New Phytologist

Research

Fine-root respiration in a loblolly pine and sweetgum forest growing in elevated CO_2

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Received: *9 May 2003*
Accepted: *4 August 2003*

doi: 10.1046/j.1469-8137.2003.00911.x

Summary

• The loss of carbon below-ground through respiration of fine roots may be modified by global change. Here we tested the hypothesis that a reduction in N concentration of tree fine-roots grown in an elevated atmospheric CO_2 concentration would reduce maintenance respiration and that more energy would be used for root growth and N uptake. We partitioned total fine-root respiration (R_T) between maintenance (R_M), growth (R_G), and N uptake respiration (R_N) for loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) forests exposed to elevated CO_2.

• A substantial increase in fine-root production contributed to a 151% increase in R_G for loblolly pine in elevated CO_2. Root specific R_M for pine was 24% lower under elevated CO_2 but when extrapolated to the entire forest, no treatment effect could be detected.

• R_G (< 10%) and R_N (< 3%) were small components of R_M in both forests. Maintenance respiration was the vast majority of R_T, and contributed 92% and 86% of these totals at the pine and sweetgum forests, respectively.

• The hypothesis was rejected because the majority of fine-root respiration was used for maintenance and was not reduced by changes in root N concentration in elevated CO_2. Because of its large contribution to R_T and total soil CO_2 efflux, changes in R_M caused by warming may greatly alter carbon losses from forests to the atmosphere.

Key words: annual fine-root respiration, maintenance respiration, growth respiration, nitrogen uptake respiration, temperate forest, free-air CO_2 enrichment (FACE), loblolly pine (*Pinus taeda*), sweetgum (*Liquidambar styeaciflua*).

Introduction

A substantial fraction of the flux of CO_2 from the soil is from roots (Rouhier *et al.*, 1996; Thierron & Laudelout, 1996), with the rest coming from soil organisms. Published values for the proportion of total soil CO_2 efflux originating from roots vary from < 10% to > 90% (Hanson *et al.*, 2000), thus, the loss of carbon through root respiration can be an important component of forest carbon budgets. More than 50% of total net primary productivity (NPP) in forest ecosystems may be allocated below-ground (Vogt *et al.*, 1982; Fahey & Hughes, 1994), and the extent to which NPP becomes long-term carbon storage greatly affects the capacity of forests to store atmospheric CO_2. The increase in atmospheric CO_2 may alter the partitioning of respiration among functional processes, as well as its absolute magnitude, thereby affecting the carbon cycling of ecosystems.

Fine root respiration supports three important functions: maintenance, growth and nutrient uptake (Johnson, 1983; Lambers *et al.*, 1983). Maintenance respiration provides the energy to turnover proteins and to maintain ion gradients, growth respiration provides energy for construction of new cells and nutrient uptake respiration provides the energy required by epidermal root cells to actively transport ions

against a concentration gradient. The partitioning of energy among these major functions will influence water and nutrient uptake by fine roots, which will affect tree growth, yet relatively few studies have quantified the proportional investment in these processes (Veen, 1980, 1981; de Visser & Lambers, 1983; Johnson, 1983; Van der Werf *et al.*, 1988; Poorter *et al.*, 1991; Bouma *et al.*, 1996; Mata *et al.*, 1996).

Nutrient uptake respiration is as high as 60% of total root respiration for maize (Veen, 1980, 1981). By contrast, *Quercus suber* used the majority of respiration for maintenance and used only 19–31% of its total respiration for nutrient uptake (Mata *et al.*, 1996), reflecting the lower nutrient demand and greater nutrient use efficiency of this species. Nutrient uptake respiration has not been determined in an intact forest ecosystem, where the percentage of total fine root respiration used for nutrient uptake could be high, particularly for trees growing in nutrient-poor soils.

Growth in elevated atmospheric CO_2 may alter the absolute rate, as well as the partitioning of fine root respiration. Several studies have documented a decrease in the specific rate of fine root respiration for trees grown in elevated atmospheric CO_2 (Callaway *et al.*, 1994; BassiriRad *et al.*, 1997; Crookshanks *et al.*, 1998). Growth under elevated CO_2 causes a decrease in the nitrogen concentration of roots (Cotrufo *et al.*, 1998) suggesting a reduction in protein concentration. Thus, the energy required for protein turnover may decline in elevated CO_2 causing a reduction in maintenance respiration. If maintenance respiration of fine roots grown in elevated atmospheric CO_2 is reduced, then more energy could potentially be available to support growth and nutrient uptake. By contrast to maintenance respiration, elevated atmospheric CO_2 stimulates fine root production (Norby *et al.*, 1986; Pregitzer *et al.*, 1995; Crookshanks *et al.*, 1998; Janssens *et al.*, 1998; DeLucia *et al.*, 1999). The decrease in maintenance respiration with elevated CO_2 may contribute to increases in growth respiration.

The objective of this study was to estimate total fine root respiration and the proportions used for maintenance, growth and nitrogen uptake in loblolly pine and sweetgum forests growing under ambient and elevated atmospheric CO_2. In addition, a survey of the literature was conducted for values of fine root respiration to provide comparisons for the rates reported in this study. Few studies report nitrogen uptake respiration, and none, to our knowledge, have attempted to estimate this process for an intact forest ecosystem. Nitrogen was investigated in this study as it was assumed that it represents the greatest expenditure of energy for nutrient uptake (Veen, 1980, 1981). We hypothesized that a reduction in nitrogen concentration of fine root tissue grown in elevated CO_2 would reduce maintenance respiration, and that more energy would be used for fine root growth and nitrogen uptake. Fine root maintenance respiration was measured from gas-exchange of nongrowing roots in the absence of nutrients, and growth respiration was quantified from construction costs and production rate of fine roots. Nitrogen uptake respiration was estimated from the annual nitrogen uptake of trees at each site and from a literature value representing the respiration rate associated with nitrogen uptake.

Materials and Methods

Experimental sites

Measurements were made in two similar-age forests where experimental plots were fumigated with CO_2 using free-air CO_2 enrichment (FACE) technology (Hendrey *et al.*, 1999). One experimental site is an even-aged loblolly pine (*Pinus taeda* L.) plantation (Duke Forest, North Carolina, USA 35°97′ N 79°09′ W) seeded in 1983 and left unmanaged since. More than 90% of the total biomass is pine (Hamilton *et al.*, 2002), however, a diverse mixture of hardwood species has become established in the understory (Hartz-Rubin & DeLucia, 2001). The soil at this experimental site is an Ultic Alfisol and is low in total nitrogen and phosphorus. The pre-fumigation soil concentrations for nitrogen and phosphorus were 0.08% ± 0.01 (SD) and 1.23 p.p.m. ± 0.35, respectively (W. H. Schlesinger, pers. comm.). The other experimental site is Oak Ridge National Laboratory (ORNL; Tennessee, USA 35°54′ N 84°20′ W) where a plantation was established in 1988 with 1-yr-old-seedlings of sweetgum (*Liquidambar styraciflua* L.). The soil at ORNL forest is classified as an Aquic Hapludult, with higher total nitrogen and phosphorus concentrations (0.13% ± 0.01 and 8.21 p.p.m. ± 1.49, respectively) than the Duke Forest site.

The Duke site has six 30-m diameter experimental FACE plots. Three treatment plots have been fumigated with elevated CO_2 beginning 27 August 1996. At the ORNL site there are four 25-m diameter FACE plots, and the fumigation of elevated CO_2 for the two treatment plots began on 11 May 1998 (Norby *et al.*, 2001). The elevated CO_2 plots have target concentrations of 200 μl l^{-1} above ambient (global average 369 μl l^{-1} in 2000). The average daytime CO_2 concentration in 2000 in the elevated CO_2 plots was 545 ± 58 at the ORNL site and 534 ± 149 at the Duke site.

Maintenance respiration

At each FACE site the rate of CO_2 efflux of fine roots from 10 separate locations within each experimental plot was measured using a portable IR gas analysis system with the conifer needle cuvette (Li-Cor 6400; Lincoln, NE, USA) in June and July 2000. Measurements were made at one time period as fine roots of tree species respond to changes in temperature (Q_{10}) in a similar way through the growing season and no acclimation has been observed from natural diurnal and seasonal changes in temperature (Sowell & Spomer, 1986; Weger & Guy, 1991; Burton *et al.*, 1996; Zogg *et al.*, 1996; Burton *et al.*, 1998). Intact roots were

gently excavated from the organic layer and kept attached to the rest of the root system throughout the measurements. The intact mats (average 0.12 g dry mass) of fine roots (= 2-mm in diameter) were rinsed with water and blotted dry before being placed in the gas-exchange cuvette. During measurements the cuvette was darkened and the roots were kept moist by adding 10 ml of water to the soda lime tube attached to the Li-Cor 6400. This maintained a relative humidity in the cuvette of = 80% and ensured constant respiration rates for at least 30 min without reductions from drying (data not shown). All measurements were taken when the rate of CO_2 efflux had stabilized, typically within 10 min of enclosing the roots in the cuvette. The air temperature within the cuvette was 25°C. To minimize CO_2 diffusion between the air space inside the cuvette and the atmosphere (Burton & Pregitzer, 2002), measurements were made at the atmospheric CO_2 concentration in each plot. The CO_2 concentration within the cuvette was 360 µl l^{-1} in the ambient plots and at 560 µl l^{-1} in the elevated plots. Measurements on excavated roots of sweetgum and potted seedlings of loblolly pine indicated that variation in atmospheric CO_2 concentration from 400 to 2000 µl l^{-1} had no affect on the rate of root respiration (K. George unpublished). After gas exchange measurements the roots within the cuvette were removed and dried at 70°C for 48 h for measurement of dry mass, nitrogen content and construction costs. It was assumed that these measurements represented maintenance respiration (R_M), as fine root growth was slow at this time (Matamala & Schlesinger, 2000).

Annual maintenance respiration (R_M^{annual}) was estimated by adjusting the instantaneous rates (R_M) measured at 25°C to the average temperature experienced by fine roots over the year and multiplying by the standing mass of fine roots at each site. Average annual soil temperatures 10 cm below the soil surface were 14°C and 15°C for 2000 at the Duke and ORNL forests, respectively. Instantaneous rates of respiration was adjusted to these temperatures using the following equation from Ryan (1991):

$$R_M = R_{25}[\exp(\ln(Q_{10})(T - 25))/10]; \quad \text{Eqn 1}$$

(R_M, instantaneous fine root maintenance respiration at temperature T; R_{25}, the rate of fine root respiration at 25°C.) A value of 2.075 was used for Q_{10}, which was an average of several values for conifers from the literature (Sowell & Spomer, 1986; Ryan *et al.*, 1996, 1997; Clinton & Vose, 1999; Tjoelker *et al.*, 1999). The same Q_{10} value was applied to sweetgum as we were unable to find estimates for this species in the literature. The Q_{10} for soil respiration in the sweetgum plots was 2.1–2.2 (P. J. Hanson, pers. comm.). The values of loblolly pine fine root standing mass for 1998 at the Duke site were from Matamala & Schlesinger (2000). The values of sweetgum fine root standing mass for 2000 at the ORNL site were from Norby *et al.* (2002).

Construction and growth respiration

Annual growth respiration (R_G) for each forest was calculated from the tissue-specific construction respiration (R_C) times the rate of production of fine roots for each FACE plot; where R_C is the energy required to make new tissue on a mass basis. Construction respiration was calculated from the heat of combustion and the carbon content of roots as in Williams *et al.* (1987) and Carey *et al.* (1996).

Construction cost (C) of fine roots (g glucose g^{-1} dry weight tissue) was quantified from the ash free heat of combustion, ash content and total organic nitrogen using the following equation from Williams *et al.* (1987):

$$C = \left[(0.6968 \times \Delta H_C - 0.065)(1 - A) + \left(\frac{kN}{14.0067}\right)\left(\frac{180.15}{24}\right)\right]\frac{1}{E_G}; \quad \text{Eqn 2}$$

(ΔH_C, the ash-free heat of combustion (kJ g^{-1}); A, the ash content (g g^{-1}); k, the oxygen state of nitrogen substrate; N, the organic nitrogen content (g g^{-1}); and E_G, the growth efficiency conversion (assumed to be 0.89).) A value of −3 was used for k; this value is appropriate for forest soils where most N is absorbed as ammonium (Christensen & MacAller, 1985). Ash-free heat of combustion was determined by combusting a 10–20 mg sample in a microbomb calorimeter (Gentry Instruments, Aiken, USA). Ash content was determined by combusting samples in a muffle furnace at 500°C for four hours (Carey *et al.*, 1996). Carbon and nitrogen content of ground root tissue were measured with an elemental analyzer (NA1500, Carlo Erba, Milan, Italy). The heat of combustion and ash content were measured on a bulked sample from each experimental plot and the nitrogen content was measured on the individual samples (10 per plot) and averaged to provide a value for each experimental plot.

Construction costs expressed in units of glucose required for tissue synthesis, include both carbon incorporated into tissue and respired during construction (Nobel *et al.*, 1992). R_C was calculated by subtracting the structural carbon incorporated in the root tissue (carbon content) from construction costs. Units of glucose were converted to CO_2 by assuming six CO_2 mol are evolved per glucose mole (Nobel *et al.*, 1992). Annual R_G was calculated as the product of fine root production (kg m^{-2} $year^{-1}$) and R_C (mol CO_2 kg^{-1}). The values of loblolly pine fine root production for 1998 at the Duke site were from Matamala & Schlesinger (2000). The values of sweetgum fine root production for 2000 at the ORNL site were from Norby *et al.* (2002).

Nitrogen uptake respiration

Annual nitrogen uptake respiration (R_N) was calculated as the product of nitrogen uptake by loblolly pine (Finzi *et al.*, 2002)

Table 1 Instantaneous maintenance respiration (R_M) rates on a mass and nitrogen basis at 25°C for loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) fine roots growing at the Duke and ORNL free-air CO_2 enrichment (FACE) sites in ambient (~360 µl l^{-1}) and elevated (~560 µl l^{-1}) atmospheric CO_2

	Loblolly pine Ambient CO_2	Elevated CO_2	% E-A	Sweetgum Ambient CO_2	Elevated CO_2	% E-A
R_M (nmol CO_2 g^{-1} s^{-1})	8.93 (1.3)	6.91 (0.6)	–22.6*	10.16 (0.2)	11.75 (1.7)	15.6
R_M (µmol CO_2 g^{-1} N s^{-1})	0.96 (0.3)	0.85 (0.1)	–11.5	1.06 (0.1)	1.08 (0.1)	2.0

Each value is a mean of three plots for loblolly pine and two plots for sweetgum (± 1 SD). The percentage difference in the rates for trees in ambient and elevated CO_2 plots is designated '% E-A'. The asterisk represents a significant ($P < 0.05$) difference between CO_2 concentrations.

and sweetgum (R. J. Norby & D. W. Johnson, pers. comm.) over a year (mol N m^{-2} yr^{-1}) for each FACE plot and an estimate of the specific cost of nitrogen uptake (0.99 mol O_2 mol N^{-1}; Mata *et al.*, 1996). Nitrogen uptake was calculated as the annual increment of nitrogen in wood plus the amount lost as litterfall minus retranslocation, expressed on ground area basis (Finzi *et al.*, 2002). The specific cost of nitrogen uptake was converted to mol CO_2 mol N^{-1} using a respiratory quotient of 0.8 (Penning de Vries *et al.*, 1974; Poorter *et al.*, 1991; Matamala & Schlesinger, 2000). There are few values in the literature for the specific cost of nitrogen uptake. The value reported by Mata *et al.* (1996) is for an evergreen woody species, *Quercus suber*, growing on nitrogen-poor soil.

Total respiration

The temperature-adjusted annual rate of R_M and the temperature-independent annual R_G and R_N were summed to calculate annual total fine root respiration (R_T) for each experimental plot.

Literature survey

A search of Biological Abstracts (Ovid, New York, USA) covering year 1980–2000 was conducted using 'respiration', 'fine' and 'roots' as keywords. The bibliographies of the articles were then scanned for further reports of fine root respiration. The survey produced 39 publications with respiration rates of fine roots (= 2 mm in diameter) from tree species dating from 1950. All rates in the literature were converted to nmol CO_2 g^{-1} tissue s^{-1} and to 15°C using Eqn 1 (Appendix 1). Studies were excluded from the survey if they did not report temperature during the measurement. The data were used to compare the rate of fine root respiration for gymnosperm vs angiosperm species, mature trees vs seedlings, and roots that were attached to the tree vs those detached during measurements.

Data analysis

Each plot was treated as an experimental unit and replicate measurements within each plot were averaged to provide a plot mean. The Duke FACE site was treated as a split plot design ($n = 3$), and a paired *t*-test was applied to each variable. There was no blocking at the ORNL FACE site and an independent samples *t*-test was used for all variables ($n = 2$). The mean distributions of data derived from the literature survey were not analyzed statistically. A meta-analysis could not be performed on the data set as individual publications did not contain data on respiration rates of roots that were both attached to the tree and detached during measurements, from mature trees and seedlings and from gymnosperm and angiosperm species (Appendix 1). Log transformations were performed where data were not normal. All statistical analyses were conducted with SPSS 10.05 (Chicago, IL, USA). Unless otherwise stated, $P < 0.05$ was the accepted probability level.

Results

Tissue-specific maintenance respiration

At the Duke FACE site, the instantaneous rate of maintenance respiration (R_M) of loblolly pine fine roots, expressed on a dry mass basis, was significantly lower in the elevated CO_2 treatment ($P < 0.05$; Table 1), but was not different between treatments when expressed on a nitrogen basis. There was no significant difference between the CO_2 treatments for instantaneous R_M of sweetgum fine roots from the ORNL site when expressed on a mass or nitrogen basis (Table 1). R_M appeared to be higher for sweetgum than for loblolly pine when expressed on a mass basis but not on a nitrogen basis. No relationship was found between nitrogen concentration of the individual fine root tissues and their respective respiration rates for either species (data not shown).

Tissue-specific construction respiration

The ash-free heat of combustion (ΔH_C) for loblolly pine fine roots was higher in the elevated CO_2 treatment ($P < 0.05$; Fig. 1c), resulting in a nonsignificant increase in construction respiration (R_C) in the elevated CO_2 treatment ($P = 0.10$; Fig. 1f). There was no difference in the other components of R_C for pine across treatments (Fig. 1a,b,d,e). For sweetgum no differences between the CO_2 treatments for R_C or any of its components could be detected ($P > 0.05$; Fig. 1a–f).

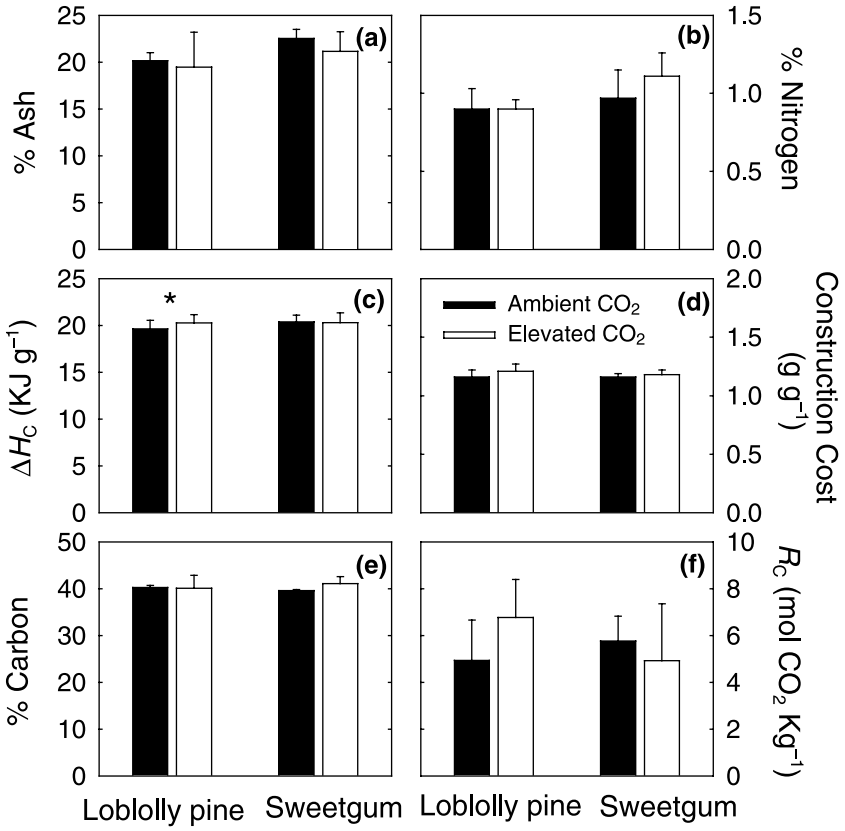

Fig. 1 Effect of ambient (~360 µl l^{-1}, closed bars) and elevated (~550 µl l^{-1}, open bars) atmospheric CO_2 on (a) percent ash (b) percent nitrogen (c) ash-free heat of combustion (ΔH_C) (d) construction cost in g glucose g^{-1} of tissue (e) percent carbon and (f) construction respiration (R_C) of loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) fine roots. The asterisk represents significant differences ($P = 0.05$) between the ambient and elevated CO_2 treatments within a species. Each bar is a mean of three plots for loblolly pine and two plots for sweetgum (± 1 SD).

Table 2 Annual total (R_T), maintenance (R_M), growth (R_G), and nitrogen uptake (R_N) respiration and fine root-standing mass, construction respiration (R_C), fine-root production and nitrogen uptake for loblolly pine (*Pinus taeda*) and sweetgum (*Liquidambar styraciflua*) growing at the Duke and ORNL free-air CO_2 enrichment (FACE) sites in ambient (~360 µl l^{-1}) and elevated (~560 µl l^{-1}) atmospheric CO_2

	Loblolly pine Ambient CO_2	Elevated CO_2	% E-A	Sweetgum Ambient CO_2	Elevated CO_2	% E-A
Annual R_T (g C m^{-2} yr^{-1})	638.6 (168.4)	531.2 (47.5)	–17	245.1 (84.1)	454.9 (182.8)	+86
Annual R_M (g C m^{-2} yr^{-1})	631.0 (168.8)	517.7 (48.2)	–18	208.1 (75.8)	400.0 (144.5)	+92
R_M (g C g^{-1} yr^{-1})	1.7 (0.3)	1.3 (0.1)	–24*	1.9 (0.0)	2.2 (0.3)	+16
[1]Standing mass (g m^{-2})	363.5 (97.3)	385.4 (35.9)	+6	112.6 (39.5)	194.8 (96.2)	+73
Annual R_G (g C m^{-2} yr^{-1})	2.6 (1.4)	6.5 (2.1)	+151*	24.1 (6.5)	41.4 (38.9)	+72
R_C (g C kg^{-1})	59.2 (20.7)	81.2 (19.6)	+37	69.3 (12.7)	59.2 (29.2)	–15
[2]Production (g m^{-2} yr^{-1})	42.8 (13.0)	80.0 (9.9)	+87*	345.3 (30.8)	612.7 (355.4)	+77
Annual R_N (g C m^{-2} yr^{-1})	5.1 (1.1)	7.0 (1.6)	+39	12.9 (1.7)	13.5 (0.6)	+5
R_N (g C g N^{-1})	1.8 (0.0)	1.8 (0.0)	0	1.8 (0.0)	1.8 (0.0)	0
[3]N uptake (g N m^{-2} yr^{-1})	2.8 (0.6)	3.9 (0.9)	+39	7.1 (1.0)	7.5 (0.3)	+5

R_M was adjusted to the annual soil temperature at each site. Each value is a mean of three plots for loblolly pine and two plots for sweetgum (± 1 SD). The percentage difference in the rates for trees in ambient and elevated CO_2 plots is designated '% E-A'. Asterisks represent a significant ($P = 0.05$) difference between CO_2 concentrations. [1]Fine root standing mass of loblolly pine in 1998 from Matamala & Schlesinger (2000) and of sweetgum in 2000 from Norby *et al*. (2002). [2]Fine root production of loblolly pine in 1998 from Matamala & Schlesinger (2000) and of sweetgum in 2000 from Norby *et al*. (2002). [3]Nitrogen uptake of loblolly pine from Finzi *et al*. (2002) and sweetgum from R. J. Norby & D. W. Johnson (pers. comm.).

Annual total, maintenance, growth and nutrient uptake respiration

Annual growth respiration (R_G $P < 0.05$) and fine root production (Matamala & Schlesinger, 2000) were significantly greater in the elevated CO_2 treatment for loblolly pine (Table 2). Annual nitrogen uptake respiration (R_N) was marginally greater in the elevated CO_2 treatment ($P = 0.06$) for loblolly pine as the uptake of nitrogen by these trees was increased in elevated CO_2 (Finzi *et al*., 2002). The uptake of nitrogen by

loblolly pine was less than half the uptake of nitrogen by sweetgum (Table 2). There was no significant difference in annual R_T and R_M between CO_2 treatments for loblolly pine ($P > 0.05$; Table 2). The high variance in R_T and its components for sweetgum resulted in no significant differences, although annual R_T and R_M were consistently higher under elevated CO_2. It appeared that annual R_T and R_M were greater for loblolly pine than for sweetgum, whereas annual R_G and R_N were lower in loblolly pine than sweetgum (Table 2).

Literature survey

To provide a context for our results, a review was conducted of fine root respiration rates in the literature for tree species. The distribution of values reported in the literature was highly skewed to lower rates, with the majority of values at 15°C were = 10 nmol CO_2 g^{-1} s^{-1} (Fig. 2). The average rate of fine root respiration for attached and severed roots was 9.1 nmol CO_2 g^{-1} s^{-1} and 6.7 nmol CO_2 g^{-1} s^{-1}, respectively, but a few high values contributed to the higher average for attached roots. Average fine root respiration rates from seedlings (9.1 nmol CO_2 g^{-1} s^{-1}) were substantially greater than for mature trees (3.7 nmol CO_2 g^{-1} s^{-1}). For seedling fine roots, 74% of respiration rates were = 10 nmol CO_2 g^{-1} s^{-1}, compared to 97% of the rates for mature trees. There was no apparent difference between the average fine root respiration rates of angiosperm and gymnosperm tree species. Data from this study are consistent with the literature. At 15°C the R_M for fine roots of loblolly pine were 4.47, and 3.46 nmol CO_2 g^{-1} s^{-1}, and 5.08 and 5.88 nmol CO_2 g^{-1} s^{-1} for sweetgum, in the ambient and elevated CO_2 treatments, respectively.

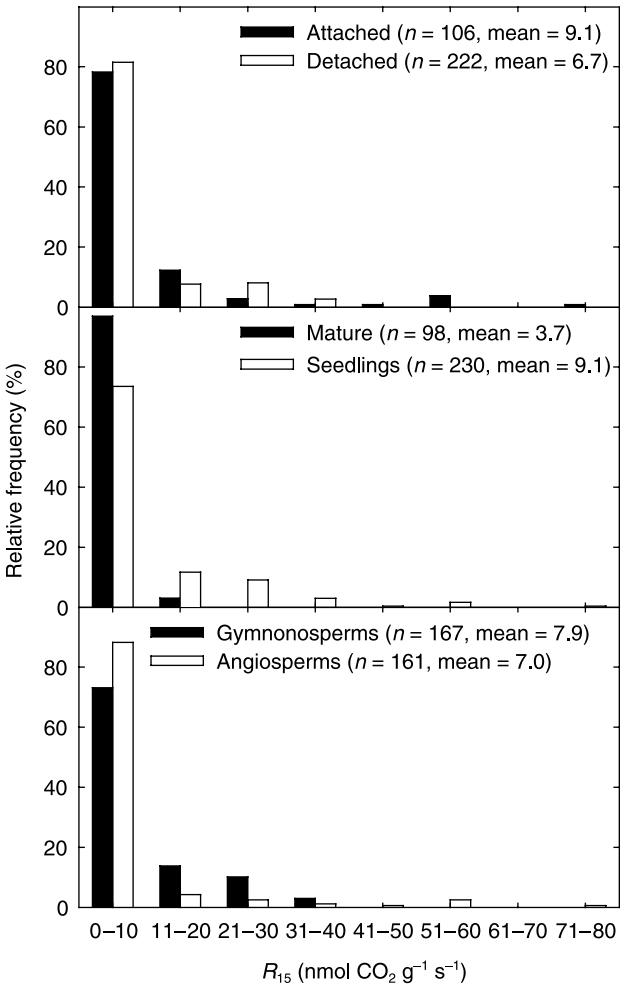

Fig. 2 Relative frequency of fine-root respiration at 15°C (R_{15}) of 328 independent measurements from 39 studies (Appendix 1) divided between fine roots that were attached or detached during respiration measurements, mature trees and seedlings and gymnosperm and angiosperm species.

Discussion

Annual growth (R_G) and nitrogen uptake respiration (R_N) of fine roots were greater in elevated CO_2 for loblolly pine but were unchanged for sweetgum. The duration of exposure to elevated CO_2 may have contributed to the difference in response of these forests; at the time of our measurements the pine forest had been exposed to elevated CO_2 for 4 yr, whereas the sweetgum forest had only been exposed for 2 yr. The increase in annual R_G and R_N in response to elevated CO_2 for loblolly pine was not apparent in total fine root respiration (R_T) because they were such small fractions of the total. Annual maintenance respiration (R_M^{annual}) accounted for 98% and 86% of R_T in the loblolly pine and sweetgum forest, respectively. It was initially predicted that a reduction in the nitrogen concentration of fine roots in elevated CO_2 would reduce R_M^{annual} and increase the energy available for growth and nitrogen uptake. There was a significant reduction in instantaneous R_M for pine grown under high CO_2 but this difference was no longer statistically significant when extrapolated to R_M^{annual}, and there was no significant change in the nitrogen concentration of fine roots. It appears that the C : N ratio of fine roots grown in elevated CO_2 was not altered and consequently did not explain the trend of reduced R_M^{annual} and the increase in annual R_G for loblolly pine.

Instantaneous R_M on a mass basis was significantly reduced by the elevated CO_2 treatment for loblolly pine but not for sweetgum. It has been suggested that a reduction in tissue nitrogen concentration, possibly caused by an increase in carbon content (Cotrufo *et al.*, 1998), reduced respiration rates of tree roots grown under elevated CO_2 (Callaway *et al.*, 1994; BassiriRad *et al.*, 1996; Crookshanks *et al.*, 1998). We were unable to detect an effect of elevated CO_2 on the nitrogen concentration of fine roots for either species. Instantaneous R_M on a mass basis was higher for sweetgum than loblolly pine and this difference was eliminated when expressed per unit N (Table 1), suggesting that the rate of CO_2 flux may have been related to nitrogen concentration. However, no relationship was apparent between individual root respiration

measurements and corresponding nitrogen concentrations (n = 53 for loblolly pine and n = 33 for sweetgum; data not shown). It appears that while expressing instantaneous R_M on a nitrogen basis reduces some of the variation in respiration rates, the observed differences in fine root respiration are not explained completely by nitrogen concentration.

There was a trend of greater construction respiration (R_C) under elevated atmospheric CO_2 for loblolly pine fine roots but not for sweetgum. The increase in the ash-free heat of combustion of loblolly pine fine roots in elevated CO_2 resulted in a small increase in construction costs and R_C. The increase in construction costs from elevated CO_2 may be related to increases in the lignin concentration of fine roots (Eissenstat, 1992). In terms of glucose equivalents, lignin is one of the most expensive compounds to produce (Penning de Vries *et al.*, 1974) and elevated CO_2 has been found to increase the lignin concentration of roots (Booker *et al.*, 2000). Elevated CO_2 also affects R_C of other plant tissues. Construction costs and R_C were reduced in leaves with increasing atmospheric CO_2 (Wullschleger & Norby, 1992; Wullschleger *et al.*, 1992; Griffin *et al.*, 1993; Ziska & Bunce, 1994), which was primarily associated with changes in non-structural carbohydrates and to a lesser extent by lignin (Griffin *et al.*, 1996). Elevated CO_2 may result in the construction of more expensive structural compounds in fine roots.

The stimulation of annual R_G for loblolly pine under elevated CO_2 was caused primarily by the increase in fine root production (Table 2). Both increased R_C and fine root production, when extrapolated to the entire forest, contributed to an increase in R_G under elevated CO_2. But, the stimulation of fine root production by elevated CO_2 (87%) was considerably greater than the stimulation of R_C (37%). There was no detectable effect of elevated CO_2 on R_C in sweetgum and only increased root production contributed to the trend of greater R_G under elevated CO_2 for this species (Table 2). For these two forests it appears that an increase in fine root production is the primary factor contributing to the increase in annual R_G under elevated CO_2. Loblolly pine had lower fine root production than sweetgum and consequently also had lower annual R_G. Trees commonly exhibit an increase in fine root growth under elevated CO_2 (Norby *et al.*, 1986; Pregitzer *et al.*, 1995; Crookshanks *et al.*, 1998; Janssens *et al.*, 1998) and in these cases we would also predict an increase in annual R_G.

The vast majority of annual R_T was used to support cellular maintenance processes (R_M), both for loblolly pine and sweetgum. On average R_M^{annual} was 98% of R_T for loblolly pine and 86% for sweetgum, leaving a small proportion of energy annually for R_G and R_N. The proportion of R_T for fine roots allocated to R_M^{annual} in this study was comparable to a 20-yr old *Pinus radiata* stand, where R_T was 1940 g m^{-2} y^{-1} and R_M^{annual} was 76% of this total (Ryan *et al.*, 1996).

Our estimates of annual R_T for loblolly pine were similar to those for another young loblolly pine stand in the Piedmont of North Carolina (663–1062 g C m^{-2} y^{-1}; Maier & Kress, 2000), but considerably higher than those reported by Matamala & Schlesinger (2000; 349.4 and 401.0 g C m^{-2} $year^{-1}$ in ambient and elevated CO_2, respectively) at the same site. Differences in methodology may have contributed to this disparity, though this remains uncertain. Unlike this study, Matamala & Schlesinger (2000) measured fine root respiration on severed roots using an oxygen electrode. Over two thirds of the studies in the survey used severed roots and the average respiration was higher for attached than for detached roots. However, the distribution of rates reported in the literature was highly skewed towards lower values, and the greater average for attached roots was caused by a few studies reporting very high rates (> 40 nmol CO_2 g^{-1} s^{-1}; Fig. 2).

Annual soil CO_2 efflux from ambient and elevated plots in the pine forest were 928 g C m^{-2} and 1176 g C m^{-2}, respectively (Andrews & Schlesinger, 2001; Hamilton *et al.*, 2002), and the values for ambient and elevated plots in the sweetgum forest were 960 g C m^{-2} and 1271 g C m^{-2}, respectively (Norby *et al.*, 2002). The values of total soil CO_2 efflux in these forests are close to the average annual value of 1050 g C m^{-2} for 34 different forest types and similar to other temperate forests (Davidson *et al.*, 2002). In the pine forest, R_T estimated from this study contributed 69% and 45% of the total CO_2 efflux from ambient and elevated plots, respectively. Using the unusual C isotopic composition of newly fixed C in the elevated plots, Andrews *et al.* (1999) estimated that 45% of total soil CO_2 efflux originated from roots. The proportion of soil CO_2 from fine roots was somewhat lower in the sweetgum forest than in the pine forest (ambient, 25%; elevated, 36%).

To calculate the proportion of respiration to support R_N annually, we multiplied estimates of total nitrogen uptake in both forests by a literature value for the specific respiration associated with nitrogen uptake. The rate of respiration per unit nitrogen uptake by the trees was taken from a study of *Quercus suber*. This slow growing evergreen tree species, from xeric, nitrogen-poor soils (Mata *et al.*, 1996), was the best match to loblolly pine and sweetgum in our study (Table 3). Mata *et al.* (1996) also found similar rates to ours for tissue specific root maintenance (7.13 nmol CO_2 g^{-1} s^{-1} at 25°C) and growth respiration (51.8 g C kg^{-1} compare to R_C Table 2). The value of R_N was 1.8 g CO_2 g^{-1} N for *Quercus suber*, which was similar to studies of herbaceous plants (Table 3). For example, five studies of herbaceous plants found a narrow range of R_N 1.0–3.2 g CO_2 g^{-1} N (Table 3; Veen, 1980, 1981; Johnson, 1983; Van der Werf *et al.*, 1988; Poorter *et al.*, 1991; Bouma *et al.*, 1996). Because R_N and the absolute rates of nitrogen uptake are relatively small, the choice of the instantaneous value of R_N is not likely to have a large effect on our annual estimate.

In our study annual R_N was much greater in sweetgum than loblolly pine. This was because the uptake of nitrogen on a ground area basis in the sweetgum stand was nearly double the uptake of nitrogen in the loblolly pine stand. Annual R_N

Table 3 Published estimates of nitrogen uptake respiration (R_N) and corresponding values of instantaneous maintenance respiration (R_M) at 25°C and construction respiration (R_C) for various species. The value of R_N from Poorter *et al*. (1991) was based on total anion uptake and is a median of 24 herbaceous species. The values of R_N from the other studies were based on the uptake of nitrate.

Species	R_M (nmol CO_2 g^{-1} s^{-1})	R_C (g C kg^{-1})	R_N (g CO_2 g^{-1} N)	References
Zea mays	3.7	104.6	3.2	Veen (1980, 1981)
Helianthus annuus	–	–	2.0	Johnson (1983)
Carex species	4.9	60.5	1.8	Van der Werf *et al*. (1988)
24 Herbaceous species	–	64.8	1.7	Poorter *et al*. (1991)
Solanum tuberosum	13.3	47.0	1.0	Bouma *et al*. (1996)
Quercus suber	7.1	51.8	1.8	Mata *et al*. (1996)

required a small expenditure of energy in relation to annual R_T, but this proportion was greater for the sweetgum stand (4.1%) compared to the loblolly pine stand (1.1%). The higher nitrogen availability in the sweetgum stand resulted in lower fine root standing mass and R_T and greater R_N per unit fine root mass compared to the loblolly stand.

In summary, the majority of fine root respiration was used for maintenance and was not reduced by changes in the nitrogen content of the fine roots grown in elevated atmospheric CO_2, as initially hypothesized. The future investment of carbon in R_M will depend upon the balance between the C : N ratio of tissues and the size of fine root standing biomass. In the loblolly pine forest annual R_T was 26% and 19% of gross primary productivity (GPP) in ambient and elevated atmospheric CO_2, respectively (Hamilton *et al.*, 2002). Because of its large contribution to R_T and total soil CO_2 efflux, changes in R_M caused by warming or other factors have the potential to greatly alter carbon losses from forests to the atmosphere.

Acknowledgements

We thank E.G. O'Neill for providing fine root standing mass and production for the sweetgum stand and A.C. Finzi for measurements of carbon and nitrogen content of fine root tissue and nitrogen uptake rates of the loblolly pine stand. This research was supported by a grant (DE-FG02–95ER62127) from US Department of Energy, Office of Science, Biological and Environmental Research Program. Additional support was provided by a Dissertation Travel Grant from the Graduate College at the University of Illinois Urbana-Champaign, and a Summer Research Fellowship from the Program in Ecology and Evolutionary Biology at the University of Illinois Urbana-Champaign to KG. We gratefully acknowledge G.R. Hendrey, K.F. Lewin, J. Nagey and W.H. Schlesinger for operating and providing access to the FACTS-1 experiment, and J. Edeburn for managing the Duke Forest.

References

Allen RM. 1969. Racial variation in physiological characteristics of shortleaf pine roots. *Silvics Genetics* **18**: 40–43.

Andrews JA, Harrison KG, Matamala R, Schlesinger WH. 1999. Separation of root respiration from total soil respiration using carbon-13 labeling during free-air carbon dioxide enrichment (FACE). *Soil Science Society of America* **63**: 1429–1435.

Andrews JA, Schlesinger WH. 2001. Soil CO_2 dynamics, acidification and chemical weathering in a temperate forest with experimental CO_2 enrichment. *Global Biogeochemical Cycles* **15**: 149–162.

Barnard EL, Jorgensen JR. 1977. Respiration of fields-grown loblolly pine roots as influenced by temperature and root type. *Canadian Journal of Botany* **55**: 740–743.

BassiriRad H, Griffin KL, Reynolds JF, Strain BR. 1997. Changes in root NH^+_4 and NO^-_3 absorption rates of loblolly and ponderosa pine in response to CO_2 enrichment. *Plant and Soil* **190**: 1–9.

BassiriRad H, Tissue DT, Reynolds JF, Chapin FS III. 1996. Response of *Eriophorum vaginatum* to CO_2 enrichment at different soil temperatures: effects on growth, root respiration and PO_4^{3-} uptake kinetics. *New Phytologist* **133**: 423–430.

Booker FL, Shafer SR, Wei C, Horton SJ. 2000. Carbon dioxide enrichment and nitrogen fertilization effects on cotton (*Gossypium hirsutum* L.) plant residue chemistry and decomposition. *Plant and Soil* **220**: 89–98.

Bouma TJ, Broeckhuysen AGM, Veen BW. 1996. Analysis of root respiration of *Solanum tuberosum* as related to growth, ion uptake and maintenance of biomass. *Plant Physiology and Biochemistry* **34**: 795–806.

Bouma TJ, Bryla D, Li Y, Eissenstat DM. 2000. Is maintenance respiration in roots a constant? In: Stokes A, ed. *Developments in plant and soil sciences, vol. 87: the supporting roots of trees and woody plants: form, function and physiology*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 391–396.

Bouma TJ, Nielsin KL, Eissenstat DM, Lynch JP. 1997a. Estimating respiration of roots in soil: Interactions with soil CO_2, soil temperature and soil water content. *Plant and Soil* **195**: 221–232.

Bouma TJ, Nielsen KL, Eissenstat DM, Lynch JP. 1997b. Soil CO_2 concentration does not affect growth or root respiration in bean or citrus. *Plant, Cell & Environment* **20**: 1495–1505.

Boyer WD, Romancier RM, Ralston CW. 1971. Root respiration rates of four tree species grown in the field. *Forest Science* **17**: 492–493.

Burton AJ, Pregitzer KS, Zogg GP, Zak DR. 1996. Latitudinal variation in sugar maple fine root respiration. *Canadian Journal of Forest Research* **26**: 1761–1768.

Burton AJ, Pregitzer KS, Zogg GP, Zak DR. 1998. Drought reduces root respiration in sugar maple forests. *Ecological Applications* **8**: 771–778.

Burton AJ, Pregitzer KS. 2002. Measurement carbon dioxide concentration does not affect root respiration of nine tree species in the field. *Tree Physiology* **22**: 67–72.

Burton AJ, Zogg GP, Pregitzer KS, Zak DR. 1997b. Effect of measurement CO_2 concentration on sugar maple root respiration. *Tree Physiology* **17**: 421–427.

Callaway RM, DeLucia EH, Thomas EM, Schlesinger WH. 1994. Compensatory responses of CO_2 exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO_2 and temperature regimes. *Oecologia* **98**: 159–166.

Carey EV, DeLucia EH, Ball JT. 1996. Stem maintenance and construction respiration in *Pinus ponderosa* grown in different concentrations of atmospheric CO_2. *Tree Physiology* **16**: 125–130.

Carpenter JR, Mitchell CA. 1980. Root respiration characteristics of flood-tolerant and intolerant trees species. *Journal of American Society of Horticultural Science* **105**: 684–687.

Christensen NL, MacAller T. 1985. Soil mineral nitrogen transformations during succession in the Piedmont of North Carolina. *Soil Biology and Biochemistry* **17**: 675–681.

Clinton BD, Vose JM. 1999. Fine root respiration in mature eastern white pine (*Pinus strobus*) *in situ*: the importance of CO_2 in controlled environments. *Tree Physiology* **19**: 475–479.

Conlin TSS, Lieffers VJ. 1993. Anaerobic and aerobic CO_2 efflux rates from boreal forest conifer roots at low temperatures. *Canadian Journal of Forest Research* **23**: 767–771.

Cotrufo MF, Ineson P, Scott A. 1998. Elevated CO_2 reduces the nitrogen concentration of plant tissues. *Global Change Biology* **4**: 43–54.

Cox TL. 1975. Seasonal respiration rates of yellow-poplar roots by diameter classes. *Forest Science* **21**: 185–188.

Crookshanks M, Taylor G, Broadmeadow M. 1998. Elevated CO_2 and tree root growth: contrasting responses in *Fraxinus excelsior*, *Quercus petraea* and *Pinus sylvestris*. *New Phytologist* **138**: 241–250.

Cropper WP, Gholz HL. 1991. *In situ* needle and fine root respiration in mature slash pine (*Pinus elliottii*) trees. *Canadian Journal of Forest Research* **21**: 1589–1595.

Davidson EA, Savage K, Bolstad P, Clark DA, Curtis PS, Ellsworth DS, Hanson PJ, Law BE, Luo Y, Pregitzer KS, Randolph JC, Zak D. 2002. Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agricultural and Forest Meteorology* **113**: 39–51.

DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Lavine M, Matamala R, Mohan JE, Hendrey GR, Schlesinger WH. 1999. Net primary production of a forest ecosystem with experimental CO_2 enrichment. *Science* **284**: 1177–1179.

Drew AP, Ledig FT. 1981. Seasonal patterns of CO_2 exchange in the shoot and root of loblolly pine seedlings. *Botany Gazette* **142**: 200–205.

Edwards NT. 1991. Root and soil respiration responses to ozone in *Pinus taeda* L. seedlings. *New Phytologist* **118**: 315–321.

Eissenstat DM. 1992. Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition* **15**: 763–782.

Fahey TJ, Hughes JW. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *Journal of Ecology* **82**: 533–548.

Finzi AC, DeLucia EH, Hamilton JG, Richter DD, Schlesinger WH. 2002. The Nitrogen Budget of a pine forest under free air CO_2 enrichment. *Oecologia* **132**: 567–578.

Griffin KL, Thomas RB, Strain BR. 1993. Effects of nitrogen supply and elevated carbon dioxide on construction cost in leaves of *Pinus taeda* (L.) seedlings. *Oecologia* **95**: 575–580.

Griffin KL, Winner WE, Strain BR. 1996. Construction cost of loblolly and ponderosa pine leaves grown with varying carbon and nitrogen availability. *Plant, Cell & Environment* **19**: 729–738.

Hamilton JG, DeLucia EH, George K, Naidu SL, Finzi AC, Schlesinger WH. 2002. Forest carbon balance under elevated CO_2. *Oecologia* **131**: 250–260.

Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* **48**: 115–146.

Hartz-Rubin JS, DeLucia EH. 2001. Canopy development of a model herbaceous community exposed to elevated atmospheric CO_2 and soil nutrients. *Physiologia Plantarum* **113**: 258–266.

Hendrey GR, Ellsworth DS, Lewin KF, Nagy J. 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. *Global Change Biology* **5**: 293–309.

Janssens IA, Crookshanks M, Taylor G, Ceulemans R. 1998. Elevated atmospheric CO_2 increases fine root production, respiration, rhizosphere respiration and soil CO_2 efflux in Scots pine seedlings. *Global Change Biology* **4**: 871–878.

Johnson IR. 1983. Nitrate uptake and respiration in roots and shoots: a model. *Physiologia Plantarum* **58**: 145–147.

Johnson-Flanagan AM, Owens JN. 1986. Root respiration in white spruce (*Picea glauca* [Moench] Voss) seedlings in relation to morphology and environment. *Plant Physiologia* **81**: 21–25.

Kelting DL, Burger JA, Edwards GS. 1995. The effects of ozone on the root dynamics of seedlings and mature red oak (*Quercus rubra* L.). *Forest Ecology and Management* **79**: 197–206.

Lafond A. 1950. The rate of respiration of jack pine root tips as influenced by extracts from different types of humus. *Soil Science Society Proceedings* **15**: 357–359.

Lahde E. 1966. Studies on the respiration rate in the different parts of the root systems of pine and spruce seedlings and its variations during the growing season. *Acta Forestalia Fennica* **8**: 5–24.

Lambers H, Szaniawski RK, de Visser R. 1983. Respiration for growth, maintenance and ion uptake. An evaluation of concepts, methods, values, and their significance. *Physiologia Plantarum* **58**: 556–563.

Maier CA, Kress LW. 2000. Soil CO_2 evolution and root respiration in 11-year-old loblolly pine (*Pinus taeda*) plantations as affected by moister and nutrient availability. *Canadian Journal of Forest Research* **30**: 347–359.

Marshall JD, Perry DA. 1987. Basal and maintenance respiration of mycorrhizal and nonmycorrhizal root systems of conifers. *Canadian Journal of Forest Research* **17**: 872–877.

Mata C, Scheurwater I, Martins-Laucao MA, Lambers H. 1996. Root respiration, growth and nitrogen uptake of *Quercus suber* seedlings. *Plant Physiology and Biochemistry* **34**: 727–734.

Matamala R, Schlesinger WH. 2000. Effects of elevated atmospheric CO_2 on fine root production and activity in an intact temperate forest ecosystem. *Global Change Biology* **6**: 967–979.

McCreary DD, Zaerr JB. 1987. Root respiration has limited value for assessing Douglas-fir seedling quality. *Canadian Journal of Forest Research* **17**: 1144–1147.

McDowell NG, Marshall JD, Qi J, Mattson K. 1999. Direct inhibition of maintenance respiration in western hemlock roots exposed to ambient soil carbon dioxide concentrations. *Tree Physiology* **19**: 599–605.

Nobel PS, Alm DM, Cavelier J. 1992. Growth respiration, maintenance respiration and structural-carbon costs for roots of three desert succulents. *Functional Ecology* **6**: 79–85.

Norby RJ, Hanson PJ, O'Neill EG, Tschaplinski TJ, Weltzin JF, Hansen RA, Cheng W, Wullschleger SD, Gunderson CA, Edwards NT, Johnson DW. 2002. Net primary productivity of a CO_2-enriched deciduous forest and the implications for carbon storage. *Ecological Applications* **12**: 1261–1266.

Norby RJ, O'Neill EG, Luxmoore RJ. 1986. Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient poor soil. *Plant Physiology* **82**: 83–89.

Norby RJ, Todd DE, Fults J, Johnson DW. 2001. Allometric determination of tree growth in a CO_2-enriched sweetgum stand. *New Phytologist* **150**: 477–487.

Penning de Vries FWT, Brunsting AHM, Van Laar HH. 1974. Products requirements and efficiency of biosynthesis: a quantitative approach. *Journal of Theoretical Biology* **45**: 339–377.

Poorter H, Van Der Werf A, Atkin OK, Lambers H. 1991. Respiratory energy requirements of roots vary with the potential growth rate of a plant species. *Physiologia Plantarum* **83**: 469–475.

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC, Zak DR. 1998. Variation in sugar maple root respiration with root diameter and soil depth. *Tree Physiology* **18**: 665–670.

Pregitzer KS, Zak DR, Curtis PS, Kubiske ME, Teeri JA, Vogel CS. 1995. Atmospheric CO_2, soil nitrogen and turnover of fine roots. *New Phytologist* **129**: 579–585.

Rakonczay Z, Seiler JR, Kelting DL. 1997a. Carbon efflux rates of fine roots of three tree species decline shortly after excision. *Environmental and Experimental Botany* **38**: 243–249.

Rakonczay Z, Seiler JR, Samuelson LJ. 1997b. A method for the in situ measurements of fine root gas exchange of forest trees. *Environmental and Experimental Botany* **37**: 107–113.

Rouhier H, Billès G, Billès L, Bottner P. 1996. Carbon fluxes in the rhizosphere of sweet chestnut seedlings (*Castanea sativa*) grown under two atmospheric CO_2 concentrations: ^{14}C partitioning after pulse labeling. *Plant and Soil* **180**: 101–111.

Ryan MG. 1991. Effects of climate change on plant respiration. *Ecological Applications* **1**: 157–167.

Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtrie RE. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* **16**: 333–343.

Ryan MG, Lavigne MB, Gower ST. 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research* **102**: 28871–28883.

Sowell JB, Spomer GG. 1986. Ecotypic variation in root respiration rate among elevational populations of *Abies lasiocarpa and Picea engelmannii*. *Oecologia* **68**: 375–379.

Steinbeck K, McAlpine RG. 1966. Inter- and Intra-specific differences in the root respiration rates of four hardwood species. *Forest Science* **12**: 473–476.

Szaniawski RK, Adams MS. 1974. Root respiration of *Tsuga canadensis* seedlings as influenced by intensity of net photosynthesis and dark respiration of shoots. *American Midland Naturalist* **91**: 464–468.

Thierron V, Laudelout H. 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. *Canadian Journal of Forest Research* **2**: 1142–1148.

Tjoelker MG, Oleksyn J, Reich PB. 1999. Acclimation of respiration to temperature and CO_2 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology* **5**: 679–691.

Tripepi RR, Mitchell CA. 1984. Stem hypoxia and root respiration of flooded maple and birch seedlings. *Physiologia Plantarum* **60**: 567–571.

Van der Werf A, Kooijman A, Welschen R, Lambers H. 1988. Respiratory energy costs for the maintenance of biomass for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. *Physiologia Plantarum* **72**: 483–491.

Veen BW. 1980. Energy cost of ion transport. In: Rains DW, Valentine RC, Hollaender A, eds. *Genetic engineering of osmoregulation. Impact on plant productivity for food, chemicals and energy.* New York, USA: Plenum, 187–195.

Veen BW. 1981. Relation between root respiration and root activity. *Plant and Soil* **63**: 73–76.

de Visser R, Lambers H. 1983. Growth and the efficiency of root respiration of *Pisum sativum* as dependent on the source of nitrogen. *Physiologia Plantarum* **58**: 533–543.

Vogt KA, Grier CC, Meier CE, Edmonds RL. 1982. Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in Western Washington. *Ecology* **63**: 370–380.

Voigt GK. 1953. The effects of fungicides, insecticides, herbicides and fertilizer salts on the respiration of root tips of tree seedlings. *Soil Science Society Proceedings* **17**: 150–152.

Walters MB, Kruger EL, Reich PB. 1993. Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. *Oecologia* **96**: 219–231.

Weger HG, Guy RD. 1991. Cytochrome and alternative pathway respiration in white spruce (*Picea glauca*) roots. Effects of growth and measurement temperature. *Physiologia Plantarum* **83**: 675–681.

Williams K, Percival F, Merino J, Mooney HA. 1987. Estimation of tissue construction cost from heat of combustion and organic nitrogen content. *Plant, Cell & Environment* **10**: 725–734.

Wullschleger SD, Norby RJ. 1992. Respiratory cost of leaf growth and maintenance in white oak saplings exposed to atmospheric CO_2 enrichment. *Canadian Journal of Forest Research* **22**: 1717–1721.

Wullschleger SD, Norby RJ, Gunderson CA. 1992. Growth and maintenance respiration in leaves of *Liriodendron tulipifera* L. exposed to long-term carbon dioxide enrichment in the field. *New Phytologist* **121**: 515–523.

Ziska LH, Bunce JA. 1994. Direct and indirect inhibition of single leaf respiration by elevated CO_2 concentrations: interaction with temperature. *Physiologia Plantarum* **90**: 130–138.

Zogg GP, Zak DR, Burton AJ, Pregitzer KS. 1996. Fine root respiration in a northern hardwood forests in relation to temperature and nitrogen availability. *Tree Physiology* **16**: 719–725.

Appendix 1

Literature survey of fineroot respiration rates of tree species at 15°C (R_{15}). Respiration rates measured on seedlings are indicated by 'S' and rates measured on mature trees are indicated by 'M'. Respiration rates measured on roots detached from the plant are indicated by 'D' and rates measured on roots that remained attached to the plant are indicated by 'A'

Species	Category	R_{15} (nmol CO_2 g^{-1} s^{-1})	Author
Abies lasiocarpa	S, D	25.00–29.37	Sowell & Spomer (1986)
Acer rubrum	S, D	23.79	Steinbeck & McAlpine (1966)
Acer rubrum	S, D	0.53–0.97	Carpenter & Mitchell (1980)
Acer rubrum	S,D	0.98–1.47	Tripepi & Mitchell (1984)
Acer rubrum	M, A	1.90	Rakonczay *et al*. (1997b)
Acer rubrum	M, D	2.07–6.40	Rakonczay *et al*. (1997a)
Acer saccharum	S, D	0.27–0.98	Carpenter & Mitchell (1980)
Acer saccharum	S, D	0.82–0.85	Tripepi & Mitchell (1984)
Acer saccharum	S, A	3.98–35.05	Walters *et al*. (1993)
Acer saccharum	M, D	2.91–5.89	Burton *et al*. (1996)
Acer saccharum	M, D	2.26–5.31	Burton *et al*. (1997)
Acer saccharum	M, D	0.90–6.42	Pregitzer *et al*. (1998)
Betula alleghaniensis	S, A	6.37–56.08	Walters *et al*. (1993)
Betula nigra	S, D	3.86–8.05	Boyer *et al*. (1971)
Betula nigra	S, D	0.74–1.38	Tripepi & Mitchell (1984)
Betula papyrifera	S, A	5.29–79.66	Walters *et al*. (1993)
Betula pendula	S, D	0.83–1.09	Tripepi & Mitchell (1984)
Citrus volkameriana	S, A	2.50–12.50	Bouma *et al*. (1997a)
Citrus volkameriana	S, A	1.06–12.37	Bouma *et al*. (1997b)
Citrus volkameriana	S, A	0.40–5.37	Bouma *et al*. (2000)
Fraxinus excelsoir	S, D	6.50–7.30	Crookshanks *et al*. (1998)
Larix laricina	S, A	6.26–9.35	Conlin & Lieffers (1993)
Liquidambar styraciflua	M, A	5.08–5.88	George *et al*. (this study)
Liriodendron tulipifera	S, D	6.97–13.57	Boyer *et al*. (1971)
Liriodendron tulipifera	S, D	17.46	Steinbeck & McAlpine (1966)
Liriodendron tulipifera	S, D	1.30–4.35	Cox (1975)
Malus spps.	M, D	5.42–15.12	Bouma *et al*. (2000)
Ostrya virginiana	S, A	6.37–58.63	Walters *et al*. (1993)
Picea abies	S, D	3.93–7.80	Lahde (1966)
Picea engelmannii	S, D	27.48–35.61	Sowell & Spomer (1986)
Picea glauca	S, D	0.39–1.72	Johnson-Flanagan & Owens (1986)
Picea glauca	S, A	3.90–8.07	Conlin & Lieffers (1993)
Picea mariana	S, A	3.50–9.72	Conlin & Lieffers (1993)
Pinus banksiana	S, D	5.55–6.40	Lafond (1950)
Pinus banksiana	S, D	19.40	Voigt (1953)
Pinus banksiana	S, A	4.17–11.04	Conlin & Lieffers (1993)
Pinus contorta	S, A	5.61–12.78	Conlin & Lieffers (1993)
Pinus echinata	S, D	11.26–22.52	Allen (1969)
Pinus elliottii	M, D	0.91–1.66	Cropper & Gholz (1991)
Pinus ponderosa	M, D	0.56–0.92	Marshall & Perry (1987)
Pinus ponderosa	S, D	4.72–6.05	BassiriRad *et al*. (1997)
Pinus resinosa	S, D	27.02	Voigt (1953)
Pinus radiata	M, A	2.10–13.90	Ryan *et al*. (1996)
Pinus strobus	M, D	2.17–4.31	Rakonczay *et al*. (1997a)
Pinus strobus	M, A	0.09–5.72	Clinton & Vose (1999)
Pinus sylvestris	S, D	4.16–8.09	Lahde (1966)
Pinus sylvestris	S, D	8.19–8.45	Crookshanks *et al*. (1998)
Pinus sylvestris	S, D	3.42–4.95	Janssens *et al*. (1998)
Pinus taeda	S, D	6.29–11.10	Boyer *et al*. (1971)
Pinus taeda	S, D	1.55–7.66	Barnard & Jorgensen (1977)
Pinus taeda	S, D	2.05–29.60	Drew & Ledig (1981)
Pinus taeda	S, A	0.10–0.20	Edwards (1991)
Pinus taeda	S, A	7.74–10.28	BassiriRad *et al*. (1997)
Pinus taeda	M, A	3.46–4.47	George *et al*. (this study)
Prunus serotina	M, A	1.40	Rakonczay *et al*. (1997b)

Appendix 1 *Continued*

Species	Category	R_{15} (nmol CO_2 g^{-1} s^{-1})	Author
Pseudotsuga menziesii	S, D	0.04–0.09	McCreary & Zaerr (1987)
Quercus petraea	S, D	7.50–8.50	Crookshanks *et al*. (1998)
Quercus rubra	S, A	3.19–25.49	Walters *et al*. (1993)
Quercus rubra	S, D	1.83–4.71	Kelting *et al*. (1995)
Quercus rubra	M, D	1.37–4.54	Rakonczay *et al*. (1997a)
Quercus rubra	M, A	2.00	Rakonczay *et al*. (1997b)
Quercus suber	S, A	3.75–5.53	Mata *et al*. (1996)
Robinia pseudoacacia	S, D	31.33	Voigt (1953)
Salix babylonica	S, D	25.83	Steinbeck & McAlpine (1966)
Salix babylonica	S, D	2.37–4.54	Boyer *et al*. (1971)
Salix nigra	S, D	29.75	Steinbeck & McAlpine (1966)
Taxodium distichum var. distichum	S, D	0.60–1.21	Carpenter & Mitchell (1980)
Tsuga canadensis	S, A	11.05–16.74	Szaniawski & Adams (1974)
Tsuga heterophylla	S, A	1.38–29.75	McDowell *et al*. (1999)
Mixed hardwoods	M, D	5.57–9.85	Fahey & Hughes (1994)
Mixed hardwoods (75% *Acer sacharum*)	M, D	4.63–6.08	Zogg *et al*. (1996)