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Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status

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Summary We measured respiration of 20-year-old *Pinus radiata* D. Don trees growing in control (C), irrigated (I), and irrigated + fertilized (IL) stands in the Biology of Forest Growth experimental plantation near Canberra, Australia. Respiration was measured on fully expanded foliage, live branches, boles, and fine and coarse roots to determine the relationship between CO_2 efflux, tissue temperature, and biomass or nitrogen (N) content of individual tissues. Efflux of CO_2 from foliage (dark respiration at night) and fine roots was linearly related to biomass and N content, but N was a better predictor of CO_2 efflux than biomass. Respiration (assumed to be maintenance) per unit N at 15 °C and a CO_2 concentration of 400 μmol mol^{-1} was 1.71 μmol s^{-1} mol^{-1} N for foliage and 11.2 μmol s^{-1} mol^{-1} N for fine roots. Efflux of CO_2 from stems, coarse roots and branches was linearly related to sapwood volume (stems) or total volume (branches + coarse roots) and growth, with rates for maintenance respiration at 15 °C ranging from 18 to 104 μmol m^{-3} s^{-1}. Among woody components, branches in the upper canopy and small diameter coarse roots had the highest respiration rates. Stem maintenance respiration per unit sapwood volume did not differ among treatments.

Annual C flux was estimated by summing (1) dry matter production and respiration of aboveground components, (2) annual soil CO_2 efflux minus aboveground litterfall, and (3) the annual increment in coarse root biomass. Annual C flux was 24.4, 25.3 and 34.4 Mg ha^{-1} $year^{-1}$ for the C, I and IL treatments, respectively. Total belowground C allocation, estimated as the sum of (2) and (3) above, was equal to the sum of root respiration and estimated root production in the IL treatment, whereas in the nutrient-limited C and I treatments, total belowground C allocation was greater than the sum of root respiration and estimated root production, suggesting higher fine root turnover or increased allocation to mycorrhizae and root exudation. Carbon use efficiency, the ratio of net primary production to assimilation, was similar among treatments for aboveground tissues (0.43–0.50). Therefore, the proportion of assimilation used for construction and maintenance respiration on an annual basis was also similar among treatments.

Keywords: biomass, carbon use efficiency, CO_2 efflux, dry matter production, fertilization, irrigation, nitrogen content.

Introduction

Little is known about the mechanisms underlying the large variability in measured shoot and leaf respiration rates, or about the relationship between respiration rates and other components of leaf physiology (e.g., photosynthetic activity, enzyme content) or the environment. A better understanding of respiratory physiology will enable us to improve models of leaf-level carbon exchange and aid in scaling fluxes from the leaf to the canopy. At the whole-plant and plant community levels, we need more detailed information about the magnitude of respiration fluxes, and we also need to to know whether the fraction of assimilation used for respiration varies over a relevant time scale (e.g., a year for a forest). Knowing the size of respiratory fluxes is important for deriving carbon budgets, validating models and comparing scaled chamber measurements with ecosystem-scale flux measurements. Knowing whether the fraction of assimilation used for production (carbon use efficiency, CUE) varies is also important for validating models and potentially for simplifying models of regional and global carbon balance.

Respiration, especially maintenance respiration (R_m), has been linked with tissue nitrogen content (Jones et al. 1978, Ryan 1991, 1995), because typically 90% of the nitrogen (N) in plant cells is in protein, which needs energy for replacement and repair (about 20% of R_m, Bouma et al. 1994) and which is tightly linked with cellular activity. However, respiration rates per unit tissue N can vary (McCree 1982, 1983, Szaniawski and Kielkiewicz 1982, Ryan 1995), and the relationship fails occasionally (Byrd et al. 1992). Understanding how respiration rates vary with nutrition within a single species may help explain the plasticity of respiration rates with respect to nutrition. Such information may be critical for managing the many ecosystems that are currently receiving high N inputs from atmospheric deposition (Wright et al. 1995).

There is evidence that the annual costs of respiration are between 30 and 70% of assimilation (Edwards et al. 1980, Ryan et al. 1994), suggesting that small changes in annual fluxes could have a large impact on net production, particularly if some components (such as wood production) are more plastic than others. Because of the strong dependence of respiration rates on temperature, many models of ecosystem response to climate warming show a decrease in CUE (Ryan et al. 1996). Other analyses suggest that CUE might decrease with increasing woody biomass (Ryan et al. 1994). However, because growth, cellular activity and respiration are tightly linked in plants (Amthor 1994), changes in CUE may be fairly conservative (Gifford 1994). A conservative CUE would simplify models, particularly for deriving global scale carbon budgets.

Because nutrition affects carbon allocation and tissue nutrient concentrations in forests (Gower et al., unpublished observations), and because of the strong link between respiration and tissue nutrient contents, we hypothesized that changes in stand nutrition alter CUE. In this study, we determined how induced changes in nutrient status influence respiration rates of individual tissues (foliage, fine roots and woody tissue). We then developed relationships between respiration and nutrient content or biomass to scale chamber measurements to annual CO_2 efflux from respiration. Finally, we calculated how changes in tissue nutrient content and allocation affect CUE for *Pinus radiata* D. Don stands.

Methods

Study area

The Biology of Forest Growth experimental plantation (Benson et al. 1992, Raison and Myers 1992) is located at 630 m elevation in the Pierce's Creek Forest about 20 km west of Canberra in the Australian Capital Territory (35°21′ S, 148°56′ E). The site was cleared of the original eucalypt woodland in 1934, broadcast burned and planted with *P. radiata* in 1935. The pine crop was clear-felled in 1972, residues burned, and the second pine stand planted in 1973.

The site experiences mild winters (July average minimum and maximum temperatures are 1 and 11 °C) and warm summers (January average minimum and maximum temperatures are 14 and 28 °C). Summer maxima may reach 35–40 °C when relative humidity is low (< 10%). Annual rainfall averages 791 mm, but is highly variable, and summer droughts of 2–3 months are common.

The soil is a yellow podzolic (Stace et al. 1968) or Typic Albaqualf (Soil Survey Staff 1975) derived from granite. It has a duplex profile comprising a sandy A horizon extending to about 0.40 m depth, and a dense (bulk density 1.7 Mg m^{-3}) B horizon of clay and gravel overlaying a C horizon of weathering granite (> 1 m). The soil has a low N-supplying capacity (Raison et al. 1992*b*) but provides adequate P for tree growth (Raison et al. 1990). Soil water storage capacity is 75 mm in the A horizon where most fine roots are concentrated, and 250 mm to a depth of 2 m (Myers and Talsma 1992). Because of low soil water storage and a high probability of summer drought, trees often experience severe water stress during the late summer and early autumn (Myers and Talsma 1992).

In winter 1983, several irrigation and fertilization treatments were established on 0.25-ha plots. The treatments we used were control (C), irrigated (I) and irrigated + liquid fertilized (IL). The irrigation treatment maintained soil water near field capacity, and approximately doubled annual rainfall. The IL treatment, which commenced in spring (September) 1984, provided a balanced nutrient input weekly in the irrigation water and was varied seasonally to match tree demand; annual inputs of N totaled 300 kg ha^{-1}. After 1990, mineralization of N in the soil and forest floor of the IL treatment was considered to be in excess of tree requirements, and fertilization was halted. The stand was thinned in October 1988, removing 30% of the basal area for the IL treatment and 50% of the basal area for the I and C treatments.

We measured respiration in the C, I and IL treatments in February–June 1993, when the trees were 20 years old. Characteristics of the sample plots are given in Table 1.

Respiration measurements

At night in February and March 1993, foliar maintenance respiration (R_m, see Amthor 1989) was determined by measuring CO_2 efflux from fully expanded foliage on about 30 samples per treatment. Samples were distributed among three canopy positions (canopy thirds) and three foliage age classes (current whorl, current + 1, and older than current + 1), with about three samples for each age class at each canopy position. In the C and I treatments, shoots typically flushed once per year, whereas shoots typically flushed more than once per year in the IL treatment. Measurements were taken from scaffolding towers adjacent to three to five trees.

In March 1993, CO_2 efflux from fine roots was measured on 15 samples of roots (< 2 mm in diameter) per treatment in the litter layer or upper A horizon. Roots were isolated by gently digging the soil, removing loose organic matter, and moistening the root mat before placing roots in the measuring cuvette. Cuvette CO_2 concentration ($[CO_2]$) averaged 400 ppm during respiration measurements. The respiration from these root

Table 1. Characteristics of *Pinus radiata* stands in June 1993; C = control, I = irrigated, IL = irrigated + fertilized, and LAI = leaf area index.

Parameter	C	I	IL
Density ha^{-1}	275	304	412
Basal area (m^2 ha^{-1})	23.3	28.3	50.3
Projected LAI (m^2 m^{-2})	3.1	3.0	4.6
Average diameter (m)	0.325	0.338	0.390
Average height (m)	21.2	23.3	23.9
Stem biomass (Mg ha^{-1})	83.9	107	170
Branch biomass (Mg ha^{-1})	18.9	18.0	24.7
Bark biomass (Mg ha^{-1})	8.1	10.4	18.2
Foliage biomass (Mg ha^{-1})	9.3	7.8	13.3
Coarse root biomass (Mg ha^{-1})	25.9	33.0	64.0
Fine root biomass (Mg ha^{-1})	2.6	3.3	1.8

samples was considered to be maintenance respiration, because only 5% of the samples contained root tips. The average soil [CO_2] of pore space around the sample roots was determined by collecting, with a syringe, twenty 15-ml samples per treatment and analyzing the samples with an infrared gas analyzer (IRGA) (CI-301, CID Inc., Moscow ID) in absolute mode.

The value of R_m for woody tissues (stems, branches and coarse roots) was estimated either from CO_2 efflux in autumn or winter (stems, coarse roots), or by subtracting construction respiration (estimated from volume growth) from CO_2 efflux measured in growing tissues. Stem CO_2 efflux was measured on 15 stems in each of the three treatment plots as described by Ryan (1990) and Ryan et al. (1995). We used a fixed plate (to ensure a gas-tight seal and resampling at the same location) and a removable chamber (to allow normal ventilation of the bole between sampling). A 12-mm-wide aluminum plate (inside dimension of 100×250 mm) was attached to the bark with putty after removing loose bark. A neoprene gasket was attached to the outer surface of the plate. Plates were located on the south side of the tree 1.4 m above the ground. To measure CO_2 flux, we attached a Plexiglas mixing chamber to the plate and connected the chamber to the IRGA. Stem respiration was measured on February 27, March 8 and 17, May 3–6, and July 22–24, 1993. Additionally, CO_2 efflux was measured on March 12, at elevations of 1.4, 12 and 16 m for two trees per treatment adjacent to the scaffolding towers.

On March 12–14, CO_2 efflux from branches was measured at night on nine to ten branches per treatment. Samples were distributed evenly among canopy thirds. Chambers were made of a hollow, split Plexiglas block and were clamped onto the branch over neoprene gaskets at each end of the chamber. Efflux of CO_2 from coarse roots was measured on five samples per treatment on March 17 using chambers similar to those used for branches.

For all tissues, CO_2 efflux was measured with an open system IRGA (LCA3, Analytical Development Corp., Hoddesdon, Herts, U.K., or CI-301, CID Inc.), with flow rates through the chamber of 140–300 μmol s^{-1}. Internal volumes of the chambers ranged from 0.00005–0.0002 m^3; air inside the chambers was mixed by a small fan. For all measurements, reference air was drawn through a 0.02 m^3 mixing chamber to maintain a stable CO_2 concentration. Flux data were recorded after the difference in [CO_2] between reference air and chamber air was stable for 3 min. Tissue temperature was measured for all samples with copper-constantan thermocouples.

Temperature response

The temperature responses of foliar and fine root respiration were measured in a temperature-controlled cuvette (Hubbard et al. 1995) with measurements at 5, 15 and 25 °C. Foliage temperature response was measured on current-year foliage for three samples per treatment. Fine root temperature response was measured on three samples in the control plot. Temperature responses of stems, branches and coarse roots were estimated by continuously monitoring CO_2 efflux and temperature of one stem, midcanopy branch, or coarse root for 20–50 h. Individual flux measurements were standardized to 15 °C using tissue-specific values of temperature response (Q_{10}).

Tissue analysis

Foliage was dried at 70 °C for 24 h and weighed to ± 0.01 g. Fine roots were sorted into two size classes (> 1 mm, < 1 mm) before drying. Samples were ground in a Wiley mill to pass a 40-mesh screen, digested in H_2SO_4-H_2O_2, and analyzed for N and P colorimetrically (Heffernan 1985). For stems, we estimated sapwood volume from diameter outside the bark, using a local relationship between diameter and bark thickness (R.J. Raison, unpublished data) and assuming sapwood was 95% of the total volume (based on a sample of felled trees from an adjacent stand). Sapwood volume assigned to the chamber was estimated by multiplying sapwood volume determined for the cylinder under the chamber by the ratio of chamber width to the cylinder's circumference (Ryan 1990). Volume growth was estimated similarly, using the difference between diameter outside the bark for successive measurements. For branches and coarse roots, we measured diameter outside the bark and estimated bark thickness using samples of similar size from nearby recently felled trees.

Statistical analysis

We used regression analyses to determine how R_m of foliage and fine roots at 15 °C varied with N or P concentration, and how R_m of stems, branches and coarse roots at 15 °C varied with sapwood or total volume and wood growth. Regression slopes for the relationship between R_m at 15 °C and N concentration ([N]) or volume were also compared among treatments (all tissues), canopy position (foliage, branches), and foliage age (foliage) by the MANOVA procedure in SPSS/PC. Differences in respiration with tree height were assessed by a repeated measures analysis of variance and the MANOVA procedure in SPSS/PC. If the intercept in a linear regression was not significant, we estimated a zero-intercept slope and calculated R^2 as $1 - [\sum(Y_i - \hat{Y}_i^2)/\sum(Y_i - \bar{Y})^2]$ (Kvalseth 1985).

Scaling to an annual budget

We estimated an annual budget for respiration for each treatment from measured or estimated biomass (foliage, fine roots, branches, stems, bark and coarse roots), tissue-specific respiration rates, tissue-specific temperature response, and daily maximum and minimum temperatures. Foliage maintenance respiration in the day was estimated as 0.6 times the dark respiration rate (Kirschbaum and Farquhar 1984). Construction respiration for all tissues was estimated using dry matter production and a construction constant of 0.25 (Penning de Vries 1975, Sprugel et al. 1995).

Stem and branch biomass were estimated by allometric relationships with stand basal area, height and density (Madgwick 1994). Bark biomass was estimated with a tree-level allometric relationship using individual tree diameter and height (Snowdon and Benson 1992). Coarse root biomass was estimated by an allometric relationship with stem diameter

(Jackson and Chittenden 1981); the relationship was developed using data from a wide range of *P. radiata* sites and was conservative with respect to site fertility. Biomass estimates for bark and coarse roots were calculated for each tree in a treatment, summed and extrapolated to a hectare basis. Annual growth for a component was calculated as the difference in biomass at the beginning and end of the year. Foliage biomass was estimated from the leaf area index (LAI) determined with a DEMON leaf area analyzer (CSIRO, Canberra, ACT, Australia) and treatment-specific values for leaf area per unit mass (Raison et al. 1992*c*). Foliar N content was estimated from the N content of the respiration samples.

Fine root biomass was estimated for soil layers 0–0.05, 0.05–0.10 and 0.10–0.20 m based on 12 cores (0.1 m diameter) per treatment in August 1992 and March 1993 (S. Pongracic, unpublished data). Fine root production was estimated from fine root biomass by assuming an annual turnover of 1.45 (cf. Santantonio and Grace 1987, Santantonio and Santantonio 1987*a*). Fine root respiration was estimated from fine root N content by assuming (1) that soil CO_2 concentrations reduce respiration (Qi et al. 1994), and (2) that the measured respiration was maintenance respiration. Efflux of CO_2 from fine roots measured at a $[CO_2]$ of 400 μmol mol^{-1} was adjusted to the $[CO_2]$ (μmol mol^{-1}) of the upper mineral soil using a relationship between CO_2 efflux (R) and soil $[CO_2]$ developed from other studies of pine roots (M.G. Ryan and R.M. Hubbard, unpublished data):

$$R \text{ at } [CO_2 = x] = R \text{ at } [CO_2 = y] \times 1.00924\exp(-0.00136(y - x)). \quad (1)$$

If soil and forest floor organic matter and coarse and fine root biomass are in approximately steady state, total belowground carbon allocation (B_c) can be estimated as the difference between annual soil CO_2 efflux and aboveground litterfall (Raich and Nadelhoffer 1989). For the treatment stands, soil and forest floor organic matter and fine root biomass were approximately in steady state (S. Pongracic, unpublished data), but coarse root biomass increased substantially over the sample year. Therefore, we added coarse root annual increment to the difference between annual soil CO_2 efflux and annual aboveground litterfall to estimate B_c. Soil CO_2 efflux was measured every 2 weeks with a CO_2 absorbent (soda-lime) in a static chamber (0.4 m diameter, 0.1 m headspace, inserted 0.02 m into mineral soil). Annual soil CO_2 efflux was estimated by extrapolating the biweekly measurements using soil temperature. The static chamber fluxes were within 20% of fluxes measured in the same chambers with an IRGA (LI-6250, Li-Cor, Inc., Lincoln, NE) across a wide range of soil CO_2 fluxes (S. Pongracic, unpublished data).

We estimated canopy assimilation from winter 1992 to winter 1993 using a process-oriented model developed from earlier studies at the same site (BIOMASS, McMurtrie et al. 1990, 1992, McMurtrie and Landsberg 1992). Climate forcing was obtained from a weather station located on site, and simulations were run using treatment-specific values of LAI, woody biomass and foliar N. Canopy assimilation from biomass was compared with the sum of fluxes of respiration and productivity. Standing crops for each component are given in Table 1.

Results

Foliage

Foliar N, P and K concentrations differed significantly among treatments ($P < 0.01$), and foliar [N] differed significantly among foliage age classes and canopy positions ($P < 0.01$) (Table 2). Nitrogen concentration followed the usual pattern of decreases with leaf age and depth in the canopy (data not shown). Phosphorus concentration was significantly lower in the I treatment than in the C or IL ($P < 0.01$) treatments, but did not vary significantly with foliage age ($P = 0.32$) or canopy position ($P = 0.07$). Potassium concentration was significantly greater in the IL treatment than in the C or I treatments ($P = 0.01$), but did not vary significantly with foliage age ($P = 0.63$) or canopy position ($P = 0.12$).

Foliar dark respiration per unit leaf mass for fully expanded foliage at 15 °C varied from 0.45 to 2.7 μmol kg^{-1} s^{-1} and was strongly correlated with foliar [N] (Figure 1). Regression slopes between respiration and [N] did not differ significantly among treatments ($P = 0.28$). However, the relationship between respiration and [N] was more variable for the IL treatment than for the C and I treatments (Figure 1). Because the intercept for a regression that combined the three treatments was not significant ($P = 0.13$), we fitted a zero-intercept linear regression to data from all treatments combined: $R_m = 1.71N$ ($R^2 = 0.38$, $P < 0.01$, $n = 93$), where R_m is CO_2 efflux from foliar maintenance respiration at 15 °C (μmol kg^{-1} s^{-1}), and N is foliar [N] (mol kg^{-1}). Foliar P concentration ([P]) was correlated with foliar [N] ($r = 0.59$, $P < 0.01$), but [P] did not explain significant additional variation in R_m ($P = 0.53$). There was no difference among treatments in the response of respiration to

Table 2. Mean (SE) foliar N, P and K concentrations as a percent of oven-dry mass by foliage age class for three treatments. Values are averages of all canopy positions.

Foliage age	Control	Irrigated	Irrigated + fertilized
Nitrogen			
C	1.34 (0.04)	1.08 (0.03)	1.43 (0.02)
C + 1	1.18 (0.05)	0.94 (0.06)	1.32 (0.04)
> C + 1	0.96 (0.04)	0.88 (0.04)	1.07 (0.05)
All	1.22 (0.04)	0.99 (0.03)	1.35 (0.03)
Phosphorus			
C	0.16 (0.01)	0.11 (0.01)	0.14 (0.01)
C + 1	0.14 (0.01)	0.10 (0.01)	0.14 (0.01)
> C + 1	0.14 (0.01)	0.08 (0.01)	0.12 (0.01)
All	0.15 (0.01)	0.10 (0.01)	0.14 (0.01)
Potassium			
C	0.87 (0.02)	0.77 (0.03)	0.87 (0.02)
C + 1	0.77 (0.05)	0.74 (0.03)	0.88 (0.03)
> C + 1	0.64 (0.05)	0.80 (0.07)	0.91 (0.09)
All	0.80 (0.03)	0.77 (0.03)	0.88 (0.01)

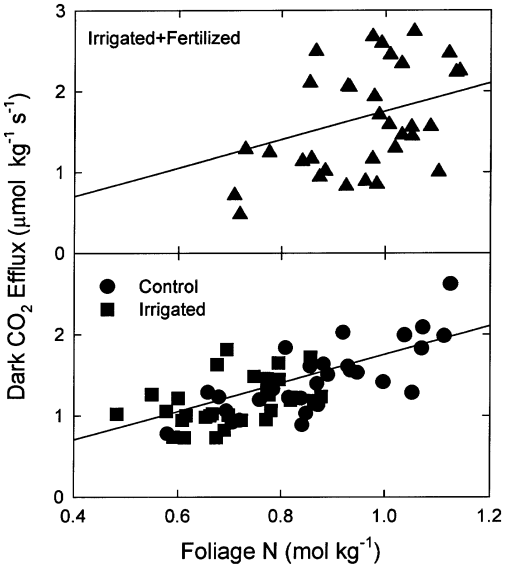

Figure 1. Carbon dioxide efflux of fully expanded foliage at night, corrected to 15 °C versus foliage N concentration for *Pinus radiata* growing in three treatments. For all treatments combined, dark CO_2 efflux (μmol kg^{-1} s^{-1}) = 1.71N (mol kg^{-1}); R^2 = 0.38. The correlation between CO_2 efflux and [N] was 0.71 for the control and irrigated treatments combined and 0.49 for the irrigation plus fertilization treatment.

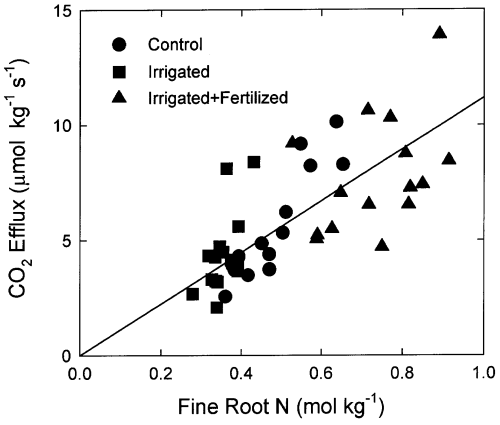

Figure 2. Efflux of CO_2 from fine roots (< 2 mm in diameter) corrected to 15 °C versus root N concentration for *Pinus radiata* growing in three treatments. For all treatments combined, dark CO_2 efflux (μmol kg^{-1} s^{-1}) = 11.2N (mol kg^{-1}); R^2 = 0.51.

temperature (P = 0.57); the Q_{10} (5–25 °C) was 2.5 (R^2 = 0.99, P < 0.01, n = 9).

Fine roots

Fine root [N] varied significantly among the three treatments (P < 0.01) and reflected the nutrient status of the stands (Table 3). Fine root [P] was significantly lower in the IL treatment than in the C treatment (P = 0.04), whereas fine root K concentration ([K]) was significantly higher in the IL treatment than in the C and I treatments (P < 0.01). Other treatment comparisons were not significant.

Fine root respiration per unit mass at 15 °C varied from 2.1 to 13.9 μmol kg^{-1} s^{-1} and was negatively correlated with sample mass (r = –0.63, P < 0.01). Fine root respiration was strongly correlated with fine root [N] (Figure 2), and respiration per unit N was only weakly correlated with sample mass (r = –0.29, P = 0.06). Slopes for a regression between respiration and [N] were not statistically different among treatments (P = 0.06). Fitting a zero-intercept linear regression to data from all treatments combined gave: R_m = 11.2N (R^2 = 0.51, P < 0.01, n = 44), where R_m is CO_2 efflux from maintenance respiration of fine roots at 15 °C (μmol kg^{-1} s^{-1}), and N is fine root [N] (mol kg^{-1}). Average soil [CO_2] in the vicinity of the sampled roots was 1500 μmol mol^{-1} (SD = 500, n = 60), whereas average [CO_2] of the fine root measurements was 400 μmol mol^{-1}. Applying Equation 1 would lower CO_2 efflux of *P. radiata* fine roots in the soil to 23% of that measured at a [CO_2] of 400 μmol mol^{-1}. Fine root respiration increased exponentially with temperature over 5–25 °C, with a Q_{10} of 2.0 (R^2 = 0.99, P < 0.01, n = 3).

Table 3. Mean (SE) fine root N, P and K concentrations as a percent of oven-dry mass for three treatments.

Treatment	N	P	K
Control	0.68 (0.04)	0.14 (0.01)	0.55 (0.03)
Irrigated	0.50 (0.01)	0.13 (0.01)	0.51 (0.02)
Irrigated + fertilized	1.03 (0.04)	0.11 (0.01)	0.76 (0.04)

Stems

Neither CO_2 efflux per unit area (P = 0.10) nor estimated maintenance respiration (P = 0.78) varied consistently with tree height (Figure 3). Stem respiration at 15 °C was highest in the IL treatment and lowest in the C treatment, but varied little within treatments from late summer to late winter (Figure 4), perhaps because an average of 74% of the annual growth had occurred before the first respiration measurement. For each

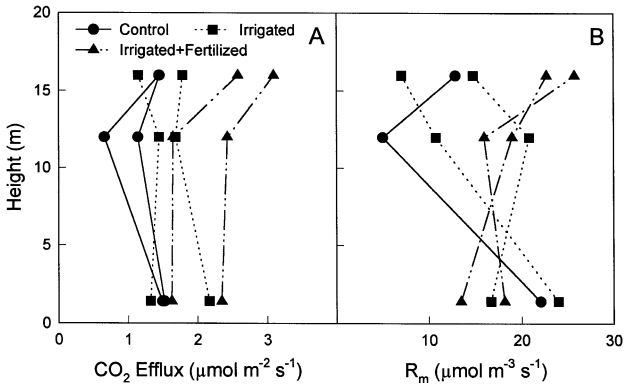

Figure 3. (A) Total CO_2 efflux and (B) estimated maintenance respiration from tree stems at different heights along the bole, corrected to 15 °C. Points are averages of measurements taken in mid-March. Lines connect measurements on the same tree.

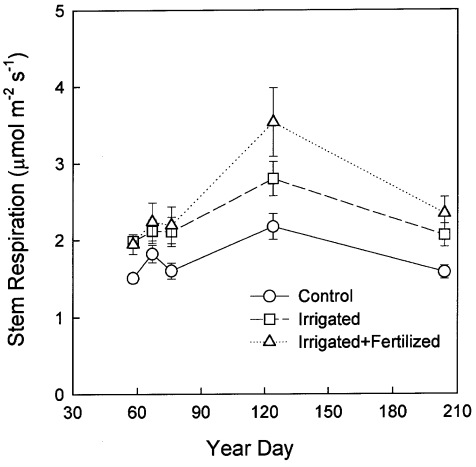

Figure 4. Average stem respiration at 1.4 m for *Pinus radiata* growing in three treatments (n = 15 per treatment). Values were corrected to 15 °C; error bars are standard errors.

sample period, stem CO_2 efflux was significantly correlated with chamber sapwood volume, chamber annual volume growth, and chamber volume growth from March to July. Correlation coefficients for the sample periods ranged from 0.44 to 0.67 for sapwood volume and from 0.57 to 0.75 for annual growth (P < 0.01). However, sapwood volume was correlated with annual volume growth (r = 0.60) and with volume growth from March to July (r = 0.72).

Estimated maintenance respiration was also positively correlated with sapwood volume and, in some cases, annual volume growth. For March 17, when measurements made using the upper chambers were included in the analysis, R_m at 15 °C (μmol s^{-1}) = 18.1V (R^2 = 0.43, P < 0.01, n = 57), where V is sapwood volume (m^3) (Figure 5). For this sample, March–July volume growth did not explain significant additional variability in R_m (P = 0.56). For the May 3–6 sample (no measurements made on upper chambers), R_m at 15 °C (μmol s^{-1}) = 39.2V (R^2 = 0.39, P < 0.01, n = 45). For May 3–6, annual volume growth for the chamber explained significant (P < 0.01) additional variability in R_m (R^2 increased by 0.11). There were no significant differences among treatments in the regression slopes for R_m and sapwood volume for either March 17 (P = 0.28) or May 3–6 (P = 0.91). The lower value of R_m (18.1 μmol s^{-1} m^{-3}) was used to develop the annual budget, because measurements on May 3–6 were substantially greater than those taken on the other four sampling dates (Figure 4) and may include growth respiration.

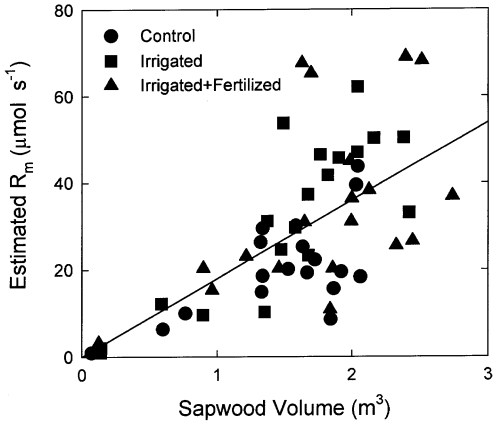

Figure 5. Estimated maintenance respiration at 15 °C on March 17 versus sapwood volume for *Pinus radiata* stems growing in three treatments. Points with values for sapwood volume less than 1 m^3 were from locations at 12 and 16 m in height; all other points are from 1.4 m height; R_m (μmol s^{-1}) = 18.1V (m^3), R^2 = 0.43.

Branches and coarse roots

Branch CO_2 efflux rate at night and estimated maintenance respiration rate were linearly related to branch volume, but branches from the upper two thirds of the canopy had substantially greater rates than branches in the lower one third of the canopy (Figure 6). For branches in the upper two thirds of the canopy, R_m at 15 °C (μmol s^{-1}) = 104V (R^2 = 0.57, P < 0.01, n = 16), where V is branch volume (m^3). For branches in the lower one third of the canopy, R_m at 15 °C (μmol s^{-1}) = 33.2V (R^2 = 0.64, P < 0.01, n = 12). Regression slopes between R_m and V did not differ among treatments for branches in either the upper two thirds of the canopy (P = 0.97) or the lower one third of the canopy (P = 0.12). The Q_{10} of the temperature response was 1.4.

Carbon dioxide efflux per unit root volume decreased exponentially with root size (Figure 7). Respiration rates for roots greater than 0.06 m in diameter were substantially lower than for roots less than 0.06 m in diameter. For coarse roots less than 0.06 m in diameter, CO_2 efflux was linearly related to root volume (R_m at 15 °C (μmol s^{-1}) = 67.8V (R^2 = 0.69, P < 0.01, n = 10), where V is root volume (m^3)). The Q_{10} of the temperature response was 1.5.

Annual budget

Table 4 shows the annual carbon balance for the C, I and IL treatments. The budget uses fine root respiration rates adjusted

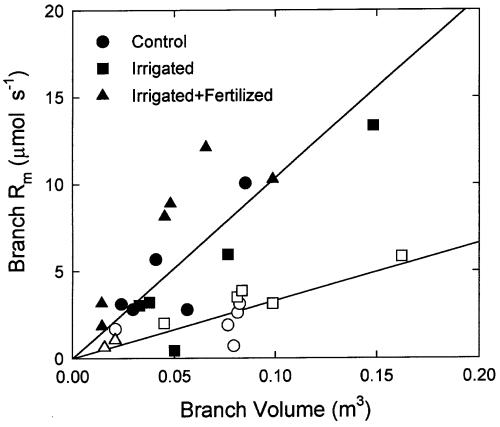

Figure 6. Estimated maintenance respiration versus branch volume for *Pinus radiata* branches at three different canopy positions. Solid symbols are branches in the upper two thirds of the canopy; open symbols are branches in the lower one third of the canopy.

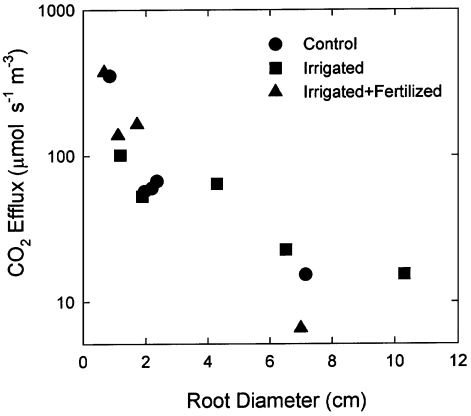

Figure 7. Efflux of CO_2 per unit root volume at 15 °C versus root diameter (D) for *Pinus radiata* coarse roots growing in three treatments. The equation is: ln(CO_2 efflux) = 5.27 – 0.333D; R^2 = 0.73.

Table 4. Annual carbon budget (1992–1993) for three *Pinus radiata* stands. Respiration was partitioned into construction (R_c) and maintenance (R_m) respiration. Total belowground carbon allocation (B_c) was estimated as the difference between annual soil respiration and aboveground litterfall plus coarse root increment. The unknown sink was estimated as the difference between B_c and root respiration and production. All values are given in Mg C ha^{-1} $year^{-1}$; C = control, I = irrigated, and IL = irrigated + fertilized.

Parameter	C	I	IL
Foliage production	0.84	1.13	2.13
Foliage R_c	0.21	0.28	0.53
Foliage R_m	4.00	2.67	6.28
Branch production	0.22	0.22	0.27
Branch R_c	0.05	0.05	0.07
Branch R_m	1.11	1.20	1.87
Stem wood + bark production	4.93	6.15	10.51
Stem wood + bark R_c	1.23	1.54	2.63
Stem wood R_m	1.34	1.71	2.70
Total belowground carbon allocation	10.22	10.36	7.40
Coarse root production	1.19	1.56	2.96
Coarse root R_c	0.30	0.39	0.74
Coarse root R_m	0.50	0.64	1.24
Fine root production	1.85	2.35	1.33
Fine root R_c	0.46	0.59	0.33
Fine root R_m	1.48	1.47	1.42
Unknown sink	4.43	3.36	–0.63
Total	24.2	25.3	34.4
Assimilation estimated with BIOMASS	29.5	26.9	36.9

for our measured soil [CO_2] of 1500 μmol mol^{-1} using Equation 1. Because of uncertainties in fine root respiration and production in the belowground budget, we consider the sum of dry matter production and respiration of aboveground components and total belowground carbon allocation (i.e., B_c estimated as annual soil CO_2 efflux minus aboveground litterfall plus coarse root production) to be the best estimate of annual carbon flux (F_a). This calculated total flux is conservative because we did not estimate losses to herbivory or leaching of dissolved carbon. Total annual flux of carbon was 82% of assimilation estimated with BIOMASS in the C treatment, and 93–94% in the I and IL treatments.

The sum of production and construction + maintenance respiration for coarse and fine roots nearly equaled B_c in the IL treatment, but was only 57 and 68% of B_c in the C and I treatments, respectively. If fine root respiration is not adjusted for soil CO_2 (i.e., rates measured at 400 ppm CO_2 are used), fine root respiration would be 4.4 times greater. In this case, the sum of production and construction + maintenance respiration for coarse and fine roots would be 6, 16 and 74% greater than B_c in the control, irrigated and irrigated + fertilized treatments, respectively. If we use fine root respiration rates adjusted for soil [CO_2], the difference between B_c and the total of coarse and fine root production and respiration was 43% of B_c (18% of F_a) in the C treatments, 32% of B_c (13% of F_a) in the I treatment, and negligible in the IL treatment. This difference between B_c and the total of coarse and fine root production and respiration is an unknown sink that may estimate increased fine root turnover or carbon allocation to root exudation and mycorrhizae, but may also represent cumulative errors in sampling or extrapolation.

The treatments caused shifts in carbon allocation in coarse and fine root production, fine root respiration, foliage production, foliage R_m, wood + bark production, and in the unknown belowground sink (Figure 8). Branch production and wood and branch R_m were consistent among treatments. Construction respiration for all tissues was 9–13% of assimilation for all treatments; the fraction of assimilation used for R_m was slightly lower in the I treatment (30%) than in the C and IL treatments (35 and 39%, respectively). Woody-tissue (stem + branch + coarse root) respiration was 22–26% of the annual assimilation, and woody tissue R_m was 15–17% of annual assimilation for all treatments (Figure 8). We did not calculate CUE for the whole plant because of uncertainty in the belowground budget. However, if we subtract B_c from F_a to estimate assimilation allocated to aboveground components and calculate CUE for aboveground respiration, CUE is conservative among treatments (0.43, 0.50 and 0.48 for C, I and IL treatments, respectively).

Discussion

Foliage

Altering nitrogen availability altered foliar R_m and foliar [N] in *P. radiata*. The fertilization (IL) treatment increased both foliar N and R_m, but also increased variability in R_m/N. Two explanations could account for the increased variability in R_m/N. First, the amount of N in protein could vary if fertilization increased the proportion of foliar N in amino acids (Nasholm and Ericsson 1990, Billow et al. 1994) and also increased variability in the ratio of amino acids to total N within the IL canopy. Second, fertilization could have increased the variability in the activation of Rubisco. Stitt and others (e.g., Stitt and Schulze

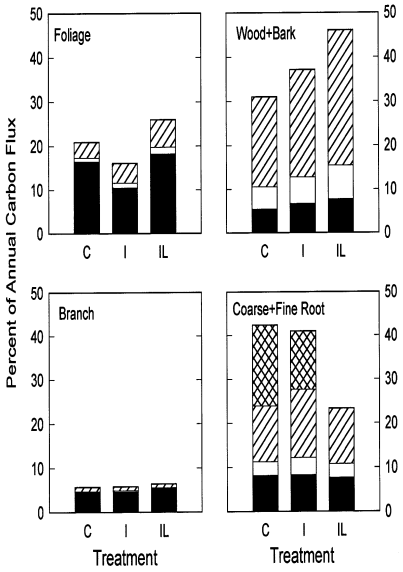

Figure 8. The fraction of the annual carbon flux (estimated as the sum of (1) dry matter production and respiration of aboveground components, (2) annual soil CO_2 efflux minus aboveground litterfall, and (3) the annual increment in coarse root biomass) by component for three *Pinus radiata* stands growing in different nutrient regimes. Legend: solid bars = maintenance respiration, open bars = construction respiration, and diagonal lined bars = dry-matter production. In the root panel, cross-hatched bars are the difference between total belowground allocation (calculated as the sum of (2) and (3) above) and the sum of root respiration and root production.

1994) showed that the carboxylating enzyme in photosynthesis (Rubisco) can readily switch between active and inactive states. In an inactive state, Rubisco functions as a storage protein, presumably with low maintenance costs.

Our value of foliar R_m per unit N (1.71 μmol s^{-1} mol^{-1} N at 15 °C) was similar to that of crop and wildland species (2.09 μmol s^{-1} mol^{-1} at 15 °C (Ryan 1991)), but only 46% of that of boreal and subalpine trees and shrubs (3.70 μmol s^{-1} mol^{-1} at 15 °C (Ryan 1995)). The lower rate in temperate species compared to boreal and subalpine species is consistent with high respiration rates of cold-adapted species at a given temperature (Lechowicz et al. 1980, Earnshaw 1981).

Fine roots

The strong relationship between fine root respiration and root [N] suggests that root activity varies with root protein content. The composition of the root samples (a few samples included growing root tips, but most samples comprised only mature fine roots) and the strong relationship with root [N] suggests that most of the respiration measured was maintenance respiration. A study of seasonal changes in *P. radiata* fine root biomass showed that peak biomass occurred in midsummer (Santantonio and Santantonio 1987*b*), suggesting that, at the time of our measurements in late summer, root growth was minimal.

Fine root biomass was low (Table 1), but fine root respiration rate per unit N was 6.6 times greater than the rate for foliage. It is unclear whether the high rates represent substantially greater metabolic activity in roots than in leaves or whether the measured high rates represent a transient response to a lower CO_2 environment during measurement. However, several factors suggest a transient response to lower CO_2 concentration: (1) elevated CO_2 can suppress CO_2 efflux from foliage (e.g., Amthor 1991) and fine roots (Qi et al. 1994); (2) fine root CO_2 efflux was also strongly inhibited in *Pinus resinosa* Ait., *Pinus strobus* L. and *Tsuga heterophylla* (Raf.) Sarg. (Equation 1); (3) extrapolating fluxes measured at a [CO_2] of 400 μmol mol^{-1} to a year would yield a much greater annual soil CO_2 efflux than was measured for two of the three treatments; and (4) if the fine roots respired at 23% of the measured rate *in situ*, R_m/N at 15 °C would be 2.6 μmol mol^{-1} s^{-1}, or 1.5 times that of foliage. Although fine root respiration was not measured at the CO_2 concentration of the soil in which the root was growing, it seems reasonable to suppose that respiration measurements made at a [CO_2] far lower than the soil environment would be artificially high. Further work to clarify the role of roots in soil respiration will be especially important, given the high rates at which roots respire.

Woody tissue

If it is assumed that the wood in branches and coarse roots was largely sapwood, then stems, coarse roots > 0.06 m in diameter, and lower branches had similar rates of maintenance respiration per unit of sapwood volume (15–39 μmol m^{-3} s^{-1}). These rates are similar to those reported for other conifers. For example, R_m ranged from 6.4–11.5 μmol m^{-3} s^{-1} at 15 °C for three pines and western hemlock (Ryan et al. 1995), and R_m in lodgepole pine was 17.1 μmol m^{-3} s^{-1} (Ryan 1990). Respiration rates of branches from the upper two thirds of the canopy were larger than those of coarse roots < 0.06 m in diameter, but rates for both tissues were similar to those reported for young *Abies amabilis* Dougl. ex J. Forbes. trees (86 μmol m^{-3} s^{-1} at 15 °C, Sprugel 1990).

The high rates of stem respiration in the May samples in the well-watered trees in the I and IL treatments may be associated with late-autumn growth because the average temperature for the 2 weeks before sampling was 14 °C. The trees in the C treatment may have been drought stressed because only 19 mm precipitation fell in the 30 days before measurement and, therefore, they may not have been able to respond to the higher temperatures.

Differences in R_m/volume between branch positions and with coarse root size might have been caused by differences in sapwood volume among the samples or by differences in the activity of the ray parenchyma cells. Additionally, the correlation between stem R_m and annual growth suggests physiological differences in R_m related to growth. Differences in tissue N content might explain some of the differences in rates because R_m has been shown to increase with wood N content in *Pinus taeda* L. (Maier and Dougherty 1994).

Annual budget

Differences in N availability among treatments (Raison et al. 1990, 1992*a*) caused differences in carbon allocation patterns,

particularly in allocation to wood + bark and in total belowground allocation. Of the 42% increase in assimilation in the IL treatment compared with the control, roughly half was allocated to increased wood production.

Increased nutrient availability in the IL treatment decreased fine root biomass and, hence, allocation to fine root production and respiration. These results are consistent with observed decreases in absolute and relative allocation to fine root production in response to fertilization (Keyes and Grier 1981, Gower et al., unpublished observations). In our study, the decreased allocation to fine roots in the IL treatment was offset by increased allocation to coarse roots. Therefore, the sum of production and respiration of coarse and fine roots was greater in the IL treatment (8.0 Mg C ha^{-1} $year^{-1}$) than in the C treatment (5.8 Mg C ha^{-1} $year^{-1}$). Total root production and respiration as a fraction of F_a were similar for all treatments.

The belowground portion of the carbon budget was based on several assumptions. Calculation of B_c depends on robust estimates of annual soil CO_2 efflux, annual litterfall, and annual changes in soil and litter carbon and root biomass. Annual soil CO_2 efflux was estimated from fluxes measured twice each month with a static chamber technique and a CO_2 absorbent, and static fluxes were within 20% of fluxes measured with an IRGA (S. Pongracic, unpublished data). Soil and litter carbon were measured and found to be roughly constant from year to year. Coarse root increment was estimated with an allometric equation developed from a wide range of *P. radiata* sites, with very different site fertilities; coarse root increment is likely to be accurate for the different treatments. Therefore, we conclude that B_c is a reasonably accurate estimate of total belowground carbon allocation.

Fine root biomass measurements were similar in the spring and fall. However, turnover may differ with treatment. If turnover rates were greater in trees in the infertile C and I treatments than in trees in the fertilized IL treatment, allocation to fine root production would increase in the C and I treatments and lower the estimate of the unknown sink. Fine root turnover would need to be 4.2 times biomass in the C treatment and 3.1 times biomass in the I treatment to balance the belowground budget.

We assumed that fine root respiration was affected by soil CO_2 concentration and that the soil [CO_2] (1500 μmol mol^{-1}) was constant throughout the year. These assumptions seem reasonable, given the known response of root respiration to [CO_2] (Qi et al. 1994). However, if we used the response of fine root respiration to soil [CO_2] reported by Qi et al. (1994), respiration at 1500 μmol mol^{-1} would be 67% of that at 400 μmol mol^{-1} (compared with 23% using Equation 1). If we estimate annual budgets by assuming fine root respiration was not affected by soil [CO_2], the annual total of root production and respiration would exceed B_c in the C and I treatments. Additionally, the fraction of root respiration to total soil respiration for unadjusted rates would be larger than that reported for other studies. In this study, root/total soil respiration was 28–60% for fine root respiration adjusted for soil CO_2 versus 79–137% for unadjusted root respiration. Other conifer studies estimate root/total soil respiration at 33 (Bowden et al. 1993), 47–51 (Nakane et al. 1983) and 62% (Ewel et al. 1987). We did not adjust coarse root respiration for soil [CO_2] because the internal [CO_2] of sapwood is high (1.5–8%, Hari et al. 1991).

An increase in fine root turnover or a decrease in the response of fine root respiration to soil [CO_2] would lower the unknown sink in the belowground budget. However, allocation to mycorrhizae and root exudation might also differ among treatments and provide an alternative explanation for the unknown sink. Mycorrhizae use a substantial fraction of belowground carbon allocation in nutrient-poor ecosystems (Vogt et al. 1982). Additionally, fertilization has been shown to reduce mycorrhizal infection and activity (Blaise and Garbaye 1983), and mycorrhizal infection appeared to be lowest in trees in the IL treatment.

Annual budgets estimated by summing aboveground production and respiration and total belowground allocation agreed well with annual assimilation estimated by the BIOMASS model. However, the agreement between model prediction and field measurements is not surprising because the model was developed from data at the Biology of Forest Growth site (see Ryan et al. 1996).

Carbon use efficiency appears to be conservative with respect to nutrition. Nutrition altered the fraction of annual assimilation used for foliage and fine root respiration, but increased foliar respiration in the IL treatment was offset by a decrease in fine root respiration. The canopy in the I treatment appeared to be slightly more efficient than the canopies in the C and IL treatments, i.e., foliar R_m used only 11% of annual assimilation in the I treatment, compared with 17–18% in the C and IL treatments. As a fraction of total assimilation, construction and maintenance respiration were both conservative across treatments (9–13% for construction, and 30–39% for maintenance).

The strong link between photosynthesis, cellular activity, growth and respiration (Amthor 1994) may explain the conservative CUE. Photosynthesis supplies the substrate for respiration, and photosynthetic capacity is linked with foliar enzyme levels. Growth and respiration are linked, and growth is limited to some extent by the supply of carbohydrates produced by photosynthesis. Therefore, more rapid growth is linked with an increased supply of carbohydrates, the maintenance respiration required to support higher cellular activity, and higher growth respiration at greater growth rates. Additionally, the low cost for maintenance of structural tissue indicates that support costs are unlikely to change much with treatment differences in woody biomass. The lack of change in CUE with large changes in assimilation, standing biomass, tissue N concentrations and annual allocation suggests that, at a given annual temperature, CUE may be conservative for forests.

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