re-visited for at least two successive measurement intervals to ensure that the loss was permanent. P_t and L_t could be considered in terms of root number (n_t), total length (mm) or root length density (L_v) defined as root length per unit volume of soil (km m^{-3}).

In each of two plots located outside the chambers, an additional tree was planted directly above a minirhizotron tube installed horizontally at 0.3 m and supplied with fertiliser and

irrigated in a manner identical to the trees growing inside the chambers. In May 1995 and January 1996, the number of roots for each 100 mm length of the tube (n_r) was counted from recorded images, and L_v was independently and destructively measured by taking rectangular soil cores (100 mm long \times 70 mm wide \times 40 mm deep) immediately adjacent to the tubes at 100 mm intervals, using the procedures described by Thomas *et al.* (1996). Data for the two dates were pooled (33 samples) to give the linear relationship $L_v = 1.05 n_r \text{ km m}^{-3}$ ($r^2=0.85$, $p<0.001$). This relationship was used to estimate L_v from measurements of n_r made from minirhizotrons in the ambient and elevated CO_2 treatments at each sample date. Estimates of L_v in this paper are calculated using the average L_v along the length of each minirhizotron tube.

Model of root growth and loss

Net root growth over a time interval t (N_t) is the difference between root growth and loss, such that

$$N_t = P_t - L_t. \quad (1)$$

The seasonal growth of roots was explained using a model based on temperature. Preliminary investigation suggested that a function driven by growing degree days was appropriate, such that

$$\begin{aligned} P_r &= 0, & T &\leq T_o \\ P_r &= a_p(T - T_o), & T &> T_o \end{aligned} \quad (2)$$

where P_r is the rate of root growth, T is the soil temperature, T_o is the base temperature below which no growth occurs, set at 7 °C, and a_p is the maximum P_r .

Changes in soil temperature with time at a given depth were approximated by the sine function

$$T = T_a + b \sin \left(\frac{2\pi t}{p} + \phi \right) \quad (3)$$

where, T_a is average annual temperature, b is the amplitude, t is the day number, ϕ is the phase and p is the period (365 days). Substituting equation (3) into equation (2) and integrating gives

$$P_t = a_p \left\{ (T_a - T_o)(t - t_o) - \frac{bp}{2\pi} \left[\cos \frac{2\pi(t + \phi)}{p} - \cos \frac{2\pi(t_o + \phi)}{p} \right] \right\} \quad (4)$$

where t_o is the time when $T = T_o$.

The model was fitted to the root growth data independently for the first and the second years using measurements of T at the depth of each minirhizotron. For each growth period, root growth was initiated when $T > T_o$ and stopped when $T < T_o$.

Examination of root loss data showed that this was best described by an exponential function with time, t , as

$$L_t = a_1 e^{(-k_1 t)} \quad (5)$$

where a_1 is the maximum loss of roots and k_1 is the relative change in root loss.

Mean relative growth rates (R_p) and mean relative loss rates (R_l) were calculated for intervals ($t_2 - t_1$) of approximately 28 days following Hunt (1982), as $R_p = (\ln P_{t,t2} - \ln P_{t,t1}) / (t_2 - t_1)$ and $R_l = (\ln L_{t,t2} - \ln L_{t,t1}) / (t_2 - t_1)$.

Fine root longevity

For two cohorts of roots, those produced either in the first half (July to December) or in the second half (January to April) of the first growing season, the ratios of surviving roots to the initial number of roots were calculated for each 2-weekly period. The results were analysed using least squares regression for four periods after the appearance of the first cohort. The periods were from mid-summer (January) to late-autumn (April), late-autumn to mid-winter (July), mid-winter to early summer (November), and early-summer to late-autumn. The half-life of the root cohorts (time taken for 50% of the roots to disappear) was calculated by $\ln(2)/b$, where b was the slope of the regression of the logarithm of the fraction of surviving roots against time for the final period (December to March).

Vertical distribution of fine roots

The distribution of net root growth with depth (N_{tz}) was estimated from measurements of roots at depths of 0.1, 0.3, and 0.5 m and the data were fitted to an exponential function of the form

$$N_{tz} = a_z e^{(-k_z z)} \quad (6)$$

where a_z is the maximum N_{tz} at $z = 0$, and k_z describes the relative decrease in roots with depth, z .

Statistical analysis

Parametric techniques were used to compare treatment, year and depth effects, where initial investigation of the distributions did not reveal any significant departures from normality or lack of homogeneity in variances. When required, L_v data were transformed logarithmically to correct for non-homogenous variance and arcsin transformations were used to normalise the distributions of survivorship data. In the case of a_z and k_z , the variables were non-normally distributed and the Mann-Whitney U test was used to compare the treatments. Repeated

measures ANOVA was used to compare the treatment, depth and time effects for relative rates of stem growth (R_s), root growth (R_p), and root loss (R_l), a_p , a_l and k_l . Where significant interaction effects were detected these were further explored using Independent t-tests. Treatment comparisons of cumulative root growth (P_i) and root loss (L_i) at each depth, after each year, were made using Independent t-tests. The treatment means reported have been back transformed.

Results

Mean annual soil temperature changed slightly with depth and was lower at all depths in the second year (Table 3-1). The minimum and maximum soil temperatures occurred in June and January in the first year of growth, and in July and February in the second year. Maximum daily average soil temperatures at a depth of 0.1 m were 26.0 °C in the first year and 20.5 °C in the second year. Minimum daily average temperatures were 3.7 °C in the first year and 3.3 °C, in the second year (Figure 3-1a). There was no difference between the daily mean air temperature (12.6 °C) between the two years.

Table 3-1 Mean annual soil temperature (T_a), amplitude (b), and phase (ϕ), at depths of 0.1, 0.3 and 0.5 m derived using Equation 4 for the two year study period.

| Depth (m) | Period | T_a (°C) | b (°C) | ϕ (d) | r^2 |
|--------------|-----------------|---------------|-------------|---------------|-------|
| 0.1 | Apr 94 - Mar 95 | 14.2 | 7.1 | 179 | 0.89 |
| | Apr 95 - Mar 96 | 12.6 | 5.9 | 176 | 0.88 |
| 0.3 | Apr 94 - Mar 95 | 14.1 | 6.5 | 173 | 0.91 |
| | Apr 95 - Mar 96 | 12.7 | 5.7 | 172 | 0.91 |
| 0.5 | Apr 94 - Mar 95 | 14.0 | 6.0 | 170 | 0.93 |
| | Apr 95 - Mar 96 | 12.8 | 5.4 | 168 | 0.93 |

The depth to the water-table ranged from 2.4 m in November 1994 to 1.2 m in July 1994 and averaged 1.84 m (Figure 3-1b). Depth to the water table decreased from late autumn (April) to reach a minimum in winter (June and July), and fell during summer. However, rapid changes occurred throughout the study period such as the decrease of 0.69 m in depth to the water table during a 21 day period in early winter in 1995 (Figure 3-1b). The water table did not rise above the minirhizotrons but, during the winter, it rose to within 0.2 m of the deepest tubes at 0.9 m. This resulted in a seasonally fluctuating root zone water content at that depth.

There was high variability in the number of fine roots at 0.9 m, with a large number observed from some of the minirhizotrons (Figure 3-2d). There was evidence to indicate that this was an artefact of the seasonally fluctuating water-table and capillary fringe. Gravimetric soil water measurements made at and above the water table showed that the capillary fringe extended to between 0.4 and 0.6 m (S M Thomas, unpublished data). Furthermore, excavation of the soil profile from 1 m to the water-table at 1.5 m (made from the access pits to the

minirhizotron tubes) revealed mottling and reduced colours, and fine roots were observed between 1 and 1.4 m. Observations also indicated that many of the deeper roots had senesced. Since fine root growth at 0.9 m was likely to have been influenced by fluctuations in soil water content, these data were excluded from subsequent analyses for treatment effects.

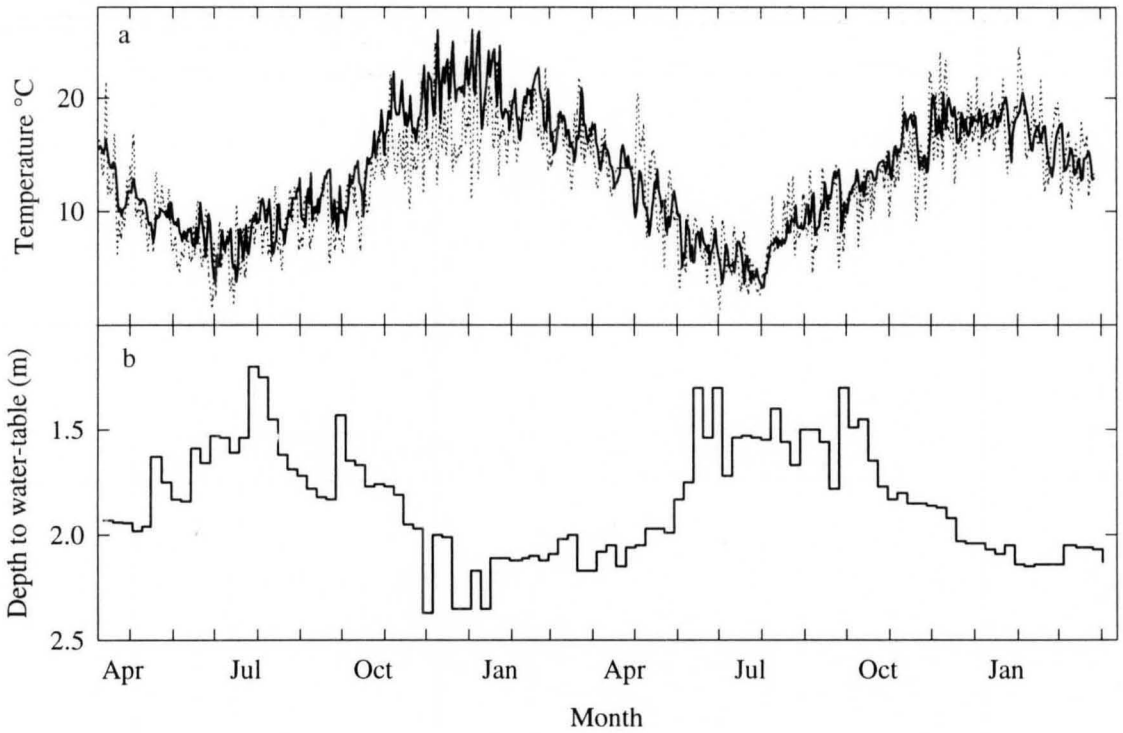


Figure 3-1 (a) Daily average soil temperature, at a depth of 0.1 m (solid line), and daily average air temperature in the open-top chambers (dotted line) for the two-year study period from April 1994 in the large open-top chambers. (b) Water-table fluctuations below the soil surface at the site.

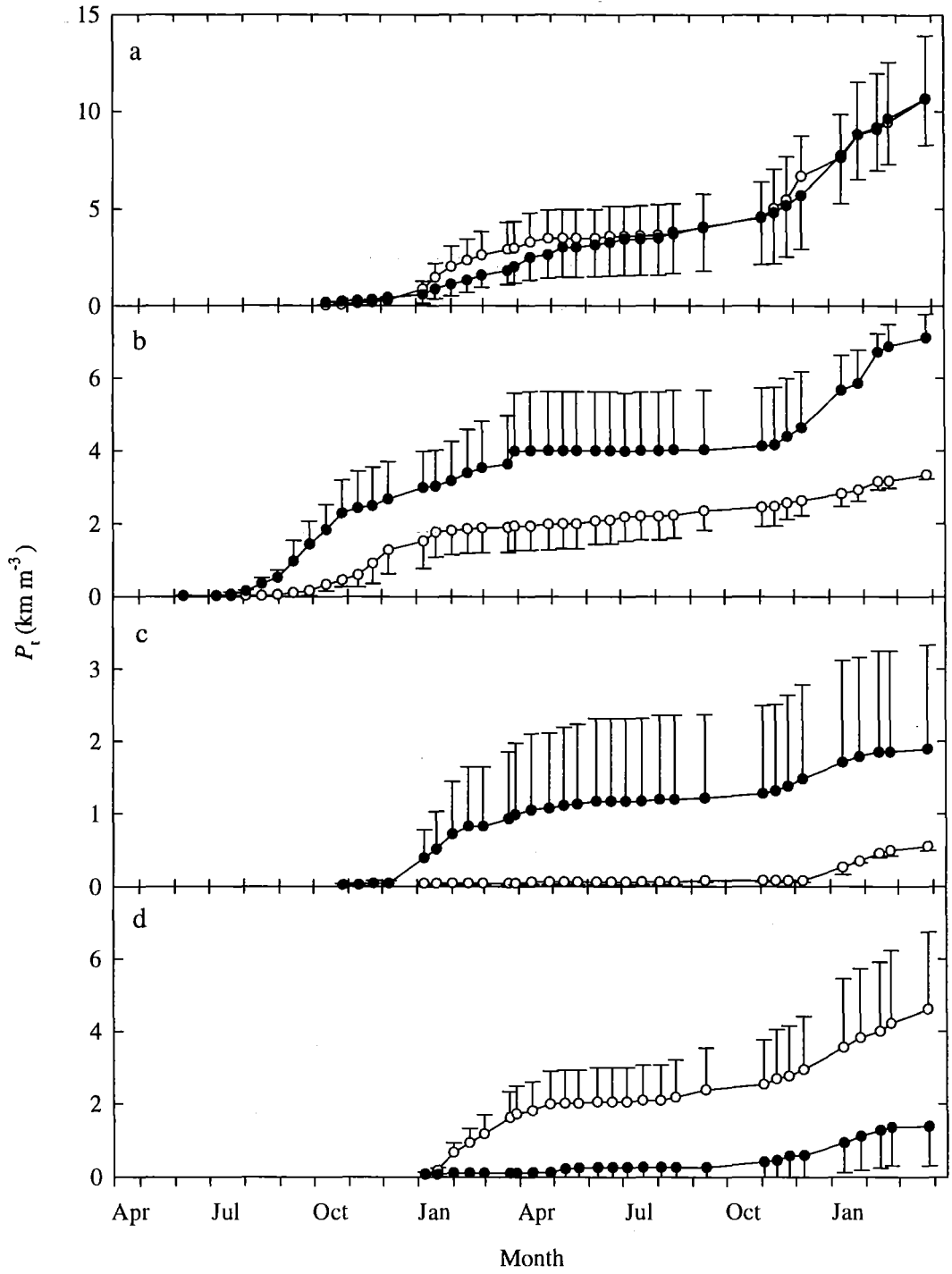


Figure 3-2 Cumulative increases in fine root growth (P_t) at depths of (a) 0.1, (b) 0.3, (c) 0.5 and (d) 0.9 m for *Pinus radiata* trees grown at ambient (O) and elevated (●) CO_2 concentration. The data are means \pm standard error for three replicates.

Stem basal area

At the start of the measurements, mean stem basal area (\pm standard error) was highest for trees growing in the ambient treatment ($114 \pm 13 \text{ mm}^2$) than for those at elevated CO_2 treatment ($78 \pm 3 \text{ mm}^2$). However, two years after planting, mean stem basal areas had increased to $3626 \pm 380 \text{ mm}^2$ for the ambient and $4150 \pm 454 \text{ mm}^2$ for the elevated CO_2 treatment (Figure 3-3). The increase was 16% greater for the trees growing at elevated CO_2 concentration, although the difference was not significant ($p>0.1$). Growth occurred throughout the year until late autumn, then decreased to a minimum in late winter (Figure 3-4). In the first year, maximum R_s was $1.2 \times 10^{-2} \text{ d}^{-1}$ for trees grown at ambient CO_2 (occurring in January) and $1.4 \times 10^{-2} \text{ d}^{-1}$ for trees growing at elevated CO_2 in November (Figure 3-4). In the second year the rates decreased and the maxima, occurring in January, were $7 \times 10^{-2} \text{ d}^{-1}$ for the ambient and $8 \times 10^{-2} \text{ d}^{-1}$ for the elevated CO_2 treatment, although the differences were not significant ($p>0.1$).

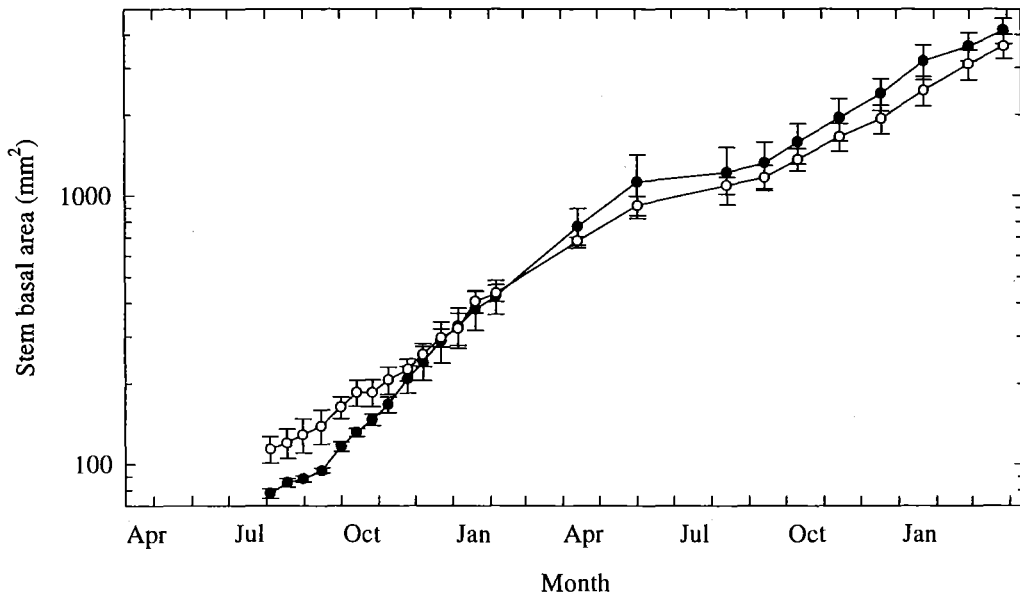


Figure 3-3 Cumulative increase in stem basal area for *Pinus radiata* trees grown at ambient (O) and elevated (●) CO_2 concentration. The data are means \pm standard error for three replicates.

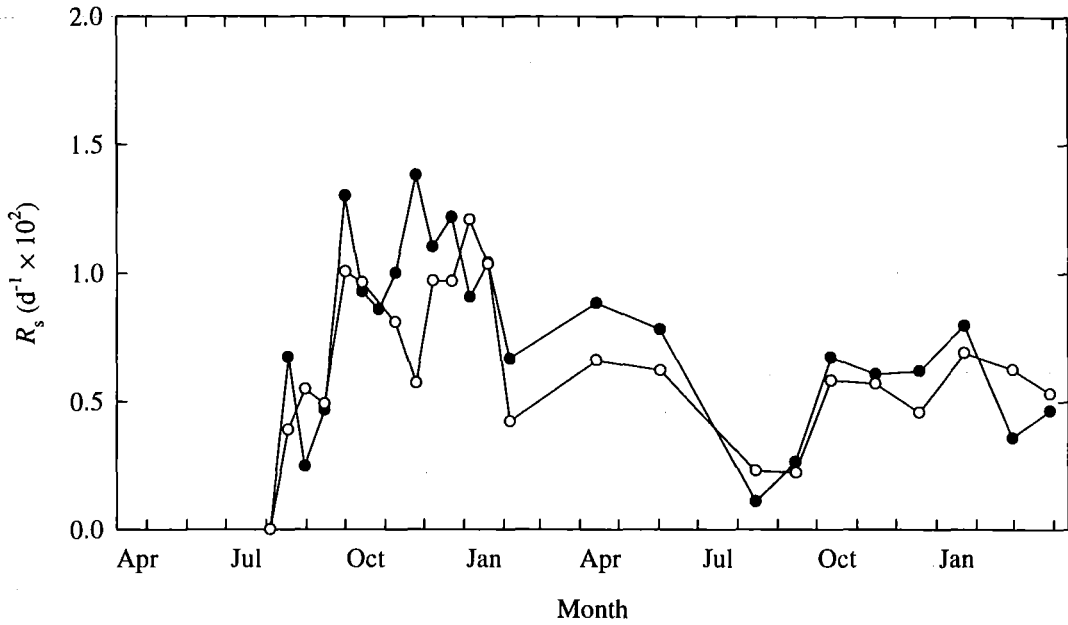


Figure 3-4 Relative rates of increase of stem basal area (R_s) for *Pinus radiata* trees grown at ambient (O) and elevated (●) CO_2 concentration. The data shown are means for three replicates.

Fine root growth

A total of 2263 fine roots were observed during the two year study. Roots were often white when they were first observed and soon changed to a darker colour, normally within 2 to 6 weeks. Mycorrhizal roots were often brown when first observed. At the start of the experiment fine roots appeared in the elevated CO_2 treatment earlier than those growing in the ambient treatment. Fine roots grew throughout the year, with most growth occurring from early spring to late-autumn and very low rates of growth during winter (Figure 3-2a-d P_1 at a depth of 0.3 m was significantly greater in the elevated CO_2 treatment than the ambient treatment after the second year ($p < 0.01$), but not the after the first year ($p > 0.1$).

Rates of root growth in the winter were low, but were greatest at a depth of 0.1 m. In the second year, root growth at all depths increased in spring at the same time (Figure 3-2b). At the end of the study, cumulative root growth for trees growing at elevated CO_2 concentration was 114% greater at 0.3 m ($p < 0.05$) than for the ambient treatment. The large difference in root growth between the treatments at 0.5 m (241%) was not significant ($p > 0.1$) and there was no difference at a depth of 0.1 m ($p > 0.1$). When the data from all the minirhizotrons in each treatment were pooled (excluding data at a depth of 0.9 m), 36% more fine roots were produced in the elevated than in the ambient CO_2 treatment ($p > 0.1$).

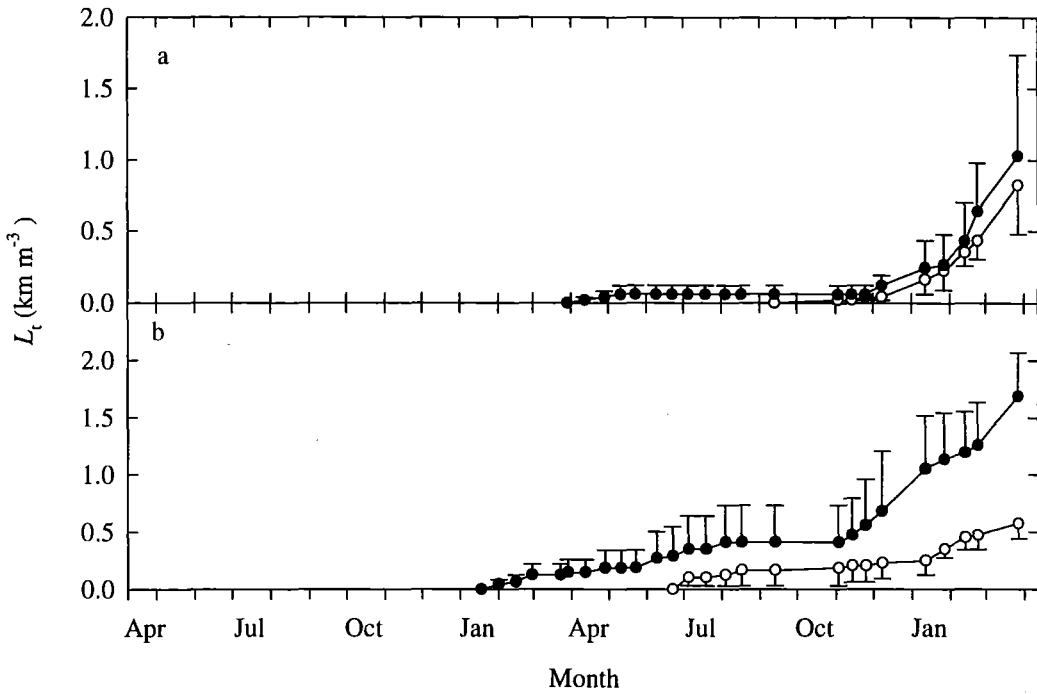


Figure 3-5 Cumulative loss of fine root length density, L_r , measured at depths of (a) 0.1 m and (b) 0.3 m for *Pinus radiata* trees grown at ambient (○) and elevated (●) CO_2 concentration. The data shown are means \pm standard errors for three replicates.

The model of root growth based on temperature in Equation 4 accounted for the seasonal variability. For data from individual minirhizotrons, the model accounted for between 43 and 97% of the variability in the first year. This improved slightly in the second year to between 64 and 99% of the variability. The parameter a_p differed between depths, although treatment differences were not significant (Table 3-2). Values of a_p were significantly greater in the second year than in the first year for the ambient ($p < 0.05$) and elevated ($p < 0.01$) treatments at a depth of 0.1 m, but not at the other depths. Values of a_p were greater nearer the surface although the differences were not significant in the first year. In the second year, values for a_p were significantly greater at a depth of 0.1 m than at 0.5 m for both treatments ($p < 0.05$).

Fine root loss

Root loss was low in the first year and was only detectable at a depth of 0.3 m for trees growing at elevated CO_2 concentration (Figure 3-5). A rapid increase in root loss occurred from the beginning of the second growth period. Roots disappeared at all depths except at 0.9 m. By the end of the study, total root loss was significantly greater (192%) at 0.3 m ($p < 0.05$). There was no difference between treatments at 0.1 m ($p > 0.1$) and, at 0.5 m, root loss was only observed for half of the chambers and occurred only towards the end of the second year.

Loss started earlier, and cumulative loss as a proportion of total root growth, tended to be greater for roots-grown in the elevated CO₂ treatment. By the end of the study, 10% in the ambient and 16% in the elevated treatment of all fine roots had disappeared ($p>0.1$). At 0.3 m, 17% of roots grown in the ambient treatment and 24% in the elevated treatment of the fine roots had disappeared after 2 years, although the difference was not significant ($p>0.1$).

Table 3-2 Values for the parameter a_p from Equation 1 for *Pinus radiata* root growth for each of the two years after planting. Data shown are means of three measurements for trees growing at ambient and elevated CO₂ concentration with standard errors shown in parentheses.

| Depth | a_p (km m ⁻³) | | | |
|-------|-----------------------------|-------------|-------------|-------------|
| | Year 1 | | Year 2 | |
| | Ambient | Elevated | Ambient | Elevated |
| 0.1 | 2.12 (0.02) | 2.22 (1.04) | 5.91 (1.51) | 6.74 (0.83) |
| 0.3 | 1.44 (0.49) | 2.83 (1.11) | 1.08 (0.55) | 2.86 (1.18) |
| 0.5 | 0.06 (0.01) | 1.11 (0.89) | 0.42 (0.07) | 0.75 (0.32) |

Roots loss, at a depth of 0.3 m, first occurred in late summer 1996, nearly 6 months before roots in the ambient CO₂ treatment began to disappear, and 4 months before the first loss occurred at a depth of 0.1 m. The first root growth, in the first year, also occurred at a depth of 0.3 m.

The exponential model of root loss in relation to time from Equation 5 accounted for between 74 and 99% of the variability at 0.1 m, and between 86 and 96% at 0.3 m. Mean values (\pm standard error) for the parameter k_1 for the ambient CO₂ treatment were 0.021 ± 0.004 at 0.1 m and 0.022 ± 0.003 at 0.3 m, and for the elevated CO₂ treatment were 0.010 ± 0.004 at 0.1 and 0.024 ± 0.008 at 0.3 m. There were no significant difference in the value of the parameters (a_1 and k_1) between treatment or depths ($p>0.1$).

Relative rates of root growth and loss

While there were trends in the timing and magnitude of maximum R_p between treatments (Figure 3-6a-c) the variability was large and the differences were not significant ($p>0.1$). The timing of the initial increase in R_p at different depths tended to vary between the treatments in the first year, but the increase in R_p occurred within a period of 2 weeks in November for all depths during the second year. In the first year, maximum R_p ($3 \times 10^{-3} \text{ d}^{-1}$) at 0.3 m occurred in September in the elevated CO₂ treatment, two months earlier than the maximum in the ambient

treatment ($1.4 \times 10^{-3} \text{ d}^{-1}$). At the same depth, the maximum rates in the second year were $1 \times 10^{-3} \text{ d}^{-1}$ for the ambient and $3.3 \times 10^{-3} \text{ d}^{-1}$ for the elevated treatment. These values occurred in February for both treatments, much later than the maximum rates in the first year.

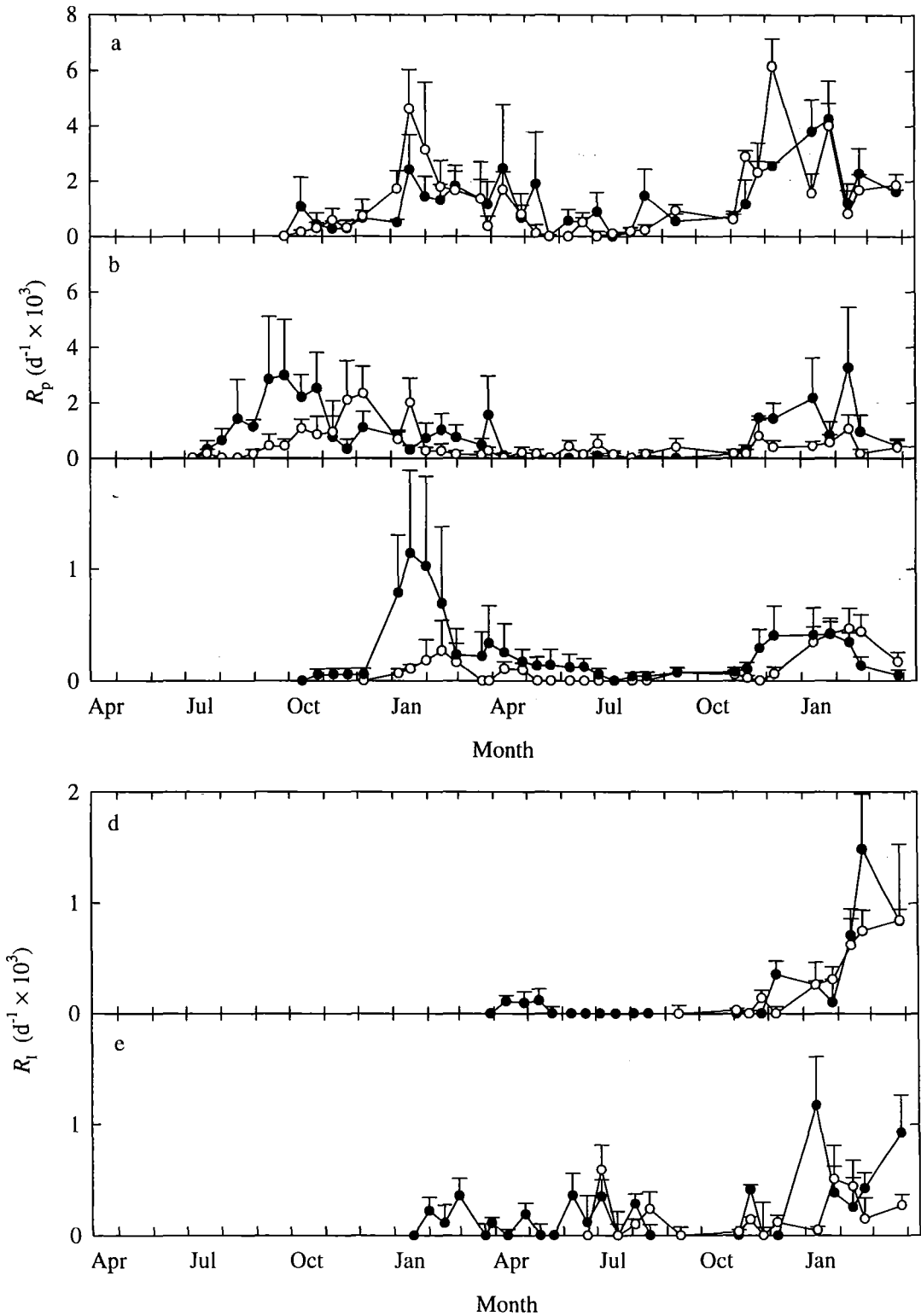


Figure 3-6 Relative rates of increase of root growth (R_p) at depths of (a) 0.1 m, (b) 0.3 m (c) 0.5 m and relative rates of root loss, R_l at depths of (d) 0.1 m and (e) 0.3 m. The data shown are means for three replicates.

In the second year, at a depth of 0.1 m, maximum R_p was greater by 33% for the ambient and 73% for the elevated treatment, than for the first year. The maximum rate occurred one month later for roots in the elevated treatment than for roots in the ambient treatment, although the differences were not significant ($p>0.1$). In contrast, at 0.3 m, maximum R_p in the elevated CO_2 treatment was similar for both years, while R_p in the ambient CO_2 treatment was consistently lower in the second year.

Between November and December of the second year, R_i at a depth of 0.3 m was significantly ($p<0.05$) greater for trees in the elevated CO_2 treatment, than for those growing in the ambient treatment (Figure 3-6e). The highest values of R_i occurred in late summer. No differences between the treatments were observed at depths of 0.1 m (Fig. 3-6d) or 0.5 m, where root losses were small.

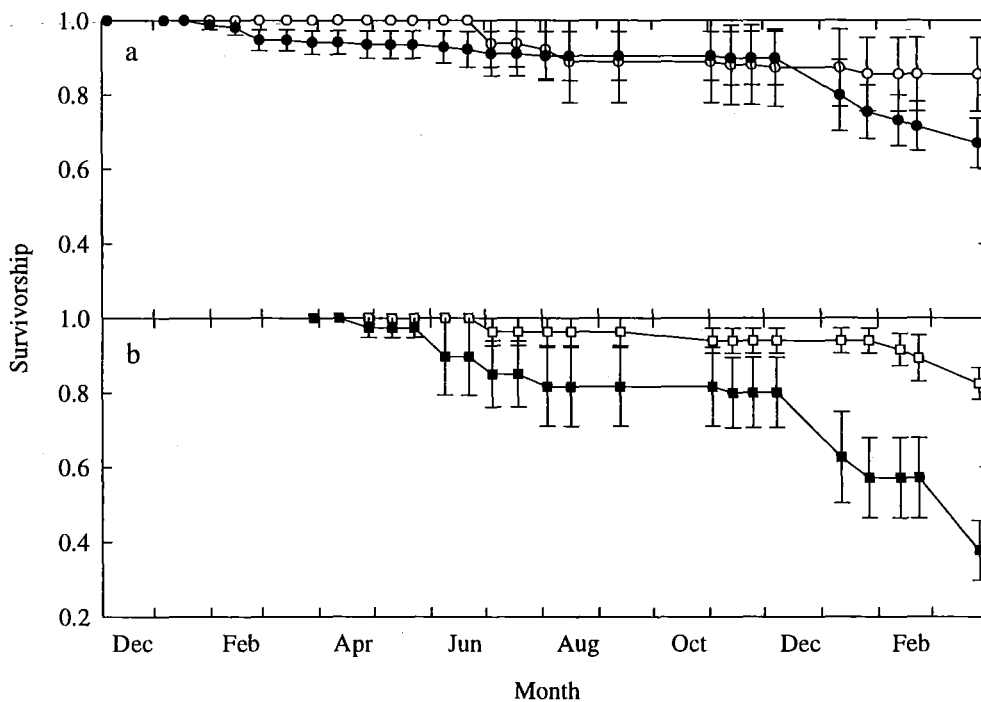


Figure 3-7 Fractional survivorship for two cohorts of fine roots in the first year after planting for *Pinus radiata* trees grown at ambient (O) and elevated (●) CO_2 concentration. Data shown are for roots grown (a) before (cohort 1) and (b) after (cohort 2) mid-summer and each point is the mean \pm standard error for three replicates.

Fine root longevity

At a depth of 0.3 m in the first year, roots in the two cohorts (those that had first appeared between July and December and those that had appeared between January and March) tended to disappear more rapidly for trees growing at elevated CO_2 concentration than for the ambient

treatment (Figure 3-7). At the end of the study, for the first cohort, the percentage of roots (mean \pm standard error) surviving did not differ between the ambient treatment ($86 \pm 7\%$) and the elevated CO₂ treatment ($67 \pm 10\%$). For the second cohort, however, survivorship was significantly ($p > 0.01$) less in the elevated treatment ($38 \pm 8\%$) than the ambient CO₂ treatment ($82 \pm 4\%$).

Between December and March the survivorship of fine roots for trees growing at elevated CO₂ concentration was significantly less ($p < 0.05$) than for trees in the ambient treatment (Table 3-3). Furthermore, roots first observed after mid-summer of the first year disappeared more rapidly between December and March, in both the ambient ($p < 0.1$) and the elevated ($p < 0.01$) treatments, than those first observed before mid-summer. Estimated half-lives for roots in the first cohort were 2446 d for the ambient and 474 d for the elevated CO₂ treatment. For the second cohort of roots, half-lives decreased to 951 d for the ambient and 333 d for the elevated treatment.

Table 3-3 Rates of loss of two cohorts of fine roots of *Pinus radiata* trees growing at ambient and elevated CO₂ concentration in the first year after the trees were planted. Cohort 1 was comprised of roots grown before mid-summer and cohort 2 was those grown after mid-summer. Mean slopes ($n=3$) are presented for four periods after roots in cohort 1 were observed with standard errors given in parentheses and p is the probability of significance between the treatments.

| | Rate of loss ($d^{-1} \times 10^4$) | | |
|-----------------|---------------------------------------|---------------|-------|
| | Ambient | Elevated | p |
| <i>Cohort 1</i> | | | |
| Dec - Mar | 0 | 6.30 (3.38) | ns |
| Apr - Jul | 5.23 (5.23) | 2.95 (2.95) | ns |
| Aug - Nov | 2.32 (1.40) | 0.51 (0.51) | ns |
| Dec - Mar | 1.91 (1.91) | 20.51 (3.54) | 0.009 |
| <i>Cohort 2</i> | | | |
| Apr - Jul | 3.06 (3.06) | 11.77 (11.95) | ns |
| Aug - Nov | 2.56 (2.56) | 1.32 (1.32) | ns |
| Dec - Mar | 10.40 (2.81) | 34.58 (12.64) | 0.036 |

Vertical distribution of roots

Changes in the vertical distribution of roots in relation to time are shown in Figure 3-8. Values for the parameter k_z tended to increase with time, and a_z increased in the ambient CO_2 treatment, but decreased towards the end of the study for trees growing at elevated CO_2 concentration (Table 3-4). By the end of the study, there tended to be relatively more fine roots at depths of 0.3 and 0.5 m for the elevated CO_2 treatment than for trees in the ambient treatment, although the difference was not significant ($p>0.1$).

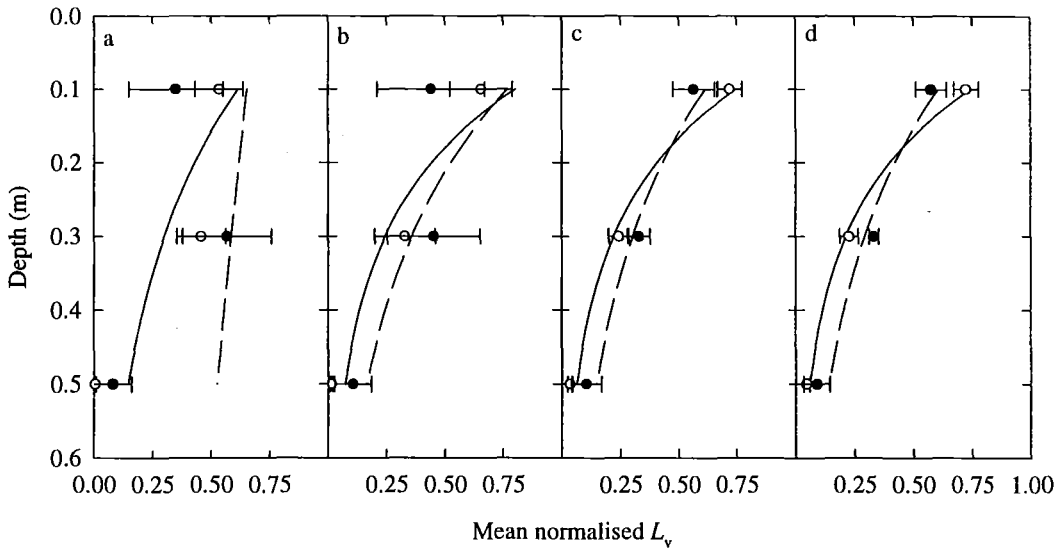


Figure 3-8 Vertical distribution of L_v for *Pinus radiata* fine roots grown at ambient (O) and elevated (●) CO_2 concentration at (a) March 1995, (b) November 1995, (c) January 1996 and (d) March 1996. Measurements were made at depths of 0.1, 0.3 and 0.5 m. The data have been normalised with respect to the sum of the average L_v at the three depths, and means \pm standard errors for three replicates are shown. The exponential model in Equation 5 was fitted to the data from the ambient (solid lines) and elevated (dashed lines) treatments.

Discussion

Data from this study indicate that more carbon was allocated to the fine roots of trees growing at elevated CO_2 concentration. Two years after planting cumulative root growth was 36% greater for trees at elevated CO_2 than at ambient CO_2 (Figure 3-2), however there was large variability and the difference was not significant. In a study with *Populus × euramericana* growing at high and low nitrogen availability over a 158 day period, cumulative root growth increased by approximately 41 and 69% in the elevated CO_2 , high and low nitrogen treatments (Pregitzer *et al.* 1995). Similar results have been found from other work using minirhizotrons

with *Populus grandidentata* (Zak *et al.* 1993; Curtis *et al.* 1994b). In a two year study with *Pinus ponderosa*, cumulative root growth was consistently greater by 35 to 40% for trees growing at elevated CO₂ concentration (Tingey *et al.* 1995; 1996).

Table 3-4 Values of parameters for the exponential model of root distribution with depth, from Equation 5 at four times during the two year period. The model was fitted to root data at 0.1, 0.3 and 0.5 m depths. Mean values for three trees grown at ambient and elevated CO₂ concentration are shown with standard errors given in parentheses and p is the probability of significance between the treatments.

| Date | a_z | | | k_z | | |
|----------|-------------|-------------|----------------|-------------|-------------|----------------|
| | Ambient | Elevated | p ¹ | Ambient | Elevated | p ¹ |
| Mar 1995 | 0.88 (0.23) | 0.69 (0.35) | 0.51 | 3.58 (1.19) | 0.54 (0.34) | 0.51 |
| Nov 1995 | 1.46 (0.63) | 1.13 (0.77) | 0.28 | 5.96 (2.62) | 3.83 (1.55) | 0.28 |
| Jan 1996 | 1.38 (0.26) | 0.88 (0.26) | 0.28 | 6.10 (1.14) | 3.56 (1.35) | 0.28 |
| Mar 1996 | 1.40 (0.28) | 0.87 (0.18) | 0.28 | 6.26 (1.17) | 3.61 (0.93) | 0.28 |

¹Mann-Whitney U test.

Stem and root growth occurred throughout the year, but slowed during the winter (Figures 3-2 and 3-3). The importance of soil temperature in regulating root growth (Bowen 1991) was confirmed by the success of the model (Equation 4) in explaining the seasonal changes in P_t . The empirical model provides a simple way of predicting seasonal changes in the rate of root growth when tree growth is not limited by water and nutrients.

After planting, the first roots appeared at a depth of 0.3 m in early spring in the elevated CO₂ treatment and late spring in the ambient CO₂ treatment (Thomas *et al.* 1996). The first roots to appear on the minirhizotrons at all depths were for trees grown at elevated CO₂ concentration. The early root growth at 0.3 m was less adequately explained by the model, but this probably resulted from the early, rapid initial root growth in the winter at low soil temperatures (Figures 3-1, 3-2 and 3-6) that may have occurred only during the establishment phase. Consistent with these findings, the relative root growth rate early in the growth season with *Populus grandidentata* was higher for trees growing at elevated CO₂ concentration (Curtis *et al.* 1994b). Earlier root growth at elevated CO₂ concentration was also observed for *Picea sitchensis* (Murray *et al.* 1996). The explanation proposed was that earlier autumnal bud set allowed relatively more carbon to be allocated to the roots as the shoot sink was reduced.

However, in contrast, Tingey *et al.* (1996) showed that there were no differences in the timing of root growth in *Pinus ponderosa* over two years.

Much less attention has been directed to measuring L_1 as an individual component for cohorts of roots. Prior to loss, almost all roots turned very dark brown or black. This colouration has been used for some other tree species as an indicator of root senescence (Hendrick & Pregitzer 1992). However, dark colouration of *Pinus radiata* roots was not a good indicator of root senescence as new growth was sometimes observed from these roots. We identified root disappearance directly and found that the rate of root loss was greater in the elevated CO₂ treatment (Figure 3-5) largely as a result of reduced root longevity (Table 3-3). Root half-lives from trees at elevated CO₂ decreased to 35% of the value for roots growing in the ambient treatment in the second year. Therefore, measurements of net root growth, when turnover had occurred, would underestimate cumulative root growth. Furthermore, measurements of net root growth would fail to show any differences of carbon allocation between the CO₂ treatments.

First root disappearance occurred largely during the second year and started earlier in the elevated CO₂ treatment. Root loss occurred at the same time, or slightly later than the increase in root growth. Maximum rates of root loss tended to occur later than maximum rates of root growth. Similar differences in the timing between maximum root growth and loss have been observed for other species, including *Pinus ponderosa* (Tingey *et al.* 1996) and *Betula papyrifera* (Berntson & Bazzaz 1997). In our study, most of the root loss occurred at the shallower depths of 0.1 and 0.3 m (Figure 3-5). Root loss at 0.5 m was low and occurred towards the end of the study. Root loss did not occur at 0.9 m, which is likely to be attributable to the soil hydrology at this depth. However the pattern of loss with increasing depth is still consistent with those observed for a temperate deciduous forest (Hendrick & Pregitzer 1996b).

There have been few studies on the effects of elevated CO₂ concentration on root longevity and these have led to conflicting results for different species and growing conditions. Pregitzer *et al.* (1995) found that root longevity in *Populus* was only reduced at elevated CO₂ concentration when grown in a low nitrogen availability treatment. In contrast, longevity was increased at elevated CO₂ in a two-year study with *Pinus ponderosa* (Tingey *et al.* 1997), and in an oak-palmetto scrub system (Day *et al.* 1996). However, no difference in longevity was found for *Betula papyrifera* or *Acer rubrum* (Berntson & Bazzaz 1996a).

Fine root longevity may vary with season (Eissenstat & Yanai 1997) and with root function (Fitter 1996). In our study, seasonal differences in longevity were more pronounced at elevated CO₂ concentration. Roots grown in spring and early summer were more likely to survive than those grown after mid-summer (Figures 3-7a and 3-7b). Support for differences in the functional role of these cohorts of roots is suggested by the observation that the first roots to be recorded were often coarser than 1 mm in diameter (Thomas *et al.* 1996). Similarly, for *Pinus*

ponderosa, mean fine root diameter decreased from 1.2 to 0.7 mm during a period of 12 months as the number of roots increased (Tingey *et al.* 1995).

Our estimates of the half-lives for roots grown at elevated CO₂ concentration of 474 d and 333 d for the two cohorts are greater than other estimates for a range of other woody and non-woody species (Eissenstat & Yanai 1997). It is probable that the estimates of half-lives for root cohorts in the ambient CO₂ treatment were over-estimated because of the non-linear nature of cohort survivorship with time. Root survivorship for Cohort 2 was much lower in the elevated than the ambient CO₂ treatment because of a rapid increase in the rate of root loss from mid-summer (Figure 3-7). Hendrick and Pregitzer (1992) estimated a half-life of 304 d for *Acer saccharum* roots grown in spring, and Fitter *et al.* (1996) estimated half-lives of 268 and 162 d for cohorts of *Populus × euramericana* grown at ambient and elevated CO₂ concentration at low nitrogen availability from data published by Pregitzer *et al.* (1995). At high nitrogen availability, the half-lives were even shorter at 116 d in the ambient and 107 d in the elevated CO₂ treatment.

The processes regulating root longevity are poorly understood. Most models assume that roots have an indeterminate life-span and that senescence is dependent on environmental conditions (Bloomfield *et al.* 1996), including nutrient availability (Pregitzer *et al.* 1993), soil temperature (Hendrick & Pregitzer 1993); soil aeration (Reid & Petrie 1991) herbivory (Santantonio & Santantonio 1987) and mycorrhizal association (Harley & Smith 1983). However, Marshall & Waring (1985) proposed that longevity is determined largely by the initial starch concentration of roots, and that senescence occurs once the carbon source is exhausted. In our study, both treatments were well supplied with nutrients and water, soil temperature and aeration were similar for all chambers, mycorrhizae were present and there was no indication of herbivory. The most likely explanation for the high values for half-life is that the trees were young and the roots were newly exploiting the soil profile. Root longevity might be expected to decrease as the root system becomes progressively larger because of decreased hydraulic conductance and increased maintenance costs. Shorter fine root half-lives and increased turnover in the elevated CO₂ treatment may be a response to increased carbon allocation to the root system, because of higher rates of photosynthesis in the foliage (Hogan *et al.* 1996). Investing increased carbon in new fine roots which are more effective at obtaining nutrients may be more efficient than maintaining older roots.

Because of the large spatial variability in root distribution and limitations on the number of minirhizotrons from which images can be analysed, it is not uncommon in studies of this nature for the differences between treatments to lack statistical significance. The horizontal placement of the minirhizotron tubes was chosen to maximise the number of roots recorded at each depth. By increasing the volume of soil sampled, apparent temporal variability is decreased, thus

increasing the sensitivity of the techniques to distinguish differences with depth and between treatments (Reid & Bowden 1995).

Greatest fine root proliferation occurred at shallow soil depths (0.1 and 0.3 m), but tended to decrease exponentially with depth after two years (Figure 3-8). This type of distribution is similar to other studies of *Pinus radiata* (Nambiar 1983; Santantonio & Santantonio 1987; Whitehead *et al.* 1994). There tended to be relatively more roots grown at the elevated CO₂ treatment at 0.3 and 0.5 m allowing greater acquisition of nutrients and water for increased productivity (Prior *et al.* 1994b). Vertical root distribution responses for elevated CO₂ treatments have been observed for *Quercus scrubland* (Day *et al.* 1996) and *Gossypium hirsutum* (Rogers *et al.* 1992; Prior *et al.* 1994a). Root distribution patterns may also have important implications for soil carbon sequestration. The turnover time for soil organic matter increases with depth with a considerable global pool of organic carbon deeper than 1 m, and with over one-third of soil organic carbon between 0 and 2 m found below 1 m (Batjes & Sombroek 1997). Significant deep carbon turnover (15% on an annual to decadal timescale) has been measured for some tropical ecosystems (Nepstad *et al.* 1994). Trees in temperate coniferous forests tend to be deep rooting (Canadell *et al.* 1996a) and, compared to other forest ecosystems, relatively more roots are found deeper in the soil profile (Jackson *et al.* 1996).

One possible explanation for increases in root growth and loss, and relative changes to root distribution may be that tree growth is accelerated at elevated CO₂ concentration, indirectly increasing below-ground carbon allocation (Gebauer *et al.* 1996). If this is the case, then an increase in the rate of ontogeny will result in trees reaching maturity and senescence earlier. This could potentially lead to an increase in soil carbon as a result of faster tree growth cycles but this would be highly dependent on the rate of carbon loss from the soil.

Conclusions

Over a period of two years of growth, with non-limiting nutrient and water conditions, cumulative root growth tended to be greater at elevated CO₂ concentration, indicating that carbon allocation below-ground was increased. Root longevity decreased for the roots growing at elevated CO₂ concentration, suggesting that root turnover would also be increased. More roots grown at elevated CO₂ concentration tended to occur deeper in the profile. Greater carbon allocation and a relatively deeper distribution of roots indicate the potential for increasing carbon input to the soil by young *Pinus radiata* trees. Increased below-ground carbon allocation may be a size-dependent effect related to enhanced tree growth at elevated CO₂. This is likely to result in reduced harvesting cycles for plantation crops and may lead to increases in soil carbon sequestration.

There is a need for longer studies to determine whether enhanced root growth and turnover would be maintained and further studies are required to determine the mechanisms of positive and negative feedbacks resulting from increased soil carbon availability (van Veen *et al.* 1991; Berntson & Bazzaz 1996b), particularly in conditions of sub-optimal water and nutrient supply.

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CHAPTER 4

SEASONAL SOIL SURFACE CARBON FLUXES FROM THE ROOT SYSTEMS OF YOUNG *PINUS RADIATA* TREES GROWING AT AMBIENT AND ELEVATED CO₂ CONCENTRATION §

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Abstract

Increased below-ground carbon allocation by trees at elevated CO₂ concentration may alter soil carbon cycling. Seasonal estimates of soil surface carbon flux were made to determine whether carbon losses from trees growing at elevated CO₂ concentration were higher than at ambient CO₂ concentration, and whether this was related to increased fine root production

Monthly soil surface carbon flux density (f) measurements were made on plots with trees growing at ambient (350) and elevated (650 $\mu\text{mol mol}^{-1}$) atmospheric CO₂ concentration in large open-top chambers. Before the trees were planted both the soil carbon concentration (0.1%) and f (0.01 $\text{g m}^{-2} \text{h}^{-1}$ at 15°C) were low. A model that described the radial pattern of f with distance from the tree stems was used to estimate the annual carbon flux (F) and annual average f from the tree plots. Seasonal fine root production was measured from minirhizotrons. Radial root distribution measurements were compared with radial measurements of f . A one-dimensional gas diffusion model was used to estimate f at the stem from soil CO₂ concentrations at four depths.

For the second year of growth, estimated F was 13% higher at elevated CO₂ concentration (1895 g y^{-1}) than at ambient CO₂ concentration (1671 g y^{-1}). Higher f at elevated CO₂ concentration was largely explained by the increased fine root production. There were strong positive relationships between f and root production and f and stem production. Both f and root length density declined exponentially with distance from the stem, and had similar length scales. Diurnal changes in f were largely explained by changes of soil temperature at a depth of 0.05 m.

Ignoring the change of f with increasing distance from tree stems could result in underestimates of soil surface carbon fluxes, especially in young stands when roots are poorly distributed.

Keywords: *Pinus radiata*, elevated CO₂ concentration, soil CO₂ flux, fine roots

§ Prepared for *Plant and Soil*.

Introduction

In temperate forests it has been estimated that between 25 and 65 % of net primary production is allocated to fine roots (Landsberg & Waring 1997). Between 28 and 70% of carbon returned to the atmosphere from the soil surface is from autotrophic root respiration for maintenance and growth (Raich & Schlesinger 1992; Ryan *et al.* 1996). The balance of this carbon efflux to the atmosphere is from heterotrophic respiration, either through the symbiotic relationship of mycorrhizae to the tree or as microbial respiration. This soil surface CO₂ efflux (f), sometimes described as soil respiration, has been shown to be positively related to root biomass (Haynes & Gower 1995; Ryan *et al.* 1996) and mycorrhizal associations (Rygiewicz & Andersen 1994; Vose *et al.* 1997). It may also be regulated by soil temperature and water (Gordon *et al.* 1987), and nutrient availability (Ryan *et al.* 1996; Zogg *et al.* 1996).

In a number of tree species, increased below-ground carbon allocation has been observed at elevated atmospheric CO₂ concentrations (Ceulemans & Mousseau 1994; Eamus & Jarvis 1989), although there is still considerable uncertainty about the effects of potential increases of carbon in the soil system, its component carbon pools and the fluxes between them (Canadell *et al.* 1996; van Veen *et al.* 1991). In the long-term carbon could potentially accumulate in the soil as a result of enhanced carbon allocation below-ground (Tate & Ross 1997). However, there is evidence that the rate of turnover of the soil carbon pools may also increase in some ecosystems (Fitter *et al.* 1996; Hungate *et al.* 1997; Körner & Arnone 1992).

In order to predict ecosystem responses to elevated CO₂ concentration it is important to determine the plant-soil carbon fluxes (Curtis *et al.* 1994a). Fine root production is the main carbon flux into the soil and is often stimulated at elevated CO₂ concentration (Berntson & Bazzaz 1997; Pregitzer *et al.* 1995; Tingey *et al.* 1997). If fine root growth is stimulated at elevated CO₂ concentration, then root (and mycorrhizal) respiration losses may also be expected to be higher. Recently, several studies have shown that f increases at elevated CO₂ concentrations for tree species (Johnson *et al.* 1994; Pajari 1995; Thomas *et al.* 1996; Vose *et al.* 1997). However, there are few studies that have investigated both seasonal patterns of root growth and f at elevated CO₂ concentrations.

Seasonal estimates of f are often made using measurements from soil surface chamber systems. But f may also be determined using soil CO₂ concentration measurements and models of CO₂ gas diffusion (De Jong & Schappert 1972). Measurements of f have been related to fine root distribution patterns and activity (Ben-Asher *et al.* 1994a; Ben-Asher *et al.* 1994b). Minirhizotron camera systems (Upchurch & Ritchie 1983) enable non-destructive measurements of seasonal fine root production. By combining these techniques the seasonal contribution of roots to f may be elucidated.

This study was undertaken as part of a larger, long-term project to estimate the carbon balance of trees growing at elevated CO₂ concentration. *Pinus radiata* D. Don trees are growing in large open-top chambers at a site near Christchurch, New Zealand. In a previous study we reported that *Pinus radiata* root production was enhanced at elevated CO₂ concentration (Thomas *et al.* 1997). The first objective of this study was to determine whether the estimated annual carbon efflux from plots (F) with *Pinus radiata* trees growing at elevated CO₂ concentration was higher than from plots with trees growing at ambient CO₂ concentration. Soil chamber measurements of f and estimates of f calculated using a CO₂ gas diffusion model (Cook *et al.* 1997) were used to model the pattern of radial f with distance from the tree stems and estimate F . The second objective was to investigate the effect of seasonal fine root and stem production on seasonal f at ambient and elevated CO₂ concentrations.

Materials and Methods

Site description

Measurements were made for four *Pinus radiata* D. Don trees grown at ambient (350 $\mu\text{mol mol}^{-1}$) and four at elevated (650 $\mu\text{mol mol}^{-1}$) CO₂ concentrations, each in identical large open-top chambers at Christchurch, New Zealand (latitude 43° 32' S, longitude 172° 42' E, 9 m elevation above sea level). Each chamber was 4.7 m in diameter and 4.3 m high. Air at ambient or elevated CO₂ concentration was supplied by large fans to chambers at approximately two to three air exchanges per minute. The design of the carbon dioxide enrichment system and the performance of the open-top chambers have been described by Whitehead *et al.* (1995). Clonal propagation from a single bud from a four-year old tree using tissue culture at ambient or elevated CO₂ concentration provided trees of genetically identical material (Davies *et al.* 1992). The trees were planted in the open-top chambers in April 1994 (autumn). The roots were inoculated with mycorrhizae by including litter from an adjacent forest plantation with the roots.

The mean annual temperature at the site was 12.2 °C, with a mean daily range of 3.5 °C. Mean annual rainfall was 612 mm. Air temperature was measured at half-hourly intervals at 1.5 m above the soil surface, and soil temperatures were measured hourly at 0.1, 0.3 and 0.5 m (Thomas *et al.* 1997). The soil was a Kairaki dune sand, which is a recently stabilised, weakly developed, rapidly, freely draining (New Zealand Soil Bureau 1974), also described as ustipsammments sandy mixed mesic (Soil Survey Staff 1990). When the trees were planted, concentrations of soil carbon (0.11%) and nitrogen (0.01%) were low and all surface organic

material had been removed before the chambers were installed at the site. The depth of the water-table was monitored weekly 500 m from the site, at a similar elevation. Soil water was maintained at near field capacity by applying irrigation each night. This was checked by daily measurements of calibrated electrical resistance soil water potential sensors (model Watermark, Irrrometer Co. Inc., Riverside, CA)

Nutrients were applied to the soil surface to maintain non-limiting conditions. In September 1994, a balanced fertiliser (Osmacote Plus, Grace Sierra International, Heerlen, The Netherlands) supplied nitrogen at a rate of $7.5 \text{ g m}^{-2} \text{ y}^{-1}$. This was increased to a rate equivalent to $15 \text{ g m}^{-2} \text{ y}^{-1}$ in December 1994 at 3 monthly intervals. From October 1995 the equivalent amount of nitrogen added was increased to $60 \text{ g m}^{-2} \text{ y}^{-1}$ applied at monthly intervals. Stem basal diameter at 0.01 m above the soil surface was measured at approximately monthly intervals from August 1994.

Seasonal root measurements

Before the trees were planted, rigid plastic sheets radiating from the centre of each chamber were inserted to a depth of 1.2 m. This isolated the root systems of study trees from others growing in the chamber to one-sixth of the total soil surface area within each chamber. Acrylic minirhizotron tubes were installed horizontally beneath the trees at 0.1, 0.3, and 0.5 m depths by the method described by Thomas *et al.* (1996). Each tube was 1.8 m long with an external diameter of 38 mm and internal diameter of 34 mm. Two parallel lines were etched 20 mm apart along the outer surface of the tubes and, perpendicular to these, lines were etched at 20 mm intervals. These lines provided references for fine root locations along the tube. Fine root ($< 1 \text{ mm}$ -diameter) production was measured bi-weekly for two years after planting by counting roots from images captured from the minirhizotrons using the technique and camera system described by Thomas *et al.* (1996). Images taken at 20 mm intervals along the tube were analysed using the RooTracker (Duke University, Durham, NC, USA) software package. Cumulative fine root production (P_t) was defined as the sum of roots produced at the 0.1, 0.3 and 0.5 m depths between times t and $t + 1$. A linear relationship between the number of roots, root length and root length density (L_v) has been established (Thomas *et al.* 1996).

Seasonal soil surface carbon flux density and soil CO₂ concentration

To distinguish between measurements and modelled estimates of f , the measurements are defined as f_o , and the modelled estimates defined as f_m . All values of f_o and f_m are CO₂-C flux density, i.e. the carbon flux density.

Measurements of f_o were made every 4 weeks using a portable soil respiration system placed on the soil surface. Seasonal measurements were made between 12 weeks and two years after the trees were planted. The soil respiration system consisted of a chamber (0.10 m diameter and 0.15 m tall) inserted 10 mm into the soil which was coupled to a portable infrared gas analyser (models SRC-1 and EGM-1, respectively, PP Systems, Hitchins, Herts, UK) in a closed circuit. The system was described originally by Parkinson (1981) and extensively tested recently by Jensen *et al.* (1996). Eight measurements were made in each open-top chamber at an approximate distance of 0.35 m from the tree stem. Soil temperature (T) was measured at the same time using the thermistor probe with the soil respiration system. Diurnal measurements of f_o were made during the summer before the trees were planted (December 1994); the following summer (February 1995); and in January 1996. To investigate the effect of soil temperature (T) on f_o , 15 minute averages of thermocouples attached to a datalogger via a multiplexer (Campbell Scientific Inc., Logan, UT) were measured at: 0.01, 0.02, 0.05, 0.1, 0.2 and 0.3 m when diurnal measurements of f_o were made.

For seasonal comparison, f_o data were normalised to a common temperature of $T = 15\text{ }^{\circ}\text{C}$ (f_{o15}) using the Arrhenius-type model of Lloyd & Taylor (1994):

$$f_o = Ae^{-E_o/(T-T_o)} \quad (1)$$

$$f_{o15} = Ae^{-308.56/(288.15-227.13)} \quad (2)$$

where, A is a data set-dependent parameter, E_o is a constant (308.56 °K) analogous to activation energy, T is soil temperature (°K) and T_o is a base temperature (227.13 °K). A was determined by fitting the model to f_o measurements made at the soil temperature (T) for each date (Equation 1). The normalised value of f_{o15} was then predicted by inserting $T = 15\text{ }^{\circ}\text{C}$ into the model, using the value of A calculated for each date (Equation 2). This common temperature of 15 °C was chosen as it approximated the average soil temperature at a depth of 0.05 m for the periods when f_o measurements were made.

Soil CO₂ concentrations, sampled directly beneath the stem of each tree, were measured between May 1994 and April 1996, at the same time as the measurements of f_o . Perforated, stainless steel tubes (0.30 m long by 14 mm internal diameter) connected to fine stainless steel tubing, terminated at the soil surface with a gas-tight syringe tap, were installed at depths of 0.1, 0.2, 0.3 and 0.5 m before the trees were planted. A 10 ml soil air sample was extracted for measurements from each depth using a plastic syringe. The CO₂ concentration of the sample was

determined within 24 h using a gas chromatograph (model 8610, SRI Instruments, Torrance, CA, USA).

Modelled soil surface carbon flux density

Soil CO₂-C gas concentrations were used in a steady-state, one-dimensional model of CO₂ gas diffusion (Cook *et al.* 1997, see Appendix) to estimate f_m at the tree stem by :

$$C(z) = C_o + \frac{Qe^{-E_o/(T-T_o)}L^2}{D(n+1)(n+2)} \left[1 - (1-z/L)^{n+2} \right] \quad (3)$$

where, C is the CO₂-C concentration of the gas in the gas-filled pore space, z is depth, C_o is the soil surface atmosphere concentration of CO₂, D is the diffusion coefficient of CO₂ in air, Q is the surface soil respiration rate, L is the depth to which respiration occurs, n is a dimensionless attenuation coefficient that describes the shape of respiration rate profile with soil depth, indicating how respiration is concentrated near the soil surface. Equation 3 may be differentiated with respect to depth to give:

$$f_m = \frac{Qe^{-E_o/(T-T_o)}L}{n+1} \quad (4)$$

The values of Q , L and n obtained by fitting Equation 3 to the CO₂ concentration profiles are used in Equation 4 to determine f_m .

Radial changes in soil surface carbon flux density with distance from tree stems

At the end of the study, measurements of f_o were made with the centre of the soil respiration chamber placed at 0.15, 0.35, 0.55 and 0.75 m from the stems of four trees in March and April 1996, two years after the trees were planted. Duplicate measurements were made in the four cardinal directions at each radial distance from the stem (r). At the same time, soil CO₂ concentrations were measured so that f_m could be estimated, i.e. f at $r = 0$ m. The relationship between f with r was described using an exponential equation (Cook *et al.* 1997) of the form:

$$f = f' e^{-r/R} + \gamma e^{-E_o/(T-T_o)} \quad (5)$$

where f' is the CO₂ flux density due to the roots at $r = 0$ m, R is a length scale and γ is a component of the carbon flux density not accounted for by the shape of the root distribution, which has been described as the background carbon flux density (Cook *et al.* 1997).

Radial changes of root length density with distance from tree stems

Root length density (L_v , mm mm⁻³) was calculated using a linear relationship established between the number of root intersections (n_r) observed from the surface of the minirhizotrons and L_v measured from soil cores taken adjacent to minirhizotrons (Thomas *et al.* 1997). Root intersections were counted for each 0.1 m increment along the tube (from 0 to 1.7 m). The relationship was $L_v = 1.05 \cdot 10^{-3} n_r$ ($r^2 = 0.79$).

The relationship between L_v distribution and r was described using an exponential equation (Cook *et al.* 1997) of the form:

$$L_v = L_v' e^{-r/R} \quad (6)$$

where L_v' is the root length density at $r = 0$ m.

Estimation of carbon flux

Seasonal carbon flux was estimated from the four-weekly f_o measurements and estimates of f_m . For four-weekly periods, daily surface carbon fluxes were estimated by substituting daily average T into Equations 1 and 4. The model parameters (A , Q , L and n) were determined by fitting the four-weekly measurements of fluxes and T . The effects of using hourly average or daily average soil temperatures on f_o daily totals were compared for 7 days (winter and summer) during the course of the study. Estimates of the average carbon flux from the plot (\bar{f}) and the total carbon flux from the plot (F) were made using the relationships described by Cook *et al.* (1997):

$$\bar{f} = \frac{2f' [1 - e^{-x}(x+1)]}{x^2} + \gamma e^{-E_o/(T-T_o)} \quad (7)$$

where, $x = r/R$, and

$$F = 2\pi \left\{ f' R^2 (1 - e^{-x}[x+1]) + r^2 \gamma e^{-E_o/(T-T_o)} / 2 \right\} \quad (8)$$

Estimations of \bar{f} and F were made using the value of R derived from L_v data (Equation 6) which was assumed to approximate R from f_o data (Equation 5). The value of r was 0.95 m, the radial extent of the plot, and γ was assumed to be a constant proportion of f at $r = 0$ m. Estimates were made from November 1994; this was when roots were observed on all minirhizotrons at 0.3 m for both CO₂ treatments. Similarly to the seasonal f_o measurements and f_m estimates, R was calculated for four-weekly intervals.

Statistical analysis

Seasonal differences between f_o measurements of the two treatments were tested using repeated measures analysis of variance. Data were normalised by log transformation and independent t-tests were used to compare treatments for individual dates. Where errors are reported they are the standard error of the sample means.

Results

Relationship between soil temperature and soil surface carbon flux density

Daily average soil temperature was 14.2 °C and 12.6 °C at 0.1 m, in the first and second year after the trees were planted, respectively. At a depth of 0.1 m, maximum hourly average temperatures occurred in mid-summer (December): 35.7 °C, in the first year. As the tree canopy expanded and shaded the soil this declined to 28.5 °C in the second year at a depth of 0.1 m. The minimum hourly temperature was 1.6 °C occurring in June of the first year and 1.2 °C in August of the second year. The greatest range of diurnal temperatures occurred at the soil surface, which reduced as soil depth increased (Figure 4-1). While seasonal soil temperatures were not continually monitored at depths less than 0.1 m, measurements made four-weekly at the same time as f_o , were observed up to 37.5 °C at the soil surface.

Changes in diurnal measurements in f_o were best correlated with the changes of soil temperature at 0.05 m depth (Figure 4-2), using Equation 1. There were large differences in the diurnal f_o between the measurements made in four chambers in January 1995 ($f_{o15} = 0.029 \pm 0.002 \text{ g m}^{-2} \text{ h}^{-1}$) and February 1996 ($f_{o15} = 0.128 \pm 0.06 \text{ g m}^{-2} \text{ h}^{-1}$). For these two periods, between 18 to 93% of the variability of four chambers could be explained by temperature at 0.05 m. There were no differences in responses between the CO₂ treatments. Before the trees were planted (December 1994) f_o was low ($f_{o15} = 0.012 \text{ g m}^{-2} \text{ h}^{-1}$) and the response to soil temperature was more variable ($r^2 = 0.04$ and 0.61).

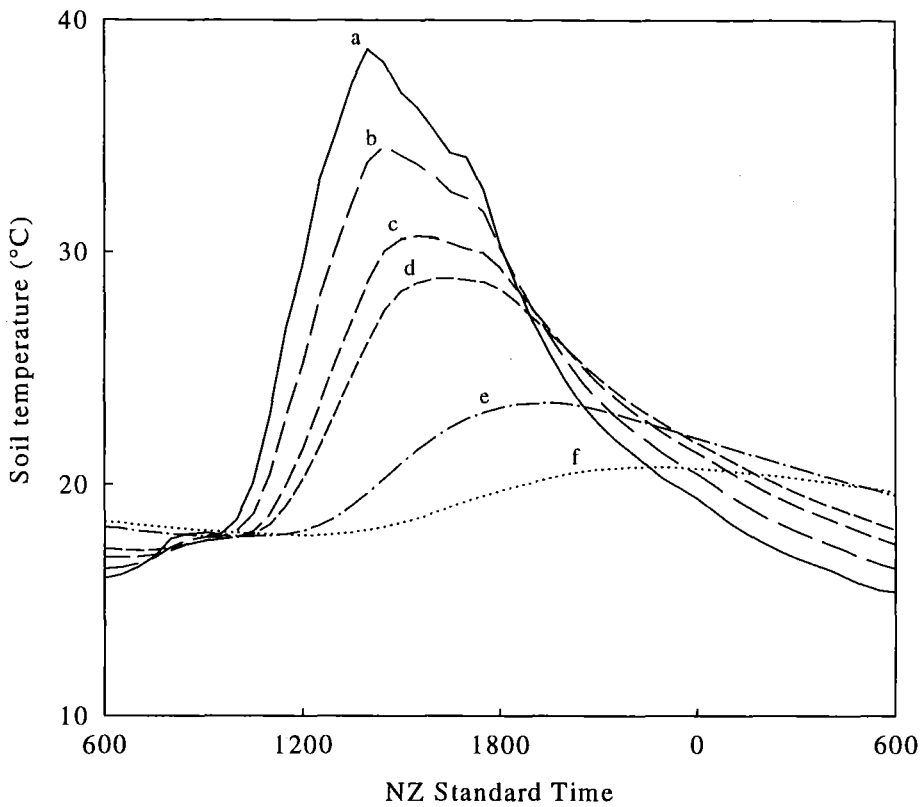


Figure 4-1 Measurements of soil temperature at depths of (a) 0.02, (b) 0.05, (c) 0.08, (d) 0.1, (e) 0.2 and (f) 0.3 m for a 24 h period in December 1994.

Soil CO₂ concentration

Soil CO₂ concentrations for all soil depths to 0.5 m were consistently higher for chambers with trees grown at elevated CO₂ concentration than those at ambient CO₂ concentration (Figure 4-3a-d). CO₂ concentration always increased with depth from 0.1 to 0.5 m for both treatments. There were large seasonal differences in measurements, with an overall trend of increasing concentration as P_t and root biomass increased. Highest concentrations were measured in March and April 1995 (Autumn). The maximum CO₂ concentration sampled at 0.5 m was 2.3 % in April 1995 (in an elevated CO₂ concentration chamber). In May and July, soon after the trees were planted, the CO₂ concentration was approximately linear with increasing depth (Figure 4-4). Greatest changes in the CO₂ concentration profile in the soil tended to occur at the shallowest depths sampled (Figure 4-4), consistent with the largest proportion of fine roots (Thomas *et al.* 1997).

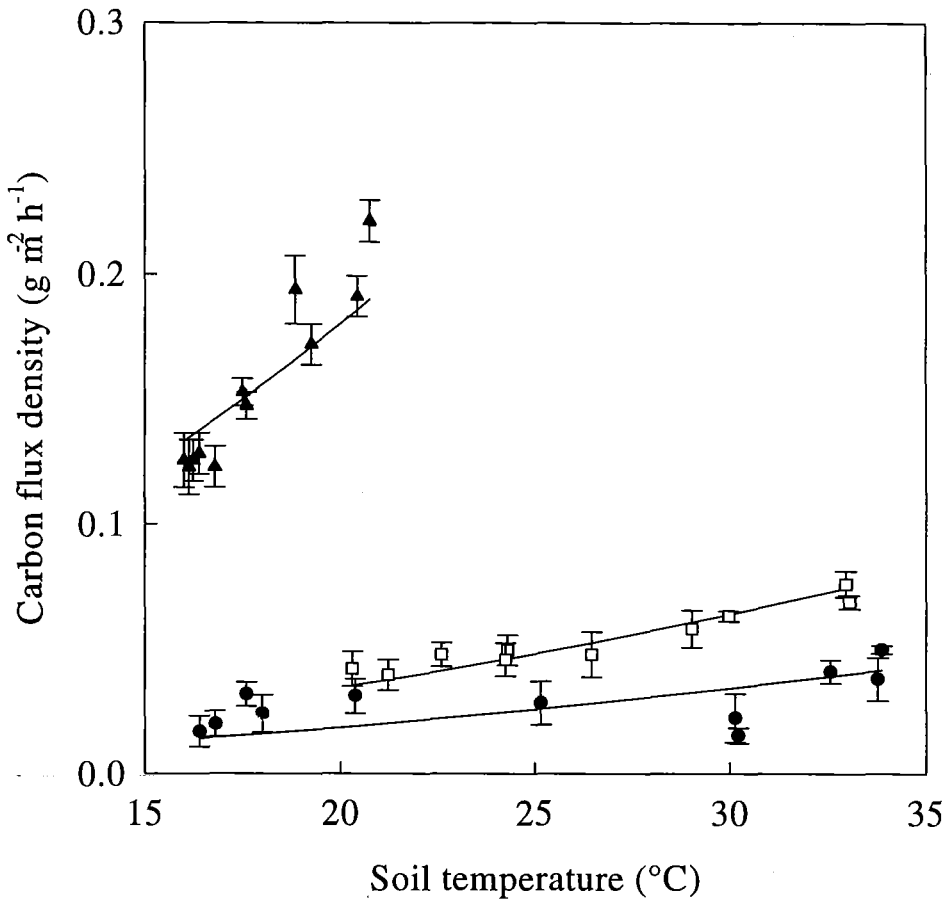


Figure 4-2 The relationship between soil surface carbon flux density and soil temperature at 0.05 m, measured: (i) before the trees were planted (December 1994, ●); (ii) in the summer of the first year of growth (January 1995, □) and (iii) the late-summer of the second year of growth (February 1996, ▲). The lines fitted are an Arrhenius-type function (Equation 1). Data are means of four measurements \pm standard error.

Seasonal changes of soil surface carbon flux density

There were seasonal changes of f_0 , after the removal of the effect of seasonal temperature at 0.05 m depth, by normalising to 15 °C (Figure 4-5). Underlying these fluctuations was a trend of increasing f_0 as stem and root production increased over the two year period. In the first year f_0 and f_m at elevated CO_2 concentration were consistently greater than at ambient CO_2 concentration. The consequence of this was the divergence of cumulative f_0 (Figure 4-6a). However, from mid-winter (July of the second year) f_0 tended to be similar for both CO_2 treatments (Figure 4-5). The average rate of increase of cumulative f_0 was slightly greater at elevated CO_2 concentration than at ambient CO_2 concentration in the second year, but much less than the first year (Figure 4-6a). Apart from f_0 measurements made in December 1994, there were no significant differences between the two treatments ($p < 0.05$).

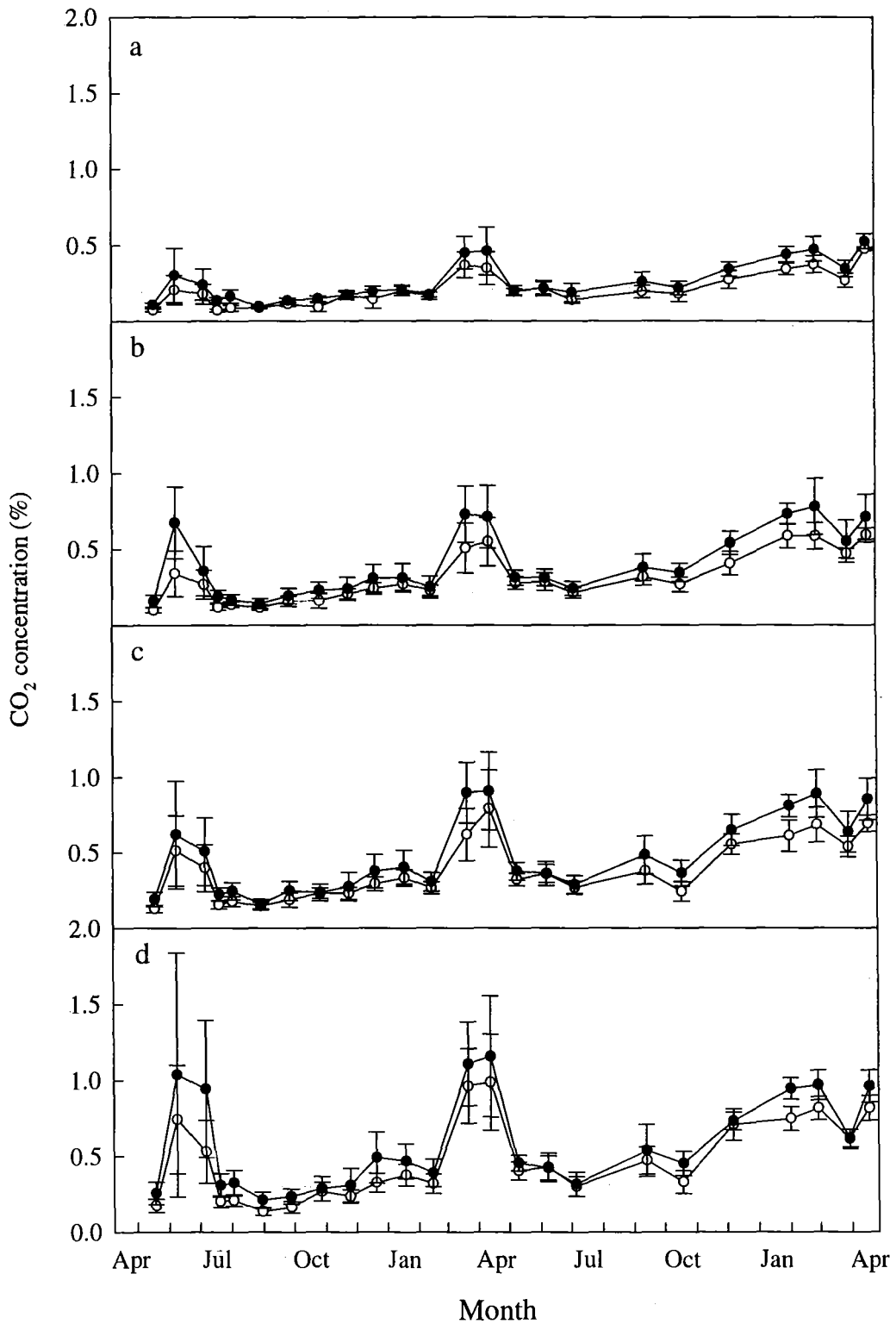


Figure 4-3 Soil CO₂ concentrations (% by volume) measured beneath *Pinus radiata* tree stems at depths of (a) 0.1, (b) 0.2, (c) 0.3 and (d) 0.5 m. Trees were grown at ambient (○) and elevated (●) CO₂ concentrations. Data are means of four measurements \pm standard error.

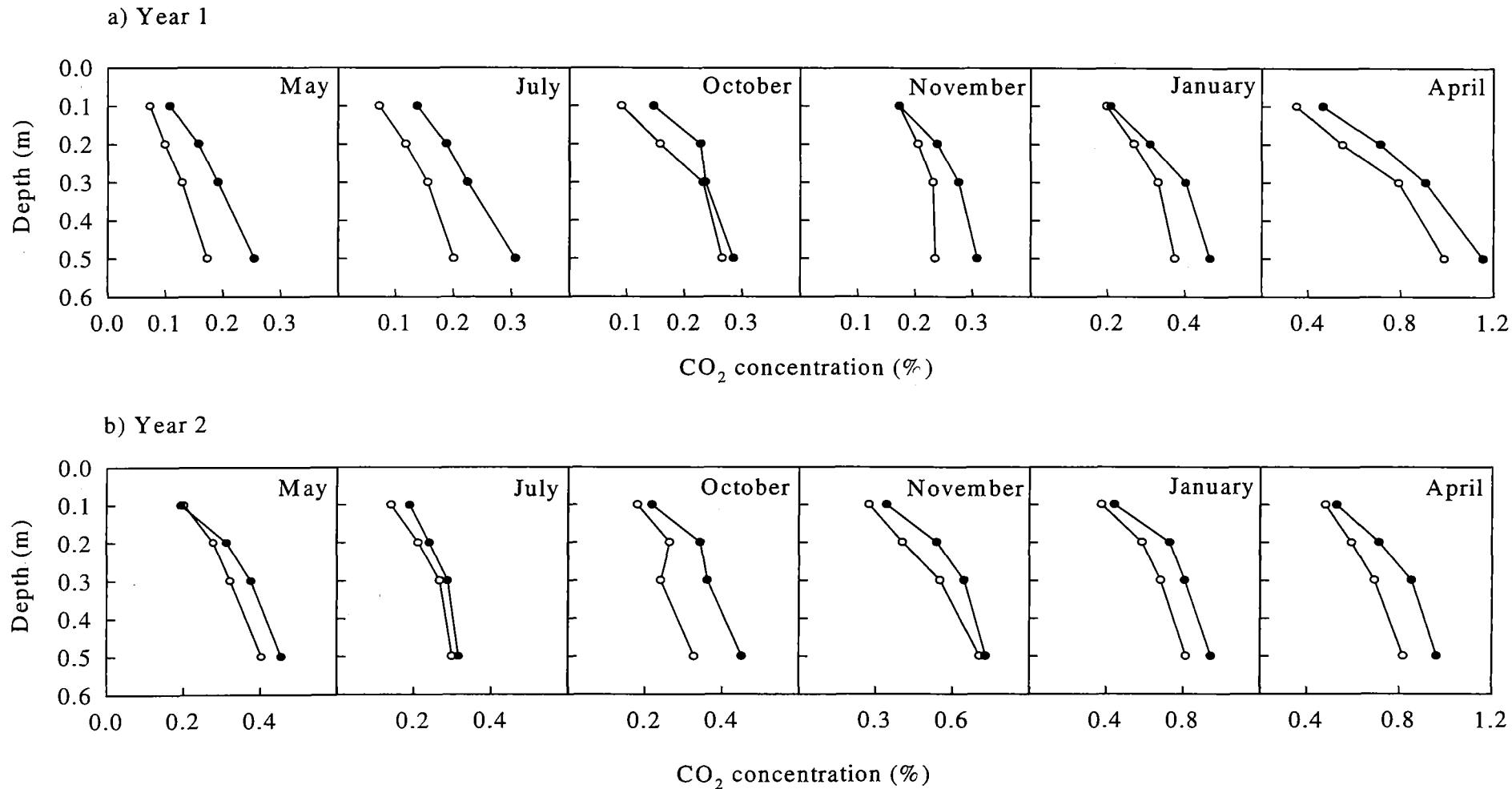


Figure 4-4 Seasonal soil CO₂ concentration profiles with depth beneath the stem of *Pinus radiata* trees for two years after the trees were planted. Trees were grown at ambient (O) and elevated (●) CO₂ concentrations. Data are means of four measurements \pm standard error.

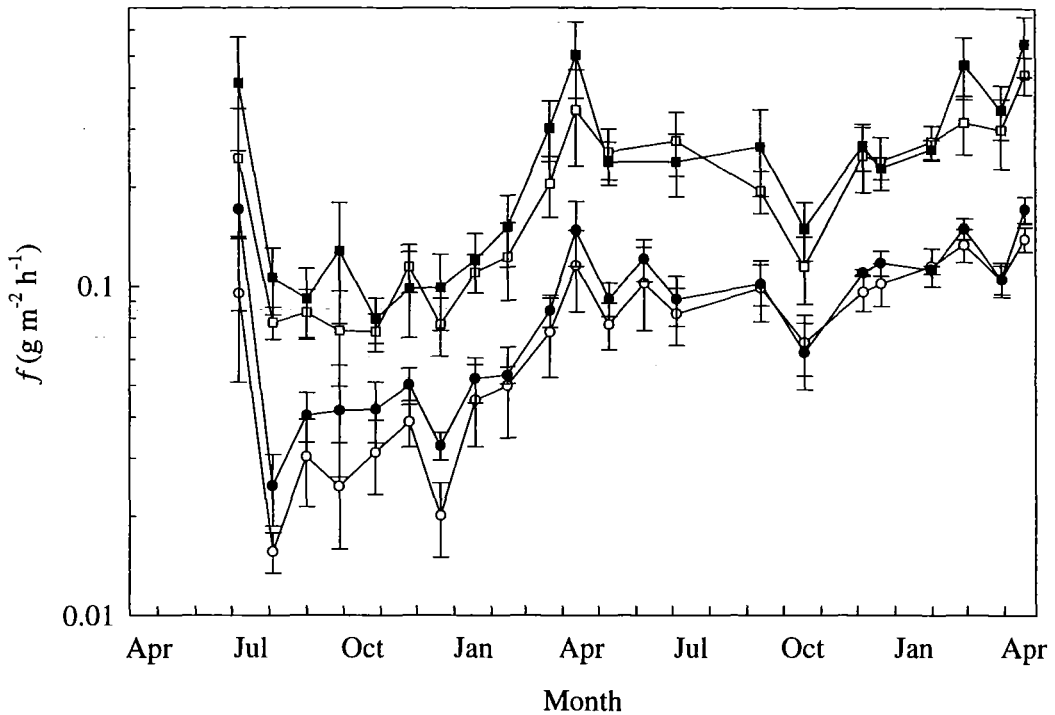


Figure 4-5 Seasonal changes in soil surface $\text{CO}_2\text{-C}$ efflux measured at a distance of 0.35 m from the tree stems (\circ , \bullet) and modelled at the stem ($r = 0$ m, \square , \blacksquare). Fluxes have been normalised to a soil temperature of 15 °C. The trees were grown at ambient (open symbols) and elevated (closed symbols) CO_2 concentration. Data are means of four measurements \pm standard error.

There was a strong positive, approximately linear, relationship between stem basal diameter and cumulative f_0 for the measurement period between August 1994 and April 1996 (Figure 4-6b). Similarly there was a strong positive relationship between P_t and cumulative f_0 (Figure 4-6c) which over the two year period was approximately linear, but for each year displayed a regular seasonal oscillation. There were no significant differences between the treatments, with high variability of P_t and f_0 .

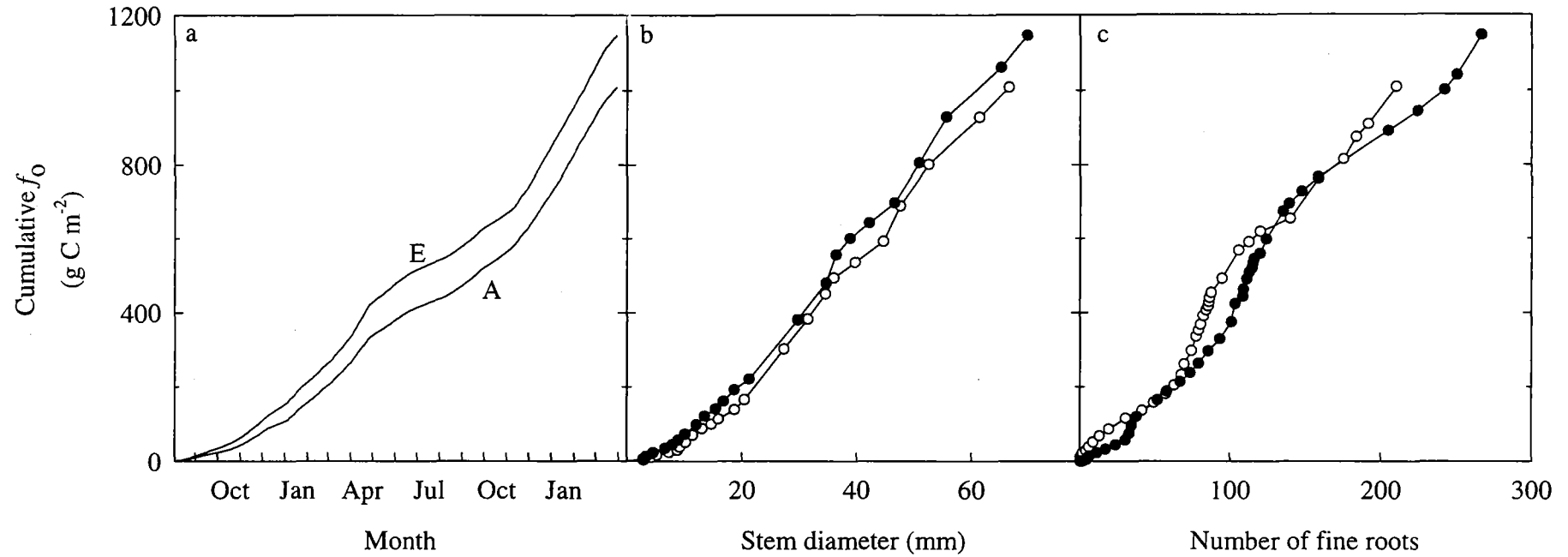


Figure 4-6 Cumulative f_0 measured at a distance of 0.35 m from *Pinus radiata* tree stems from August 1994 to April 1996 in relation to (a) time at ambient (A) and elevated (E) CO₂ concentration, and the increase in (b) stem basal diameter, and (c) cumulative root production at ambient (O) and elevated (●) CO₂ concentration. Data are means of four measurements.

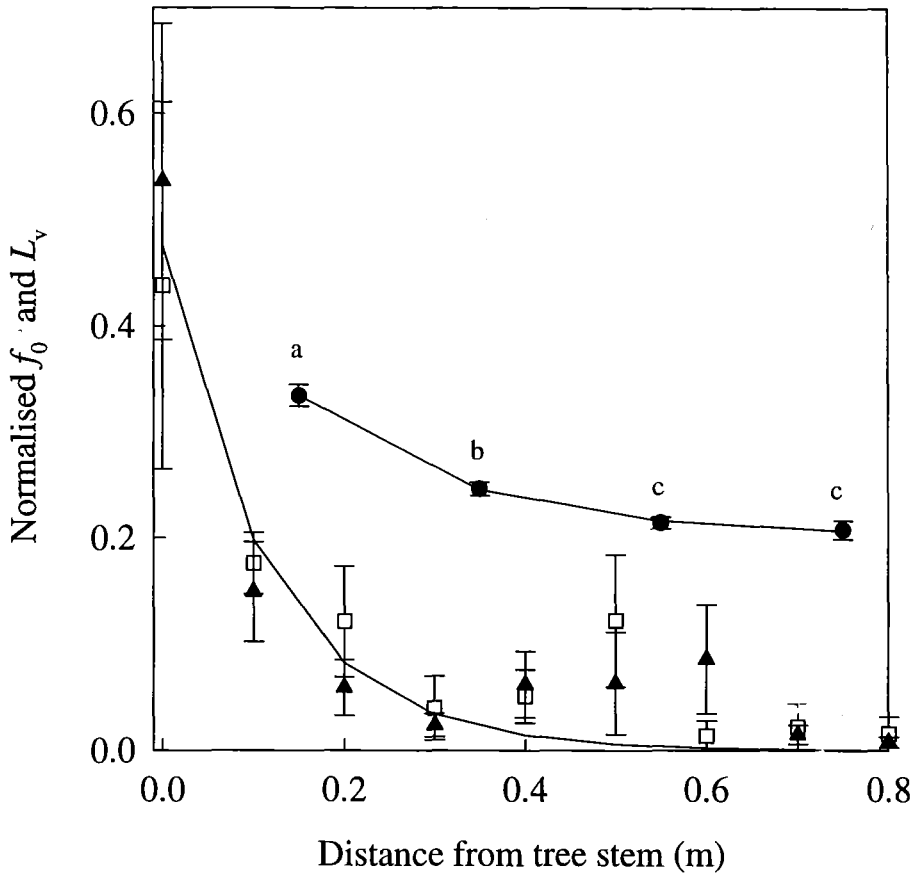


Figure 4-7 Changes in f_0 and L_v with distance (r) from *Pinus radiata* tree stems measured late-March and early-April 1996 (autumn), two years after planting. The values of f_0 (●) are data pooled from five plots. For each plot, paired measurements of f_0 were measured along transects for the four cardinal directions at $r = 0.15, 0.35, 0.55$ and 0.75 m. Data were normalised by dividing each measurement by the sum of measurements for each transect and are presented as the means (40 measurements) \pm standard error for each distance. The relationship between f and r was: $f = 0.27e^{-4.44r} + 0.19$ ($r^2 = 0.99$). L_v is data measured from minirhizotrons at 0.3 m beneath four trees growing at ambient CO_2 (□) and four trees growing at elevated CO_2 concentration (▲) at 0.1 m increments from the stem. Data were normalised by dividing the observed number of roots per 0.1 m increment by the total from each tube and are presented as means of four measurements \pm standard error for each treatment. The relationship between L_v and r , data pooled between treatments, was: $L_v = 0.48e^{-8.80r}$ ($r^2 = 0.89$). Significant differences ($p < 0.001$) in f_0 are denoted by change in letter.

Radial changes of soil surface flux density with distance from tree stems

At the end of the study f_0 was decreasing exponentially with increasing r (Figure 4-7). Data were pooled from both treatments from the four open-top chambers sampled. Comparison of normalised data for both treatments indicated there was no significant difference in the relationship between f_0 and r . When the data were pooled across the treatments the relationship was $f = 0.27e^{-4.44r} + 0.19$, ($r^2 = 0.99$). Comparison of data using paired t-tests at $r = 0.15, 0.35, 0.55$

and 0.75 m indicated that f_0 was significantly different ($p < 0.001$) between these distances, except between 0.55 and 0.75 m (Figure 4-7). Using this same relationship for both treatments, γ accounted for 58 % of f at $r = 0.15$ m, and 94 % at 0.75 m, after two years of growth. Including f_m (i.e. f at $r = 0$ m, estimated from Equation 4) and normalising the data in the same manner, then $f = 0.29e^{-8.64r} + 0.12$, ($r^2 = 0.99$). The ratio of γ to f , when $r = 0$ m, was 0.29 ± 0.025 . This ratio was assumed for the following calculations.

L_v , measured at the same time as the radial fluxes, likewise declined with increasing distance from the stem (Figure 4-7). There was no significant difference between the ambient and elevated CO_2 treatments so the data were pooled and normalised giving the relationship $L_v = 0.48e^{-8.80r}$ ($r^2 = 0.89$).

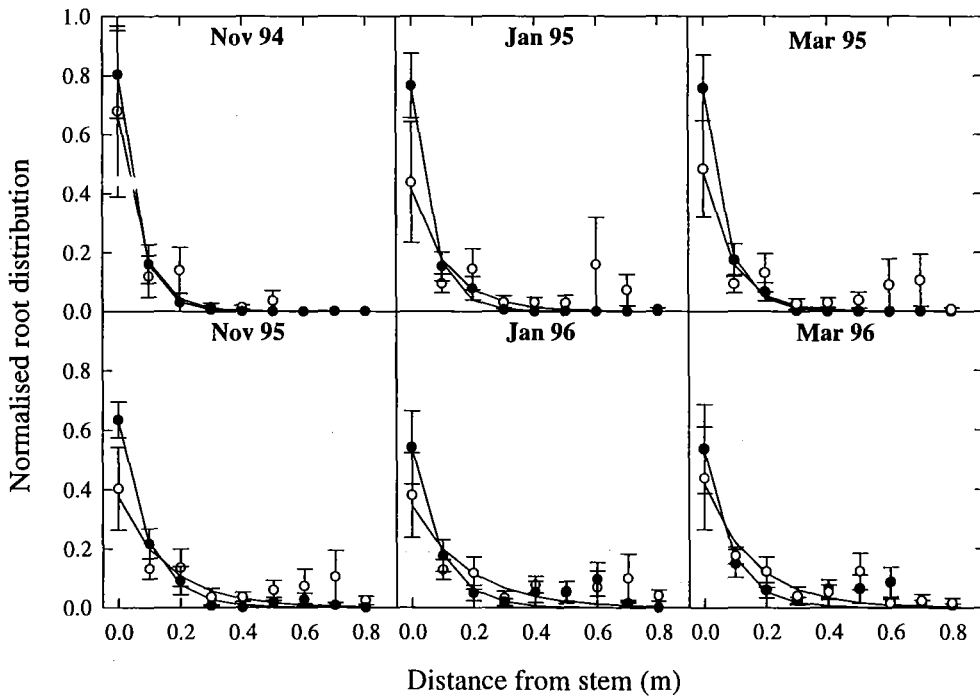


Figure 4-8 Seasonal change in the horizontal distribution of roots at 0.3 m measured using minirhizotrons. For each date, data were normalised by dividing the number of roots observed in each 0.1 m minirhizotron length increment by the sum of the total number of roots along the tube. Trees were grown at ambient (O) and elevated (●) CO_2 concentrations. Data are means of four measurements \pm standard error.

L_v increased with increasing tree basal area and as the root system expanded laterally (Thomas *et al.* 1997). Between November 1994 (spring) and March 1996 (autumn) the proportion of root length beneath the stem had declined 35 and 33 %, for trees grown at ambient and elevated CO_2 respectively (Figure 4-8). There were no significant treatment differences in the parameters L_v and R , (Equation 5). For the estimates of carbon fluxes (Equations 6 and 7) the value of R was calculated from data pooled across treatments (Table 4-1).

Table 4-1 Seasonal changes of parameters for exponentially declining fine root distribution with distance from the stems of *Pinus radiata* trees, where L_v is the fine root length density at $r = 0$ m and R is the length scale (Equation 5). Parameters (means \pm standard error) were estimated from the number of fine root roots per 0.1 m increment from the tree stem on minirhizotrons installed horizontally at 0.3 m depth. Data were normalised by dividing the number of fine roots per 0.1 m increment by the total for the length of the minirhizotron and have been pooled across ambient and elevated CO_2 treatments ($n = 8$).

| Date | L_v | R (m) | r^2 |
|----------------|-------------|-------------|-------|
| November 1994 | 0.73 (0.02) | 0.07 (0.01) | 0.99 |
| January 1995 | 0.57 (0.05) | 0.08 (0.02) | 0.94 |
| March 1995 | 0.60 (0.04) | 0.08 (0.01) | 0.96 |
| May 1995 | 0.59 (0.04) | 0.08 (0.01) | 0.97 |
| July 1995 | 0.60 (0.03) | 0.08 (0.01) | 0.98 |
| September 1995 | 0.57 (0.03) | 0.09 (0.01) | 0.98 |
| November 1995 | 0.51 (0.03) | 0.11 (0.02) | 0.96 |
| January 1996 | 0.44 (0.05) | 0.12 (0.03) | 0.88 |
| March 1996 | 0.42 (0.05) | 0.14 (0.03) | 0.87 |

Estimation of carbon flux from the soil-tree plots

It was assumed that as the values of R for both f (0.116 m) and L_v (0.114 m) were very similar after two years of growth then R estimated from L_v data would reasonably approximate the value of R from f data. For the second year after the trees were planted, the mean annual total F estimated to have been released at elevated CO_2 ($1895 \pm 290 \text{ g y}^{-1}$) was 13% greater than at ambient CO_2 concentration ($1671 \pm 277 \text{ g y}^{-1}$) (Figure 4-9). \bar{f} was estimated to be 589 ± 98 and $668 \pm 102 \text{ g m}^{-2} \text{ y}^{-1}$, for the ambient and elevated treatments respectively. Total annual flux density estimates from f_0 measurements made at $r = 0.35$ m for the same period, were approximately 23% greater: 745 ± 110 and $809 \pm 50 \text{ g m}^{-2} \text{ y}^{-1}$, for the ambient and elevated plots respectively (Figure 4-6a). In the first year of tree growth the difference was greater, between July 1994 and April 1995 there had been approximately 29% more carbon lost from the elevated CO_2 plots at $r = 0.35$ m (Figure 4-6a). These differences between treatments were not significant.

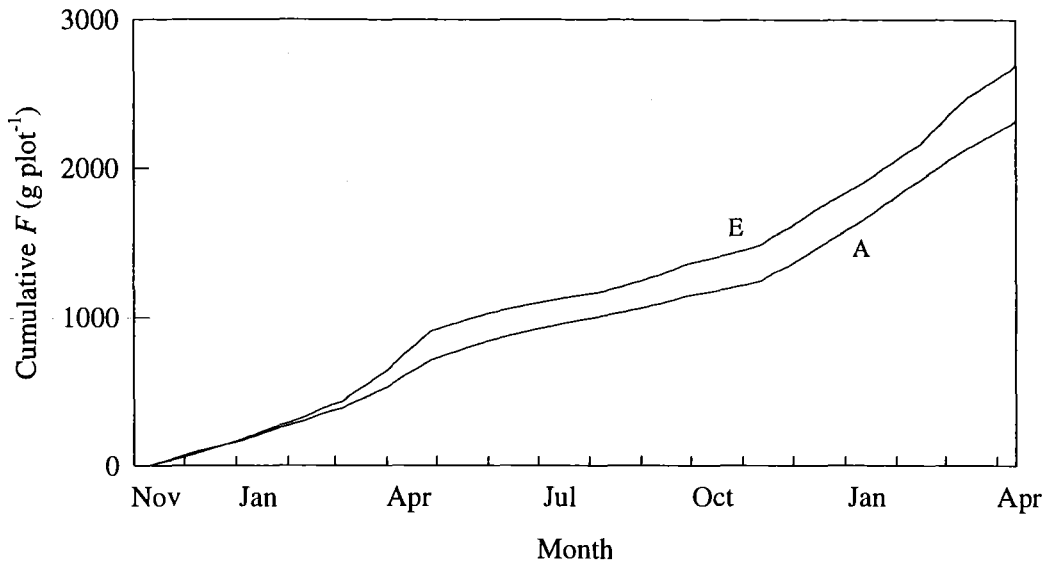


Figure 4-9 Cumulative soil surface carbon flux from plots (F) with *Pinus radiata* trees growing at ambient (A) and elevated CO_2 concentration (E). Data are means of four measurements.

Discussion

Estimated F was greater at elevated CO_2 concentration than at ambient CO_2 concentration. In the first year there was approximately 23% more carbon efflux from soil with trees growing at elevated than at ambient CO_2 concentration. In the second year this difference was reduced (Table 4-2). However, despite the carbon fluxes at the soil surface being consistently greater at elevated CO_2 there were no significant differences between treatments in both years. A similar decline in the rates of fine root production between the two years was observed by Thomas *et al.* (1997).

Table 4-2 Changes of measured f_o at $r = 0.35$ m, F and P_t between the first and second years after trees were planted. Enhancements were not statistically significant ($p > 0.1$).

| | Enhancement at elevated CO_2 concentration (%) | |
|-----------------------|---|-------------------------|
| | Year 1 (July to March) | Year 2 (April to March) |
| f_o ($r = 0.35$ m) | 30 | 9 |
| F (or \bar{f}) | 23 | 13 |
| P_t | 41 | 33 |

The larger decrease in the ratio of f_o to F between the first and second year at elevated CO_2 concentration may be partly attributed to the reducing proportion of fine root biomass at $r = 0.35$ m (see Figure 4-8 and Thomas *et al.* 1996). Throughout the study there was a higher concentration of fine roots close to the tree stem, but as the tree basal area increased more roots were observed further from the tree stems in the horizontal and vertical directions, thus allowing greater exploitation of the soil volume (Figure 4-8 and Table 4-1). This was largely a response to above-ground demand for nutrients and water. After two years, the estimated f_o , measured at $r = 0.35$ m, was higher than the plot averages by 21% for the ambient treatment and by 26% in the elevated treatment. As the root systems expanded radially then the position of the average plot flux density would have also increased radially from the stem.

There are few reported soil surface carbon flux density data for tree-soil systems at elevated CO_2 concentration. In a 3 year study of *Pinus ponderosa* growing in open-top chambers, fluxes were an average of 35% greater at elevated than ambient CO_2 concentration (Vose *et al.* 1997). They estimated the carbon flux during the growing season to be 235 g m^{-2} for the ambient treatment and 319 g m^{-2} for the elevated treatment based on measurements made over three periods. In another study, f_o increased by 22 to 102% in open-top chambers with *Pinus sylvestris* saplings growing at elevated CO_2 concentration compared with trees growing in chambers at ambient CO_2 (Pajari 1995).

Our estimates are comparable with f measurements for fertilised 31-year-old *Pinus resinosa* (red pine) ranging between 451 and $696 \text{ g m}^{-2} \text{ y}^{-1}$ (Haynes & Gower 1995) and for 9-year-old *Pinus elliottii* (slash pine) of $820 \text{ g m}^{-2} \text{ y}^{-1}$ (Ewel *et al.* 1987). In both these studies, estimates were from soda-lime static chamber measurements which were then adjusted to measurements made using dynamic chamber systems with portable gas analysers. Our estimates are much greater than the $371 \text{ g C m}^{-2} \text{ y}^{-1}$ for a mixed hardwood forest based on soda lime measurements (Bowden *et al.* 1993). Studies have shown that estimates made from dynamic chamber measurements should be more accurate than those made from static chamber - alkali absorption measurements which often underestimate f particularly when the flux rates are high (Cropper *et al.* 1985; Haynes & Gower 1995; Jensen *et al.* 1996).

The strong seasonal temperature effect was evident for measurements of both f_o and soil CO_2 concentrations (Figures 4-6a and 4-3). This can be related to the strong influence that soil temperature has on the fine root production of these trees (Thomas *et al.* 1997), and seasonal increases in the carbon fluxes were closely related to the increase in root production and biomass (Figure 4-6c). Fine root and stem production continued throughout the year but rates were lowest over the winter period (Thomas *et al.* 1997). In addition, the flux measurements could also be shown to increase approximately linearly with stem production (Figure 4-6b) which also continued throughout the year with lowest rates of increase over the winter. We found that the use of an Arrhenius-type model (Lloyd & Taylor 1994) was appropriate to predict the soil surface

carbon flux density. Changes in f_0 were largely explained by changes in temperature at a depth of 0.05 m. Most methods of estimating the seasonal f from plots with trees do not take account of the effect of changing temperature, and often assume that f_0 measurements, often made over a relatively short period, are representative of the seasonal average.

While soil temperature explained the seasonal variability for most of the study period, f and C were high in the autumn (March and April) of both growing seasons. This was noted by Thomas *et al.* (1996) for the first year and may be a result of increased root sink activity. However, this was not reflected by an increase in fine root production (Thomas *et al.* 1997). Another explanation may be related to the increased sink strength of the mycorrhizal symbiont. It has been demonstrated that ectomycorrhizal fungi are a large photosynthate sink (Söderström & Read 1987) and that they may increase photosynthetic rates (Dosskey *et al.* 1990; Rousseau & Reid 1990). We hypothesise that some of the autumn increase in carbon fluxes was related to an increased mycorrhizal demand for carbon for the late-summer - autumn growth of fungal mycelium and epigeous fruiting bodies (Smith & Read 1997). Large initial soil CO_2 concentrations and fluxes in the first winter (June and July 1994; Figures 4-3 and 4-5) were possibly related to increased below-ground carbon allocation and use related to an establishment stage of rapid root growth after the trees were planted. The first root growth was observed at 0.3 m in July at elevated CO_2 concentration (Thomas *et al.* 1996). The addition of a carbon (and nutrient) source of forest floor litter, to encourage the mycorrhizal infection of roots, may have stimulated growth of the microbial biomass in a soil system that was previously carbon limited.

Soil CO_2 concentrations were consistently higher at all the depths measured in the elevated CO_2 plots, this is consistent with greater root length density. Invariably, the soil CO_2 concentrations increased with depth. At a depth of 0.5 m concentrations were up to 35 times greater than above the surface concentrations in the elevated treatment. The maximum concentrations would have occurred deeper than 0.5 m. Root respiration and rhizodeposition would have occurred to 1.4 - 1.5 m, the depth to which fine roots were observed (Thomas *et al.* 1997). Reported maximum soil CO_2 concentrations range between 0.04 and 13% (Amundson & Davidson 1990). Seasonal changes in the depth to which soil respiration occurs and relative surface activity (i.e. model parameters L and n) are also consistent with changes in root activity (see Cook *et al.* 1997).

Both f_0 and L_v declined exponentially with distance from the tree stem. The very similar distribution patterns (i.e. similar values of R) indicate that root and rhizosphere respiration were a significant contribution to f . Similar findings have been reported by Ben-Asher *et al.* (1994a) for *Prunus amygdalus* (almond). They also used a regression model to estimate the depth of the root zone. As there was a significant decline in f with increasing distance from the stem it was appropriate that a model that described the distribution of f_0 should be used to estimate both \bar{f} and F . Low L_v and f_0 at a distance of 0.8 m from the tree stems (Figure 4-7) suggests that the

contribution of fine roots to f towards the outer limits of the plot was low. It also indicates that the use of the approximate plot radius of 0.95 m for estimates of F and \bar{f} was reasonable.

The radial decline in f with distance from the tree stems indicates the importance of the chamber measurement position for the estimation of f . Our measurements were made at a fixed radial distance (0.35 m) from the tree stems. In the second year this would have overestimated \bar{f} by approximately 23%. The trees in this study were grown in a soil with low soil carbon concentrations and there was no litter layer. In most forest ecosystems there would be considerably more soil organic carbon and surface litter, which would result in a greater contribution of microbial respiration from the decomposition of this carbon source. A likely consequence of this will be that the relationship between the radial fine root distribution of the trees and f would not be as strong as found in this study. However, since significantly higher rates of f were observed close to the tree stems, where there was the greatest concentration of fine roots, then this should be considered when developing sampling procedures to estimate the soil surface carbon fluxes from plots with individual trees, or from forest floors.

Conclusions

There was increased carbon lost from the soil surface in the plots with trees growing at elevated CO_2 concentration. This was closely related to increased root production and biomass. However, it remains uncertain whether the rate of carbon loss per unit of fine root length or mass was greater at elevated CO_2 . Soil temperature explained most of the seasonal variation in surface carbon loss. However, high carbon losses in autumn, less well explained, may be the consequence of increased mycorrhizal sink strength. Methods of seasonal estimation of carbon efflux from the soil surface should consider the effect of changing soil temperature.

Carbon loss significantly decreased with increasing distance from the tree stem. This was related to the pattern of fine root distribution; as the fine roots were the main source of carbon for f . This has important implications for using measurements of f to estimate the carbon flux from plots with tree root systems, especially in young stands with low initial soil organic matter, which is likely to limit microbial respiration.

CHAPTER 5

SYNTHESIS AND DISCUSSION

Studies of tree growth at elevated CO₂ concentrations have shown that biomass is likely to be increased and that more carbon will be allocated below-ground (Ceulemans & Mousseau 1994). However, there are relatively few studies that have investigated the below-ground carbon fluxes for trees growing at elevated CO₂ concentration. In this thesis, the two major below-ground carbon fluxes were investigated for *Pinus radiata* trees over a relatively long time period (two-years) compared with other reported studies.

Most of the below-ground carbon is allocated to fine roots. Carbon may then be lost from fine roots by several processes including respiration (root and mycorrhizal), turnover and exudation. Measurements made of CO₂-carbon efflux at the soil surface (f) are the sum of root and mycorrhizal respiration, and microbial respiration. The main source of carbon in the latter case is the fine root system. In most ecosystems above-ground litter deposition and the decomposition of soil carbon from organic pools with long-residence times are also sources of microbial carbon (Landsberg & Gower 1997). However, in this study, the site was selected so that the soil carbon content was very low (0.1%), therefore only likely to have a minimal effect on carbon efflux estimates (Figure 4-2). Also, there was no above-ground litter addition from the young trees during the study period. Therefore, reasonable estimates of f could be made.

Pinus radiata above-ground and below-ground production was increased at elevated CO₂ concentration. Stem basal areas were greater at elevated CO₂ concentration, from the end of the first year of growth; these trees had been significantly smaller when they were planted than those that had been grown at ambient CO₂ concentration (Chapter 3). Below-ground carbon allocation to fine roots (Chapters 2 and 3) and also the total carbon efflux from the tree-soil system (Chapters 2 and 4) was always greater. The relative enhancements after two years were similar at elevated CO₂ concentration: stem basal area was 13 % greater; total root production was 36% greater; and, estimated carbon efflux, based on measurements (f_0) at 0.35 m distance from each tree, was 29 % greater at elevated CO₂ concentration than at ambient CO₂ concentration.

However, there were seasonal differences in the carbon fluxes between trees growing at the two CO₂ concentrations. There was earlier, rapid root growth in the first year for the trees growing at elevated CO₂ concentration (Figure 2-4 and Figures 3-2 and 3-6), the rate of stem growth was much greater (Figure 3-3) and soil surface carbon efflux was also much greater in the first year (Table 4-2). These rates of increase were not maintained in the second year. However, the absolute rates of stem production, fine root production and soil surface carbon

efflux remained greater. By the beginning of the second year there was no apparent difference in the timing of root production between the two treatments.

The reduction in growth rates suggests that acclimation of growth at the elevated CO₂ concentration may be occurring, although, after two years, rates were still greater at elevated CO₂ concentration. Similar changes in growth rates were observed for *Pinus taeda* for a four year period (Tissue *et al.* 1997). If acclimation does occur it is unlikely that the absolute production gained during the early years of growth will be lost. In terms of commercial tree production cycles may be reduced as trees come to maturity earlier at elevated CO₂ concentration.

This is one of the few studies of trees growing at elevated CO₂ concentration that has investigated the effects on fine root turnover. Fine root longevity was significantly reduced at elevated CO₂ concentration. This may have important implications if the rates of turnover are maintained, potentially leading to increased soil carbon. However, this will also be dependent on the nature of any environmental feedback that may result from additional carbon inputs.

It is apparent from this investigation that more than one growth season is required for studies of tree growth at elevated CO₂ concentration. Particularly for young *Pinus radiata* trees growing in a well-watered and nutrient-unlimited system which had fine root life-spans greater than most other tree species that have been recorded, and root loss only occurred after 1 year. Similarly, Berntson & Bazzaz (1996a; 1997) only observed significant decreases of *Betula papyrifera* fine root longevity after the first year of growth. For another coniferous species (*Pinus ponderosa*), root longevity was increased at elevated CO₂ concentration, however, total root loss was still greater as the fine root biomass was larger (Tingey *et al.* 1997). Similar species-dependent responses have also been observed for other plants (Fitter *et al.* 1996). Therefore, longer-term investigations, or studies during later growth stages, are required to determine whether tree fine root turnover rates will remain greater or whether acclimation occurs after some period. There are practical difficulties associated with studies of large trees. There are major physical and cost considerations of exposing trees to elevated CO₂ concentrations. However, long-term exposure of older trees to elevated CO₂ concentrations from naturally occurring CO₂ springs (Hättenschwiler *et al.* 1997) may also offer opportunities for investigation of below-ground carbon processes for those tree-soil systems.

While the findings of this investigation will be important for determining and modelling the whole-tree carbon balances for young *Pinus radiata* tree responses at elevated CO₂ under favourable conditions, further information is required for longer-term or larger-scale predictions. The responses of ecosystems at elevated CO₂ are less certain due to the complex nature of soil-plant interactions and the level of understanding of key mechanisms that regulate carbon allocation. For example, there is only limited understanding of the mechanisms that determine the amount of carbon allocated to tree parts (Landsberg & Waring 1997), the control

of root life-span (Eissenstat & Yanai 1997), and the nature of feedbacks at elevated CO₂ concentration (Berntson & Bazzaz 1996b). Allocation patterns change as trees age (Gower *et al.* 1996; Ryan *et al.* 1997). It has been shown that nitrogen has a major effect on tree allocation (Beets & Whitehead 1996) and fine root turnover (Keyes & Grier 1981; Axelsson & Axelsson 1986). However, the direction of below-ground feedbacks at elevated CO₂ concentration is difficult to predict because of the often complex interactions between the soil carbon and nitrogen cycles. Perhaps it is not surprising that, to date, most carbon balance models have tended to inadequately treat the soil as a black box (Norby 1997). Evidently, greater effort is required to understand below-ground processes before ecosystem responses may be reliably modelled.

Perhaps the greatest reason for having such a limited understanding of below-ground carbon processes, especially compared with above-ground processes, is the difficulty of making measurements of the carbon pools and fluxes. However, recent technological development and improvements in measurement techniques should increase our ability to understand these processes; for instance, the minirhizotron system which has been recommended to study the carbon dynamics related to fine roots in elevated CO₂ concentration studies (Curtis *et al.* 1994a).

In this study, the minirhizotron system proved to be an effective measurement tool. In terms of the seasonal carbon allocation, patterns of fine root production were clearly shown, carbon loss from the root system was indicated by fine root loss, and the rate of root turnover indicated by root longevity. The horizontal installation of minirhizotrons increased the number of roots sampled at each depth making it easier to discriminate and show differences in growth patterns between the depths. It was also an effective means of showing the horizontal distribution of roots in relation to the tree stems. The characteristic shape of this distribution was then used to estimate the total carbon flux from the tree-soil system (Chapter 4). By using measurements at each depth, it was also possible to predict the vertical distribution of roots using an appropriate model for this tree-soil system.

A criticism of the minirhizotron technique has been the difficulty of estimating biomass from observations (e.g. Majdi *et al.* 1992). In this study, measurements of roots immediately adjacent to minirhizotron tubes were used to estimate root length density (L_v) and root carbon density using relationships established between minirhizotrons and the bulk soil (Figure 2-2). There was relatively large variability in the distribution of fine roots recorded beneath the trees, at both CO₂ concentrations (Figure 2-3 and Figure 4-7). Therefore, it would seem appropriate that L_v measurements from the bulk soil are made close to the position of the roots observed on minirhizotrons. This is likely to be even more important for a species such as *Pinus radiata* that has inherently low L_v (Nambiar 1983). As soil moisture and fertility were controlled and the soil was uniformly packed around the minirhizotron tubes prior to tree planting, then a

reasonable relationship between the minirhizotron observations and soil measurements was established.

The nature of the Forest Ecosystems Project, involving the field investigation of responses of rapidly growing trees for several years at approximately twice the ambient CO₂ concentration, meant that there were certain practical limitations. A consequence of this was the limited number of trees growing in open-top chambers that could be studied, four in each of the CO₂ concentration treatments. A number of steps were taken to reduce the variability of responses not related to the two treatments. To remove genetic variability between trees, clonal propagation techniques were used to produce trees of genetically identical material (Davies *et al.* 1992). Minirhizotrons and gas sampling chambers were installed prior to the trees being planted, eliminating installation disturbance effects on the root systems. The soil was carefully and uniformly re-packed. As the soil was a sand without structure, re-packing had not changed its physical properties. The selection of the site for its low initial carbon content has already been noted. Non-destructive measurements were made, firstly because of the need to study seasonal changes but also because of the low number of study trees, which would out-live the life of this particular study. Regular addition of a balanced fertiliser also removed the influence of soil fertility (predominantly nitrogen availability) which may affect plant responses at elevated CO₂ (Stulen & den Hertog 1993) to treatment effects.

There were large seasonal responses of fine root production and soil surface carbon efflux and soil temperature was the main seasonal environmental variable that accounted for these responses. Maintaining soil moisture at approximately constant values by irrigation during the study eliminated the potential for water-limiting responses of both root production and loss, and soil respiration. This allowed the use of temperature-based models to aid interpretation of the seasonal fine root (Chapter 3) and soil surface carbon efflux (Chapter 4) measurements. Not all the seasonal effects could be attributed to temperature. Initial early, rapid root growth at elevated CO₂ (Figure 2-4 and Figure 3-6) was hypothesised to be an ontogenetic response related to a greater supply of carbohydrate from source leaves, while the high late summer and autumn *f* was possibly a function of increased sink strength and may have been partly related to mycorrhizal growth.

While the use of horizontal minirhizotrons to measure the seasonal and depth responses of fine roots is likely to have been more successful than using angled or vertical tubes there was still considerable within treatment variability. Large spatial variability is a common problem in root studies. Calculations of the required number of minirhizotrons to give accurate estimates of root length are often unrealistic (e.g. Steele *et al.* 1997). The low number of treatment replicates and high within treatment variability meant that treatment differences in absolute fine root production or loss were not significant. However, the minirhizotron technique was clearly a powerful tool for determining the effect of the CO₂ concentrations on root longevity (Chapter

3). The data were also able to show a shift in the vertical distribution of fine roots after 2 years (Chapter 3).

Based on the results from this thesis, and from studies that have been cited, there is clearly a need for much more extensive investigation of components of the below-ground carbon balance and the mechanisms that control the fluxes between them. It is necessary to distinguish between, and estimate, the individual below-ground carbon fluxes and pools. For example, root and heterotrophic (mycorrhizal and microbial) respiration need to be separated, and this will require new or improved techniques. The importance of root exudation should be quantified. It is assumed to be small, but has been found to be greater at elevated CO₂ (e.g. Norby *et al.* 1987). The development of carbon isotopic composition methods (e.g. Paterson *et al.* 1996) may help distinguish between sources of below-ground respiration. A better understanding of the nature of feedback processes is required, particularly the effects of resource availability, especially nitrogen which is known to have a significant impact on carbon allocation and cycling (e.g. root and above-ground litter decomposition).

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APPENDIX

A MODEL OF ONE-DIMENSIONAL STEADY-STATE CARBON DIOXIDE DIFFUSION FROM SOIL*

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Abstract

An analytical model is developed for one-dimensional, steady-state diffusion of carbon dioxide (CO₂) from soil with vertical decrease of the source term described by a power function and a constant diffusion coefficient. The surface flux density of CO₂ from the soil (f_m) is derived from integration of the source term with depth. The model was tested using two years of monthly measurements of the soil CO₂ concentration profile in a sand containing a *Pinus radiata* D. Don tree. Modelled surface flux density (f_m) at the base of the tree was consistently greater than surface flux density (f_o) measured 0.35 m away with an average ratio of f_m to f_o of 2.5 ($R^2 = 0.83$). This was explained by decreasing root length density (L_v) with radial distance from the tree stem. An exponential function for decrease of L_v and the surface flux density of CO₂ with increasing radial distance from the tree stem and an analytical expression of the total CO₂ flux from the soil around a growing tree root system were derived. Length scales for both the decrease in root length density and CO₂ flux with radial distance were similar. An expression to estimate the radial distance from the tree stem that gives an average plot value of CO₂ surface flux density was also derived.

Keywords Roots, carbon dioxide flux, diffusion, soil respiration.

1. Introduction

The soil as a source or sink in the carbon budget is important for many reasons, including the contemporary spectre of possible feedback effects on global climate (Raich and Schlesinger, 1992; Kirschbaum, 1995). The need to quantify soil fluxes in global carbon budgets, and an aim to further understand the regulation of soil fluxes by environmental variables (e.g., by soil water; Orchard and Cook, 1983; Cook *et al.*, 1984), has led to the development of models. One type of model is phenomenological, and is empirically based on statistical analyses of environmental and flux measurements for modal soils (e.g., Howard and Howard, 1993). Other models are based on the processes involved that may include the concurrent transport of water and heat (Simunek and Suarez, 1993; Suarez and Simunek, 1993; Jensen *et al.*, 1996). Phenomenological models may sometimes provide better predictions of fluxes, but they are limited in their application to a range of sites. Process-based models may be deployed across all sites and, as in this study, they can also be used diagnostically to elucidate different regulating variables.

The transport of gases into or out of soil is mainly by diffusion (Glinski and Stepniewski, 1985) in response to a sink or source within the soil. For CO₂ diffusion out of unsaturated soil, the source is the respiration of micro-organisms and plant roots, collectively known as the soil respiration. The environmental factors that control this production of CO₂ and the processes by which the gas moves through soil are reviewed by Amundson and Davidson (1990). The source strength or respiration rate usually varies with depth and a power function has often been used to describe it mathematically (Romell, 1922 (cited in Glinski and Stepniewski, 1985); Wesseling, 1962). Combining this vertical function with a solution of the diffusion equation gives a one-dimensional, steady-state model of soil gas transport. A purpose of this paper is to propose an alternative form of the power function. A model is then tested using a set of field data where air and soil CO₂ concentrations at four depths, and the surface CO₂ flux density (f_o), were measured contemporaneously. The measurements were made on a monthly basis over a two year period in an irrigated sand at a site where a *Pinus radiata* D. Don tree was planted at the start. This allowed us to quantify the effects of a growing root system on spatial and temporal variation in f_o . In discussing these results, analytical theory is developed for the scaling of small chamber f_o measurements up to CO₂ flux from field plots containing trees and for estimating the location of the plot's average value of surface CO₂ flux density.

2. Material and Methods

2.1 Soil CO₂ Diffusion Model

The steady-state transport of CO₂ out of soil can be described by the one-dimensional diffusion equation:

$$\frac{d(DdC/dz)}{dz} = -q \quad (1)$$

where D is the diffusion coefficient of CO₂ in the gas-filled pore space (m² s⁻¹), z is depth (m), C is the concentration of the gas in the gas-filled pore space (kg m⁻³) and $q(z)$ (kg m⁻³ s⁻¹) is the source term that may be equated with the soil respiration rate. In order to solve eqn (1), the respiration rate as a function of depth must be defined, and this has often been done with a function of the form:

$$q(z) = Q[1 - (z/L)^k] \quad (2)$$

where Q is the surface soil respiration rate (kg m⁻³ s⁻¹), L is the depth to which respiration occurs (m) and k is a dimensionless attenuation coefficient. Generally, in a soil with growing plants, L may be interpreted as the depth of respiring roots, while k determines the shape of the respiration rate profile with soil depth. This function was first used for soil gas transport by Romell, 1922 (cited in Glinski and Stepniewski, 1985) with $k = 1$ and later by Wesseling (1962) for CO₂ transport with $k = 0.25$.

Alternatively, we propose a similar function for $q(z)$:

$$q(z) = Q g_T g_\theta (1 - z/L)^n \quad (3)$$

where n is a coefficient analogous to k , g_T is the relationship between soil respiration and temperature and g_θ is the relationship between soil respiration and water content (θ , m³ m⁻³). The relationship between soil respiration rate and temperature (g_T) used was that derived by Lloyd and Taylor (1994) which is based on kinetic theory and is:

$$g_T = \exp\left[\frac{-E_o}{T - T_o}\right] \quad (4)$$

where E_o is a constant (308.6 °K) analogous to activation energy, T is temperature (°K) and T_o is a base temperature (227.1 °K). The additional effect of θ on respiration rate (Orchard and Cook, 1983; Cook *et al.*, 1984; Linn and Doran, 1984) was not taken into account in this study because

the soil was maintained at constant θ by regular irrigation, but it could be incorporated into the model. When eqn (3) is substituted into eqn (1) the resulting equation can be subject to the following boundary conditions:

$$\begin{aligned} z = 0, \quad C = C_o, \quad q = Q g_T \\ z = L, \quad D \frac{dC}{dz} = 0, \quad q = 0 \end{aligned} \quad (5)$$

and solved for C to give:

$$C(z) = C_o + \frac{Q g_T L^2}{D(n+1)(n+2)} \left[1 - \left(1 - z/L \right)^{n+2} \right] \quad (6)$$

where C_o is the soil surface atmosphere concentration of CO_2 . In eqn (6) Q now incorporates a constant value of g_θ , as the effect of soil water content variation on q has not been included and assumes that D is invariant with depth. If D is not constant with depth, but may be considered invariant over some incremental depth, using eqns (3) and (5), eqn (1) may still be solved in a piece-wise manner following Cook (1995).

The value of D is a function of both temperature (T), water content and soil porosity (p). The temperature ($^\circ\text{K}$), dependency was estimated following De Jong and Schappert (1972) and the relationship with water content and soil porosity ($\text{m}^3 \text{m}^{-3}$) from Sallam *et al.* (1984) to give:

$$D(\theta) = D_a \frac{(p - \theta)^{3.1}}{p^2} \quad (7)$$

where D_a is the diffusion coefficient for CO_2 in air ($\text{m}^2 \text{s}^{-1}$) at $273 \text{ }^\circ\text{K}$.

For a constant D , eqn (6) may be differentiated with respect to depth and evaluated at $z = 0$ to give an expression for the CO_2 flux density from the soil to the atmosphere (f_m) as:

$$f_m = \frac{Q g_T L}{n+1} \quad (8)$$

It is also apparent that f_m is dependent on T . The soil temperature at a depth of 0.05 m, measured at the time gas samples were extracted (Thomas *et al.*, 1996) was used in eqns (4) and (7) to determine g_T and D respectively. This value of g_T , the ambient CO_2 concentration in the chamber (C_o), and the measured soil CO_2 concentration profile were then fitted to eqn (6) using the SIMPLEX algorithm (Careci and Cacheris, 1984). The values of the parameters Q , L and n derived from the fitting process were then inserted into eqn (8) along with the value of g_T in order

to estimate f_m . These modelled values of surface CO₂ flux density (f_m) were compared with measured values of surface flux density (f_n) made at 0.35 m from the base of the tree.

2.2 Measurements

Measurements were made at a flat site at Bromley, Christchurch, New Zealand (43° 32' S, 172° 42' E, 9 m above sea level; Thomas *et al.* 1996). Average annual air temperature is 12.2 °C, with a range of average daily temperature from 2.8 to 21.4 °C, and average annual rainfall is 620 mm.

The soil is a recently stabilised, weakly-developed dune sand classed as a Typic Ustipsamments Sandy Mixed Mesic (Soil Survey Staff, 1990). Throughout the study, no water-table was recorded at the site within 1.2 m of the soil surface. The plot was within a large open-top chamber that was 4.7 m in diameter and 4.2 m in height. Ambient air was supplied to the chamber by a large fan, providing two air exchanges per minute. This was sufficient to maintain temperature and humidity within the chamber close to ambient conditions (Whitehead *et al.* 1995). The root system of one tree was isolated from other trees not being studied by digging and burying rigid plastic sheets 1.2 m deep into the soil to isolate a sector of the chamber. This gave an approximately triangular shaped plot with an area 2.9 m². When the plot was established in March 1994, all vegetation and surface organic matter was removed. The total carbon content of the soil was 1.1 mg g⁻¹.

In April 1994, a *P. radiata* tree was planted in the centre of the plot. The roots were inoculated with mycorrhizae by including a small quantity of litter from an adjacent forest in the planting hole. Irrigation was supplied each night or as required to maintain the sand near field capacity throughout the year. Soil water content was measured regularly using the time domain reflectometry method (model TRASE, Soil Moisture Equipment Corporation, Santa Barbara, CA, USA).

2.3 Modelled $f(f_m)$

The air (i.e., soil surface) and soil CO₂ concentration were measured at monthly intervals from July 1994 through April 1996. The soil measurements were made directly beneath the position of the tree centre at depths of 0.1, 0.2, 0.3 and 0.5 m (Fig. 1). To facilitate this, the plot's top 0.5 m of soil was removed prior to March 1994 and perforated stainless steel tubes (0.30 m long by 14 mm internal diameter) covered in nylon mesh were buried horizontally at each depth. Stainless steel tubing connected the soil air sampler to the surface, terminated by a syringe tap preventing gas escape and enabling sample collection. The soil was carefully re-packed at the same bulk density. A 10 ml soil air sample was extracted for measurements from each depth using a plastic syringe. The CO₂ concentration of the sample was determined within 24 h by gas chromatography (model 8610, SRI Instruments, Torrance, CA, USA) and was corrected using hourly average soil temperatures measured at 0.1, 0.3 and 0.5 m using thermocouples and a datalogger (model CR-10, Campbell Scientific, Inc. Logan, UT, USA).

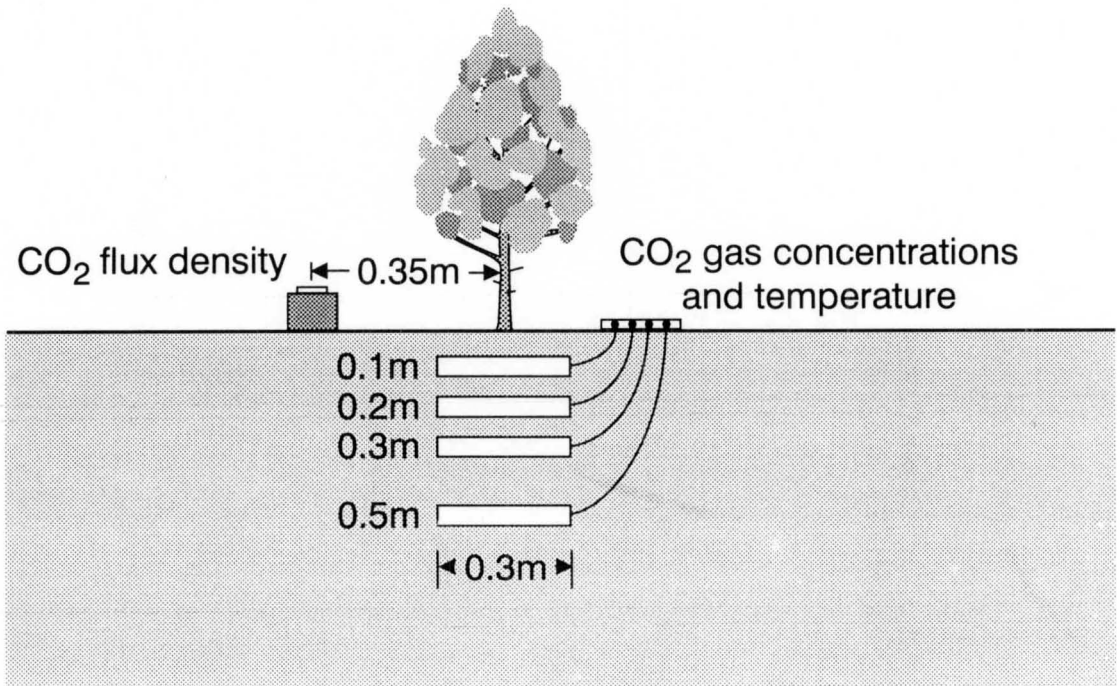


Figure 1. Schematic diagram of plot showing the placement of the gas samplers and flux density measurements in relation to the tree stem and soil surface.

2.4 Measured f (f_o)

The soil surface CO₂ flux density was measured monthly. Eight measurements were made in a circular pattern at a distance of 0.35 m from the tree stem. The measurement system consisted of a portable infrared gas analyser in a closed circuit (flow rate = ca. 0.5 l min⁻¹) coupled to a chamber (0.10 m diameter and 0.15 m tall) that was inserted about 10 mm into the soil (models EGM-1 and SRC-1, respectively, PP Systems, Hitchins, Herts, UK). The system was described originally by Parkinson (1981) and extensively tested recently by Jensen *et al.* (1996). The soil temperature at a depth of 0.05 m was measured contemporaneously.

2.5 Radial f and L_v

A functional relation between f and radial distance from the tree stem (r) may be written:

$$f = f' \exp(-r / R) + \gamma_T \quad (9)$$

where f' is the CO₂ flux density from the soil surface due to the roots at $r = 0$, R is a length scale (m) and γ is the background soil CO₂ surface flux density. The value of γ is probably mainly microbial respiration but may also include maintenance root respiration (Ben-Asher *et al.*, 1994a, b). The radial variation in f was determined by making duplicate measurements in the four cardinal directions at distances of ($r =$) 0.15, 0.35 (the standard measurement location), 0.55 and 0.75 m from the tree stem. Soil CO₂ concentrations were measured at the same time, so that f at $r = 0$ could be modelled.

Fine root length density (L_v) of roots <1 mm diameter of four trees growing in open top chambers was estimated at 0.3 m depth from acrylic minirhizotrons (length, 1.8 m), installed horizontally, directly beneath the trees. The minirhizotron methodology and calculation of L_v is described by Thomas *et al.* (1996). The radial distribution of L_v along the minirhizotron was estimated at the same time as the radial measurements of f . The relationship between L_v and r was determined from the relation:

$$L_v = L_v' \exp(-r / R) \quad (10)$$

where L_v' is the root length density at $r = 0$.

3. Results and Discussion

At the end of the two-year study, in March 1996, root length density (L_v , $\text{mm mm}^{-3} \times 10^2$) decreased exponentially with radial distance (r , m) from the tree stem ($L_v(r) = 9.65 e^{-6.44r}$, $R^2 = 0.45$, Fig. 2)(see also Thomas *et al.*, 1996). Measured soil CO_2 flux density (expressed in terms of the mass of carbon) also decreased exponentially from the stem of the tree (Fig. 2). The temperature at the time the measurements were made was 14.1°C . At $r = 0$ is shown the modelled value of $f_m = (f' + \gamma_{gT})$ based on the measurements of soil CO_2 concentration. When this modelled data point is included the regression equation ($f = 7.4 e^{-10.23r} + 2.66$) accounted for 94% of the variation. When the modelled data point is excluded the regression parameters change to ($f = 3.6 e^{-4.56r} + 2.37$) accounting for 99.8% of the variation. The proportionality between L_v and f_o is manifest in the similarity of length scales $1/6.44 = 0.15$ m for L_v and $1/10.23 = 0.10$ m or $1/4.56 = 0.22$ m for f . A proportionality between CO_2 flux and root length density was also found by Ben-Asher *et al.* (1994a). The relationship between f and r (Fig. 2) explains the difference between f_m from soil CO_2 concentration measurements made at $r = 0$ and f_o as measured by a chamber at $r = 0.35$ m (Fig. 7). Additionally, due to the radial decrease in L_v and possible radial gradient in soil CO_2 concentration, there may have been a radial flux of CO_2 , which would not be explained by the one-dimensional nature of our model. However, the vertical gradient in CO_2 concentration will be much greater than the radial gradient, due to the low soil surface concentration caused by atmospheric mixing. Hence the one-dimensional model should provide an adequate description of the CO_2 flux. Also, for the rapidly developing tree root system, there was a remarkably consistent difference between f_o measured at $r = 0.35$ m and modelled f_m at $r = 0$ over the two year study.

When $n \approx 1/k$ eqn (3) gave similar relationships as eqn (2) for normalised values of q/Q and z/L (Fig. 3). An explanation for why $n \approx 1/k$ can be found in appendix I where it is shown that in an integral sense $n = 1/k$. The effect of increasing n (i.e., > 1) on the respiration rate was to concentrate the respiration closer to the soil surface. For forests, this corresponds with the concentration of roots near the soil surface (e.g., for *Pinus radiata* plantation forest, see Whitehead *et al.*, 1994) and reflects the large contribution of roots to soil respiration (Ben-Asher *et al.*, 1994a,b; Johnson *et al.*, 1994; Haynes and Gower, 1995).

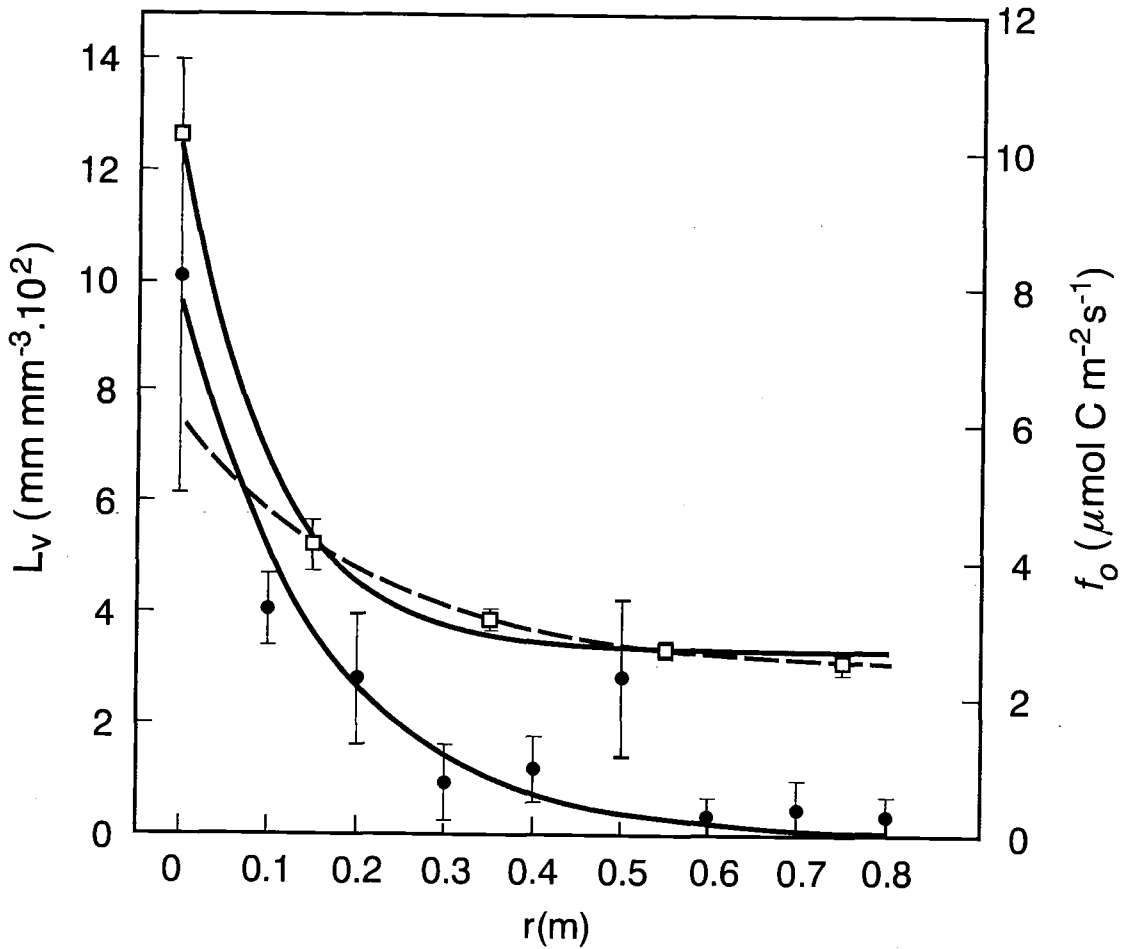


Figure 2. The relationship between root length density (L_v , $\text{mm mm}^{-3} \times 10^2$) (● bars are standard deviations) and r with a exponential curve ($L_v = 4.87 e^{-9.30r}$) (—) that accounted for 99% of the variation. Also shown is the relationship between measured soil carbon dioxide (in terms of carbon) flux density (f_o , $\mu\text{mol C m}^{-2} \text{s}^{-1}$) for irrigated Kairaki sand at distances (r , m) of 0.15, 0.35, 0.55 and 0.75 m from the stem of a 2-year-old, 4 m *Pinus radiata* tree in March 1996 (□). Eight replicate measurements were made in a circular pattern at each distance from the stem (bars are standard deviations). At $r = 0$ is shown the modelled value of f_o based on the measurements of soil CO_2 concentration at four depths as described in the text. A least-squares regression curve using both the modelled and measured data ($f_o = 7.4 e^{-10.23r} + 2.66$) (—) and with only the measured data ($f_o = 3.6 e^{-4.56r} + 2.37$) (---) accounted for 94% and 99.8% of the variation respectively. The temperature when measurements were made was 14.1 °C.

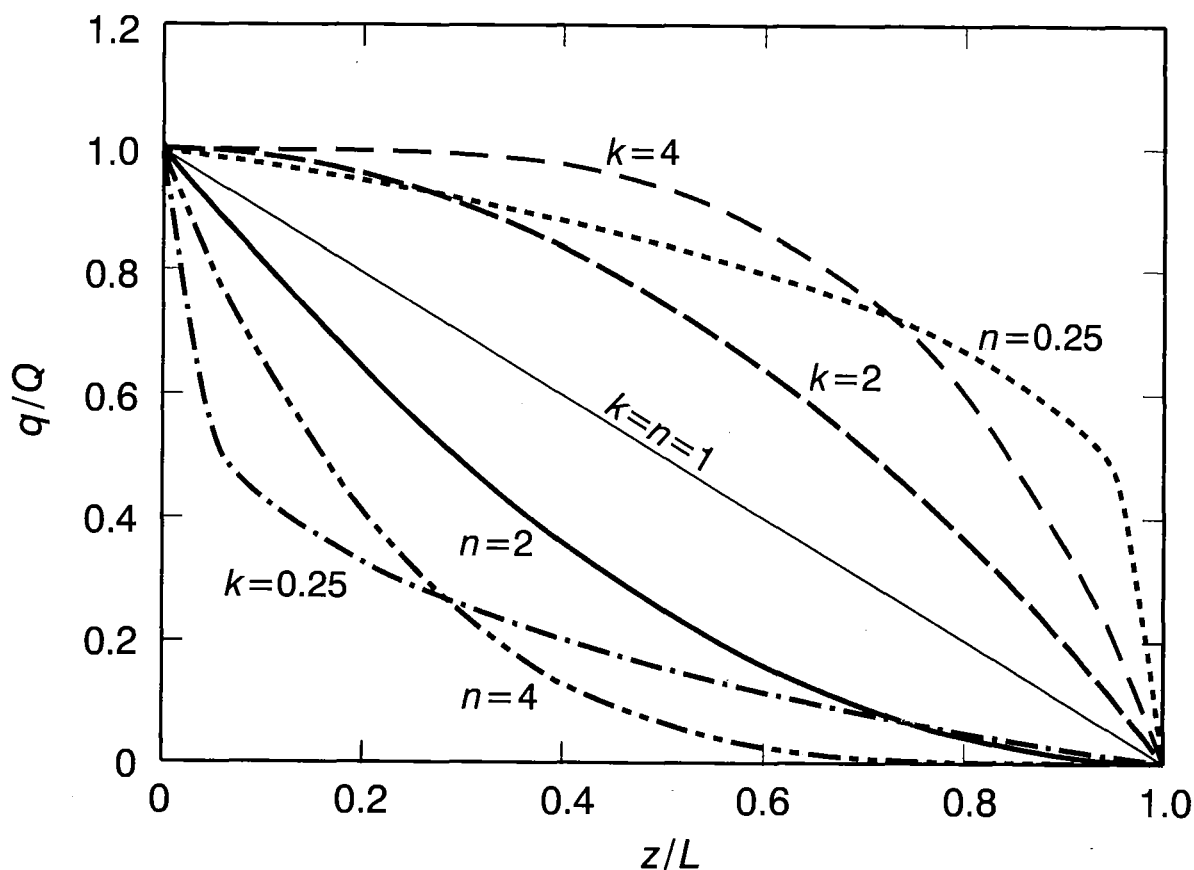


Figure 3. Relationships between normalised values of soil respiration rate (q/Q) and depth (z/L) calculated using eqns (2) and (3) with the attenuation coefficients k and n set to 0.25, 0.5, 1, 2, 3 and 4, respectively.

At the beginning of field measurements, in winter 1994 and only 2 months after planting the *Pinus radiata* tree in the plot, the slope of the CO_2 concentration profile with depth in the soil was relatively constant (Fig. 4). The smooth shape and monotonic increase in of all measured profiles indicated that the soil was at steady state with respect to CO_2 diffusion (Jury *et al.*, 1991, p. 210) and that the model (eqn (6)) should be appropriate for explaining the CO_2 profiles. There was good agreement between measured and modelled concentration profiles. The sand contained very little organic matter prior to planting of the tree and the tree root system was small at planting. Yet the CO_2 concentrations with depth at the start of the measurements July 1994 (Fig 4a) were greater than measurements made for many months after this time (Fig. 4b). We suggest this may be a result of soil and root disturbance at planting. It could also be related to the release of CO_2 from the microbial decomposition of organic carbon rich duff used to inoculate the roots with mycorrhizae at planting. Disregarding this initial point with time there was an increasing curvature of the CO_2 profile near the surface during this study, corresponding with tree growth which was nearly 4 m tall by the autumn (April) of 1996 (Figs 4b, c, d)

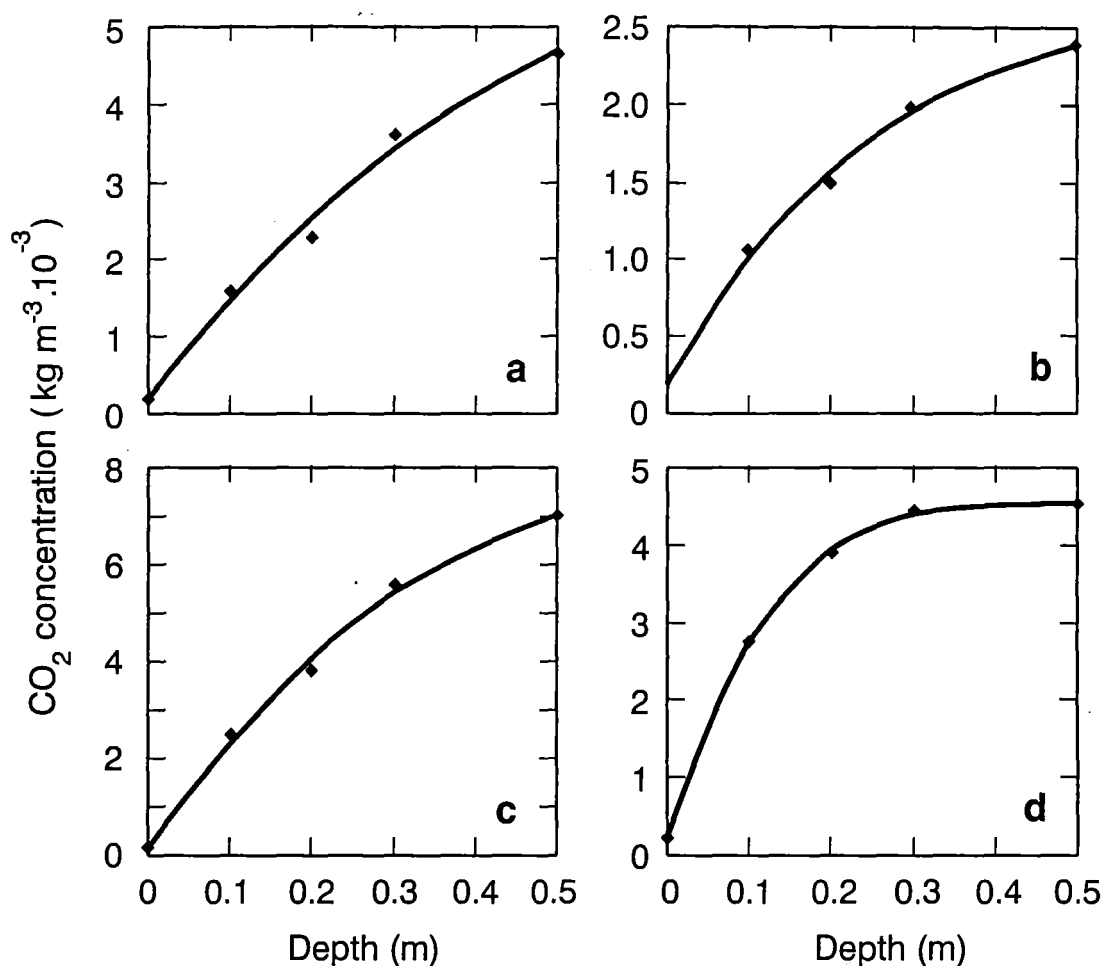


Figure 4. Typical CO₂ concentration profiles in a 2.9 m² irrigated plot of Kairaki sand at Bromley, Christchurch, New Zealand on a) 6 July 1994 (winter and soon after planting a single *Pinus radiata* seedling in the field plot), b) 18 January 1995 (summer), c) 21 March 1995 (autumn) and d) 27 February 1996 (late summer and the two-year-old tree was nearly 4 m tall). Points (◆) and curves (—) are measured and modelled values, respectively. The sand contained little organic matter prior to planting of the seedling. Note the high concentrations in a) which was the first measurement.

The model was run with the parameter L constrained to values between 0.5 and 1.5 m. This is consistent with roots observed on minirhizotrons installed at 0.9 m from January 1995 (Thomas *et al.*, 1997) and water-table depth which was on average 1.8 m (Thomas *et al.* 1997). The effect of the capillary fringe was approximately, 0.5 m in this soil and roots have not been observed deeper than 1.4 to 1.5 m (S.M. Thomas, unpublished data). The value of L attained the minimum value (of 0.5 m) on two occasions throughout the two years, the maximum value (of 1.5 m) occurred eight times. The average was $L = 1.0 \pm 0.4$ m (standard deviation) (Fig. 5a). There was a roughly

sinusoidal cycling of L with time that involved 3 - 4 months of $L \approx 1.5$ followed by 1 - 2 months of $L \rightarrow 0.5$

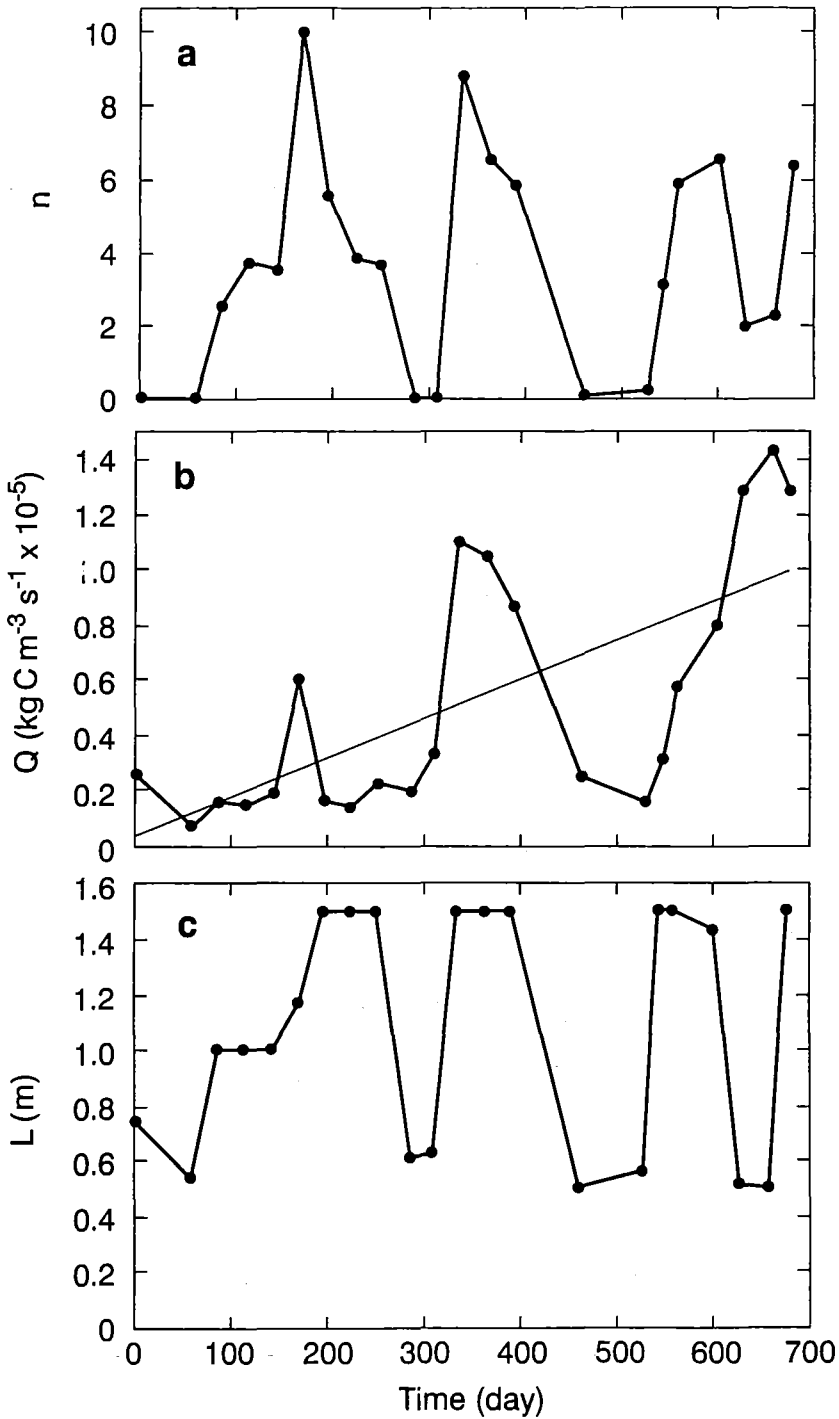


Figure 5. Courses of (a) the respiration with depth attenuation coefficient (n), (b) surface soil respiration rate (Q , kgC m⁻³ s⁻¹) and (c) the depth over which respiration occurred (L , m) between July 1994 and April 1996 in a 2.9 m² irrigated plot of Kairaki sand containing a *Pinus radiata* tree planted in April 1994. Also shown is a linear regression of Q (ordinate) and days after July 1994 (slope = 1.41×10^{-7} , offset = 3.93×10^{-6}) that accounted for 44% of the variation (—).

Values of n , indicating how respiration is concentrated near the soil surface, varied with time in a manner roughly similar to L , but the range was between 0 and 10. The maximum value was obtained only once, and the average was closer to the range midpoint at 3.7 ± 3.0 (Fig. 5b). This meant that on average, 32% of modelled soil respiration was concentrated between the surface and a depth of $z/L = 0.1$ (56 and 73% between $z/L = 0$ to 0.2 and 0 to 0.3, respectively).

We interpret changes in L and n to be strongly related to root activity. Increases in both parameters to maxima in November and December in the first year of measurements are consistent with fine root relative growth rates which peaked in December and January at depths 0.3 and 0.1m, respectively (Thomas *et al.*, 1997). From the mid-winter (July) to mid-summer (December), L increased from 0.5 m to 1.5 m and this is consistent with an observed increase in rooting depth from 0.1 m at planting to 0.9 m (Thomas *et al.*, 1997). Similar responses of n were observed in the second year of root production, with L at a maximum during the period of greatest root production. Root relative growth rates increased from early November to maxima in December and January at a depth of 0.1 m (Thomas *et al.*, 1997).

A linear regression through the values of Q indicated that it increased by a factor of eight over the two years of measurement (slope = 1.41×10^{-7} (kg m⁻³ s⁻¹) day⁻¹, $R^2 = 0.44$; Fig. 5c). This corresponded with expansion of the planted tree's root system (see Fig. 4 of Thomas *et al.*, 1996). An explanation for the relatively high initial value of Q (July 1994) is given above. Superimposed on the two-year trend of increasing Q was a sinusoidal variation of an amplitude that increased with time. Since the temperature effect had been removed with g_T this variation is related to root and the soil microbial processes. The increase in Q may be related to increased root growth in spring through to autumn (Thomas *et al.*, 1997) and the availability of rhizosphere carbon for heterotrophic respiration. Lower root growth rates were found in winter (Thomas *et al.*, 1997). Root turnover was low in the first year increasing in spring of the second year concurrently with root production.

Combining L , n and Q , f_m calculated from the soil CO₂ profiles followed Q , but with a seasonal variation (due to g_T) superimposed on the increase with time. The value of f_m increased by a factor of 2.5 over the two years. It was not possible to conduct a corresponding measurement of f at the same location because of the tree's stem. However, there was an excellent correspondence between measured f_o and f_m throughout the two years after tree planting when values were normalised with respect to the first date of comparison (Fig. 6). However, f_m was consistently a factor of 2.5 greater than the measured values ($R^2 = 0.83$)(Fig. 7).

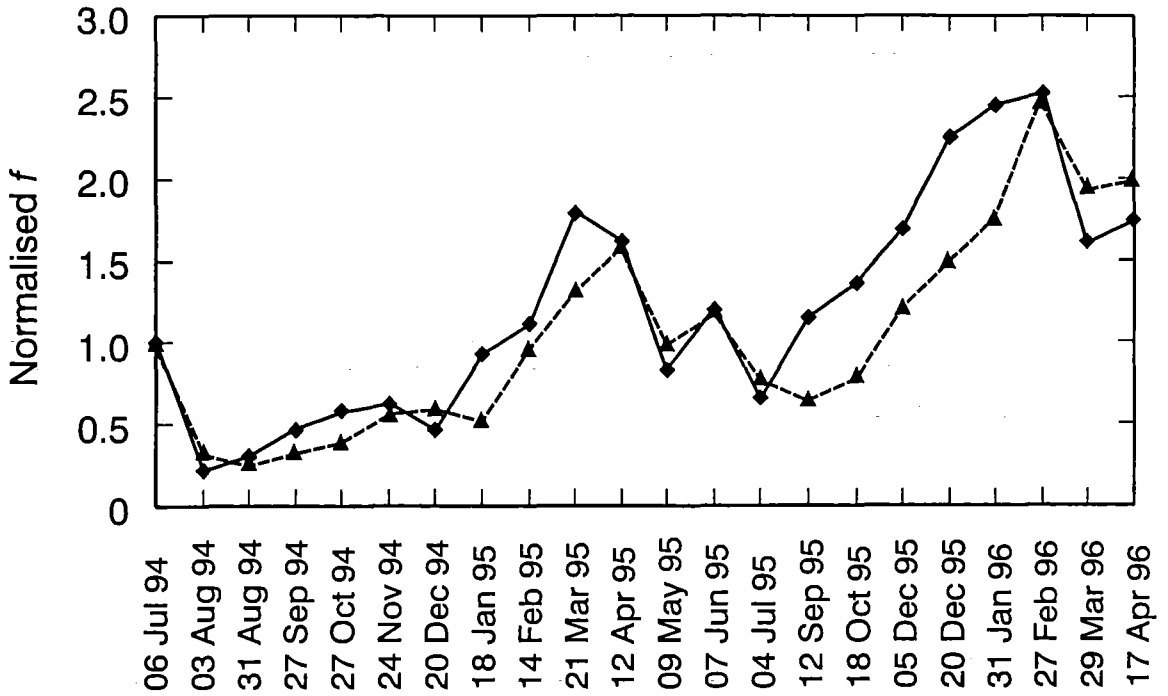


Figure 6. Courses of measured (◆—◆) and modelled (▲—▲) soil carbon dioxide flux density (f), normalised with respect to the values in July 1994 (5.58 and $1.82 \mu\text{mol.C m}^{-2} \text{s}^{-1}$), for irrigated Kairaki sand over two years after planting a *Pinus radiata* seedling that attained a height of nearly 4 m.

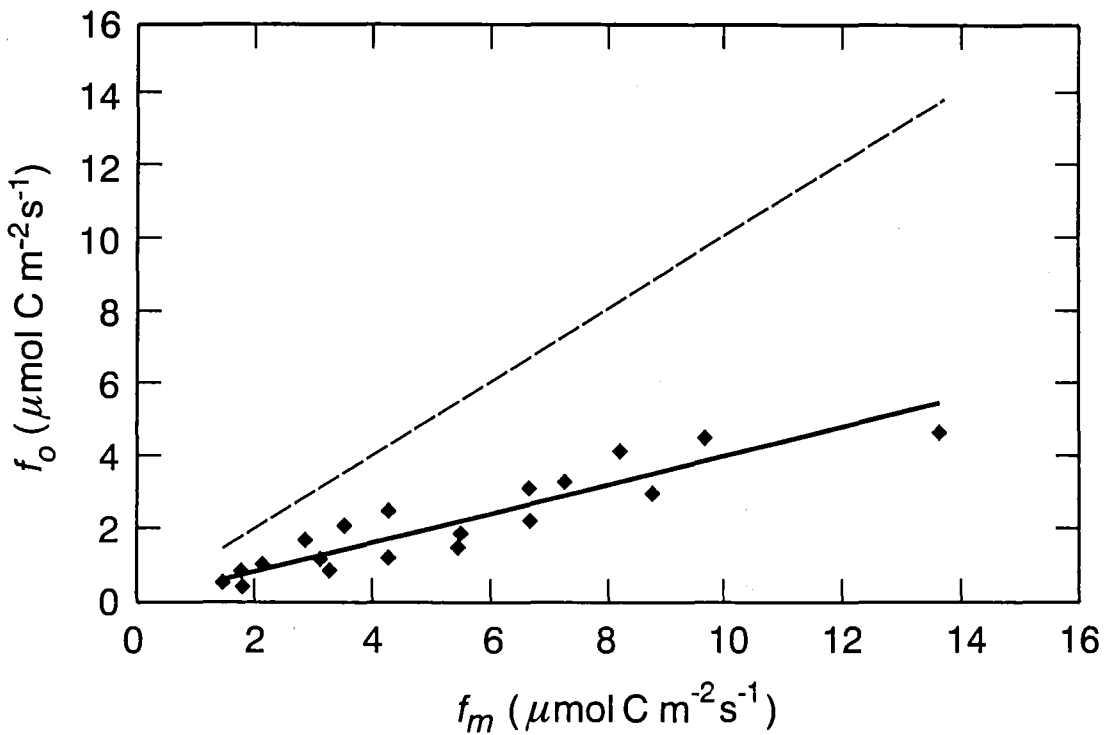


Figure 7. The relationship between mean measured and modelled CO_2 flux density ($\mu\text{mol C m}^{-2} \text{s}^{-1}$) for irrigated Kairaki sand over two years after planting a *Pinus radiata* seedling that obtained a height of nearly 4 m. The eight measurements were made in a circular pattern at a distance of 0.35 m from the tree stem (bars are standard errors), while modelled values were based on soil carbon dioxide concentrations directly beneath the stem. The linear regression through the origin had a slope of 0.39 and it accounted for 83% of the variation.

From eqn (9) and the exponential relation between f and r in Fig. 2, we find that $R = 0.22$ or 0.1 m depending on whether the modelled value of f is used to determine R . This result has implications for the sampling of and estimation of the soil CO_2 fluxes from plots of trees in carbon budget studies. The total flux of CO_2 (F) out of a plot containing a tree can be found by integrating eqn (9) with respect to r :

$$F = 2\pi \left\{ f' R^2 \left(1 - e^{-x} [x + 1] \right) + r^2 \gamma g_T / 2 \right\} \quad (11)$$

where $x = r/R$ is a dimensionless radius. Further, the average soil CO_2 flux density (\bar{f}) from the plot is simply F divided plot area (πr^2):

$$\bar{f} = \frac{2f' [1 - e^{-x} (x + 1)]}{x^2} + \gamma g_T \quad (12)$$

For a tree root system extended to $x = 3$, we can use eqn (12) to quantify $\bar{f} = 0.18 f' + \gamma g_T$.

Moreover, the radius at which $f = \bar{f}$ (\bar{r}) can be found by equating eqns (9) and (12) and solving for r to give:

$$\bar{r} = -R \ln \left\{ 2 \left[\frac{1 - e^{-x} (x + 1)}{x^2} \right] \right\} \quad (13)$$

Again letting $x = 3$, eqn (10) indicates that $\bar{r} = 1.7R$. The value of R was either 0.22 or 0.1 m depending on whether the modelled value was used in determining it. The corresponding values of \bar{r} are 0.17 or 0.37 m in our study. The location of the f measurements at $r = 0.35$ m were either too far away from the stem of the tree to give the average flux, or approximately the correct distance. Examination of Fig. 2 indicates that the difference between the flux at 0.17 m and 0.35 m is not large. Calculation of the \bar{f} values calculated from the f_m and g_T values and the values of R and γ determined in Fig. 2 are shown in Fig. 8 and compared with measured

values at $r = 0.35$ m. Both estimates of \bar{f} are close to the measured value f_o for dates after 21/3/95. Prior to this date except for the first point the values are overestimated. This is due to the value of γ being too large. This is clearly shown by the fact that the estimated values of \bar{f} are greater than f_m . This indicates that an increase in γ occurred at some time between August 1994 and March 1995. This increase occurred just prior to 21/3/95 and corresponds with the period of root growth at depths of 0.1 m to 0.3 m (Thomas *et al.*, 1997). This suggests that the increase in γ was due to either an increase in the maintenance respiration of the roots or a stimulation of the microbial respiration associated with the growth of roots. Consequently, although f_o was less than f_m , it was a reasonable approximation of the average value of CO_2 flux density from our tree plot for the period from March 1995 to April 1996.

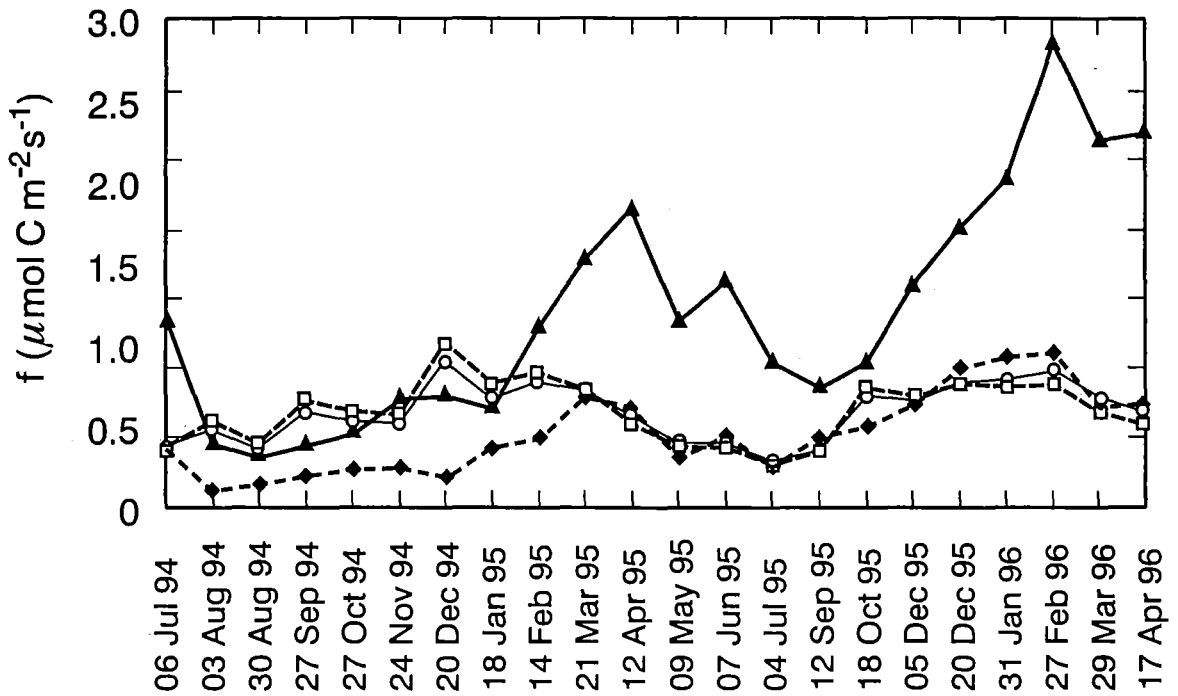


Figure 8. Comparison of the measured (\diamond — \diamond), modelled (\blacktriangle — \blacktriangle), and average flux densities ($R = 0.22$ m \square — \square , $R = 0.1$ m \circ — \circ).

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Appendix I

For the functions:

$$f(x) = (1 - x)^n \quad (\text{A1})$$

and

$$g(x) = (1 - x^k) \quad (\text{A2})$$

Integration with respect to x for the range $x = 0$ to $x = 1$ gives respectively:

$$\int_0^1 f(x) dx = \frac{1}{n+1} \quad (\text{A3})$$

$$\int_0^1 g(x) dx = 1 + 1/k \quad (\text{A4})$$

Equating (A3) and (A4) results in $n = 1/k$.