

Supply-side controls on soil respiration among Oregon forests

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Abstract

To test the hypothesis that variation in soil respiration is related to plant production across a diverse forested landscape, we compared annual soil respiration rates with net primary production and the subsequent allocation of carbon to various ecosystem pools, including leaves, fine roots, forest floor, and mineral soil for 36 independent plots arranged as three replicates of four age classes in three climatically distinct forest types.

Across all plots, annual soil respiration was not correlated with aboveground net primary production ($R^2 = 0.06$, $P > 0.1$) but it was moderately correlated with belowground net primary production ($R^2 = 0.46$, $P < 0.001$). Despite the wide range in temperature and precipitation regimes experienced by these forests, all exhibited similar soil respiration per unit live fine root biomass, with about 5 g of carbon respired each year per 1 g of fine root carbon ($R^2 = 0.45$, $P < 0.001$). Annual soil respiration was only weakly correlated with dead carbon pools such as forest floor and mineral soil carbon ($R^2 = 0.14$ and 0.12 , respectively). Trends between soil respiration, production, and root mass among age classes within forest type were inconsistent and do not always reflect cross-site trends.

These results are consistent with a growing appreciation that soil respiration is strongly influenced by the supply of carbohydrates to roots and the rhizosphere, and that some regional patterns of soil respiration may depend more on belowground carbon allocation than the abiotic constraints imposed on subsequent metabolism.

Keywords: belowground net primary production, carbon cycles, CO₂ efflux, fine roots, forest carbon dynamics, net primary production, Oregon, Pacific north-west, soil carbon, soil respiration

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Introduction

It is estimated that more than half of the carbon fixed by forest ecosystems is released back to the atmosphere through soil respiration (Davidson *et al.*, 1998; Law *et al.*, 1999; Longdoz *et al.*, 2000). Considering the importance of forests in sequestering atmospheric carbon, it is clear that assessment global carbon cycles demands an understanding of how forest soil respiration is regulated not only at individual sites but also over broad spatial and temporal scales.

Studies have shown that within individual forest stands, soil respiration is correlated with temporal patterns of soil temperature and soil moisture and it is commonly assumed that regional patterns are shaped

by these same environmental drivers (Kang *et al.*, 2000). However, it is unclear how often this is as a result of direct constraints on belowground metabolism (as in Wang *et al.*, 2002) or indirect constraints on the capacity of vegetation to supply of carbon to the soil.

As more cross-site comparisons become available, there is a growing appreciation of the role that plant production plays in regional patterns of soil respiration. In a comparison of 18 European forests, Janssens *et al.* (2001) found that between years and across sites, annual gross primary production, not temperature, was the primary factor influencing soil respiration. This point was echoed by Reichstein *et al.* (2003), who found that measures of vegetation productivity were necessary to model reliably large-scale patterns of soil respiration and Litton *et al.* (2003), who found that soil respiration in a chronosequence of lodgepole pine was correlated with measures of biomass rather than abiotic variables.

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In another study (Campbell & Law, 2004), we demonstrated that soil respiration among the conifer forests of western Oregon varied with both age class and community type. This study pointed at landscape-scale features such as the rain shadow of the Cascade mountains, and processes such as stand replacing disturbance as the factors most important in shaping regional patterns of soil respiration. Furthermore, we suggested that differences in annual soil respiration did not result from a common response to variation in soil temperature, soil moisture, or growing season but rather differences in base respiration rates specific to each forest type and age. Based on these observations, we hypothesize that landscape forces, such as edaphoclimatic gradients and stand replacing disturbances, drive soil respiration across this landscape by controlling substrate availability in the soil.

The objective of the current study was to determine how regional variation in soil respiration relates to plant production and the subsequent partitioning of carbon into various pools. Specifically, we examined the relation between annual soil respiration and net primary production and the subsequent allocation of carbon to leaves, coarse roots, and fine roots, across three climatically distinct forest chronosequences in Oregon. In addition, we evaluate the relationship between soil respiration and the accumulation of carbon in the forest floor and two physical fractions of mineral soil carbon.

Methods

Plot design

To assess annual soil respiration as a function of carbon supply, we established 36 independent forest plots arranged as three replicates of four age classes in each of three climatically distinct forest types. Each individual study plot encompassed 1 ha of structurally homogenous forest determined to be representative of its age and location. The three study sites were located along a large precipitation and elevation gradient and are best described as hemlock-Sitka spruce in the fog belt of the Coast Range near Cascade Head Experimental Forest, Douglas-fir in the Cascade Mountains near HJ Andrews Experimental Forest, and ponderosa pine in the Metolius Basin on the dry east side of the Cascade Mountains (referred to hereafter as Coast Range, West Cascades, and East Cascades, respectively). Forest ages range from 10 to 400 years and were subjectively classified as either initiation, young, mature, or old. The locations of the study sites are shown in Fig. 1. The climatic, edaphic, and compositional qualities of each forest type are given in Table 1, while the structural qualities of each age class are given in Table 2.

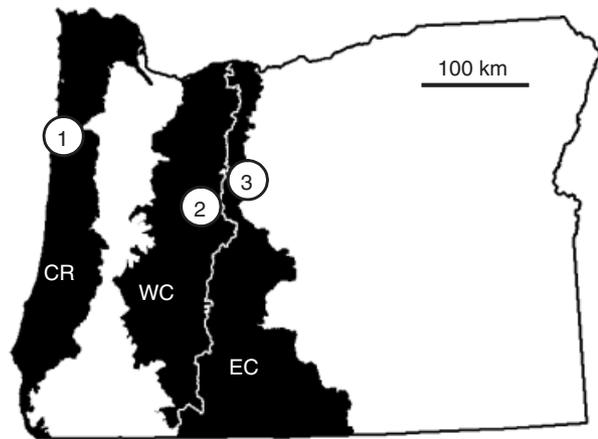


Fig. 1 Geographic location of the study sites and the extent of the forest types they represent in western Oregon. Study sites are shown as 1–3. CR, Coast Range; WC, West Cascades, and EC, East Cascades.

Annual soil respiration

Soil respiration (soil surface CO₂ efflux) was measured using a portable infrared gas analyzer coupled to a soil respiration chamber (LI-COR model 6400 and 640009, respectively, LI-COR Biosciences, Lincoln, NE, USA). To form an adequate seal between the chamber and the ground surface, permanent plastic collars that received the respiration chamber were inserted through the litter layer at each measurement point. Each individual measurement covered 75 cm² of ground surface and soil respiration was measured for approximately 90 s. For a given day, plot-wide soil respiration is based on the average of 12 point measurements regularly stratified throughout the 1 ha plot. Measurements were taken at the same 12 points in each plot on 1 day in May, July, September, November 2001 and February 2002. February measurements were taken over snow at East and West Cascade plots. Soil temperature at a depth of 10 cm was measured next to the collar coincident with each soil respiration measurement. Continuous, year-round soil temperature was measured using a single temperature logger buried at a depth of 10 cm in the center of each plot (Hobo temperature logger, Onset Computer Corporation, Warner, NH, USA). Comparisons between this continuous, single-location temperature and the plot-wide average measured at the respiration collars revealed no consistent biases.

Following Ryan *et al.* (1997) and Law *et al.* (1999), annual soil respiration for the year 2001 was computed for each plot by developing plot-specific temperature response curves and then using soil temperature to model annual soil respiration. Specifically, daily

Table 1 Climatic, edaphic, and biological characteristics of the three study sites

Site characteristic	Coast Range	West Cascades	East Cascades
Canopy composition (importance by basal area)	Western hemlock (0.36), Sitka spruce (0.34), Douglas fir (0.27)	Douglas fir (0.79), western red cedar (0.10), western hemlock (0.10)	Ponderosa pine (0.95)
Additional indicator species	Red alder, vine maple, salmonberry, salal, red huckleberry, sword fern	Vine maple, salal, red huckleberry, sword fern, Rhododendron	White fir, incense cedar, antelope bitterbrush, greenleaf manzanita, Idaho fescue
Geographic location	Salmon River drainage of Tillamook county Oregon	Blue River drainage of Linn county Oregon	Upper Metolius River of Deschutes county Oregon
Average precipitation (mm yr ⁻¹)	2800	2100	520
Average number of frost-free days	333	255	190
Soil description	Basaltic colluvium forming well drained silt loams	Igneous colluvium and residuum forming well-drained stony to cobbly clay loams	Ash over colluvium forming well-drained sandy to gravelly loams
Average age of each age class (average of the oldest 10% of trees on each plot)	Initiation: 12–14; young: 22–40; mature: 45–52; old: 170–190	Initiation: 13–20; young: 40–70; mature: 140–170; old: 400–500	Initiation: 9–20; young: 56–89; mature: 93–106; old: 190–316

Table 2 Structural qualities of each age-class averaged across three replicate stands

	Stand age	Stem diameter (cm)	Stem density (m ⁻²)	Canopy height (m)	Ontogeny
<i>Coast Range</i>					
Initiation	> 12–14	11	1830	11	Crowns closed, suppression not occurring, large shrub component
Young	22–40	20	1440	20	Suppression and self-thinning occurring, understory absent
Mature	45–52	38	600	38	Self-thinning nearly complete, understory re-establishing
Old	170–190	51	340	51	Multistory canopy, gap formation, well-developed understory
<i>West Cascades</i>					
Initiation	13–20	10	1120	10	Crowns closing, large shrub component
Young	40–70	22	740	22	Self-thinning occurring, shade-tolerant understory developing
Mature	140–170	38	340	38	Self-thinning complete, understory well developed
Old	400–450	32	510	32	Multistory canopy, gap formation, well-developed understory
<i>East Cascades</i>					
Initiation	9–20	10	320	10	Tree crowns widely spaced, understory establishing
Young	56–89	27	300	27	Crowns expanded (not closed), well-developed understory
Mature	93–106	21	980	21	Some thinning occurring, some new cohort establishment
Old	190–316	30	470	30	Open multistory canopy, understory often burned

Stand age is defined as the 90th percentile of the tree stem age distribution. Stem diameter is the average diameter at breast height (DBH) of stems >5.0 cm DBH. Stem density is number of stems >5.0 cm DBH m⁻². Height is average maximum. Sample size = three replicate plots per age class.

average soil respiration for each day of the year was computed according to the following equation:

$$R_i = R_{i10}e^{\beta(T-10)} \quad (1)$$

where R_i is the average soil respiration estimated for day i , R_{i10} is the average soil respiration for day i normalized to 10 °C (which is either a measured point or one linearly interpolated between measurements), β is from the season-wide temperature response curve $y = ae^{\beta x}$ (where y is the soil respiration and x is the soil temperature), and T is the average soil temperature measured for day i . In this procedure, the slope of the temperature response curve is kept constant throughout the year but the intercept is allowed to vary based on seasonal trends in temperature-normalized respiration. This accounts for seasonality in soil respiration not associated with temperature. Of all the daily soil respiration values (R_i), only 2% were computed for temperatures more than 1 °C beyond the range of each plot's temperature response curve. Concerns with this and similar methods for interpolating soil respiration between periodic measurements include: (a) whether or not a bias results from matching daily average temperatures to respiration measurements that are usually made at only one time of day, and (b) whether or not a single measurement date is appropriately representative of the entire intermeasurement interval. As for the first concern, hourly diel measurements (made at each forest age and type combination) give no indication of the kind of asymmetry in temperature and respiration that would lend bias to the daily aggregation of temperature. As for the second concern, we were able to compare our estimates of annual soil respiration on two of the East Cascade plots with that calculated from continuous automated chamber measurements (Irvine & Law, 2002). The two approaches produced values that were within 17% of one another at one plot and within 1% at the other. Additional details regarding this procedure are given in Campbell & Law (2004).

Biomass measurements

Forest biomass was quantified for tree boles, tree branches, tree foliage, understory wood, understory foliage, tree coarse roots (>2 cm), and total fine roots (<2 cm). In this study, trees were defined as woody plants with a stem diameter greater than 5 cm at a height of 137 cm. All remaining plants, including shrubs, forbs, grasses, and moss, were considered understory. To determine the frequency, dimensions, and species of trees and understory in each of the 36 plots, stem surveys were conducted in four regularly spaced subplots. Subplot size varied depending on the

frequency of stems and ranged between 12 and 30 m² for understory and 80 and 700 m² for trees.

The masses of tree boles and tree coarse roots were estimated using allometric equations specific to species and or location that predict wood volume from stem diameter and height combined with measures of wood density specific to each plot and or species. The masses of tree branches, bark, understory wood, and understory foliage were estimated allometrically using species-specific equations that predict mass directly from stem diameter and or leaf cover. The allometric equations were acquired largely from the BIOPACK database (Means *et al.*, 1994) and are described in VanTuyl (2003).

The mass of tree foliage was calculated by multiplying overstory leaf area by a plot-wide estimate of leaf mass per unit area (LMA). Overstory leaf area was estimated using a handheld optical meter (LI-COR model 2000, LI-COR Biosciences). LAI correction factors for crown clumping were determined from TRAC crown gap measurements (Third Wave Engineering, Ottawa, Canada), while corrections for shoot clumping and wood interception were made as in Law *et al.* (2001a).

LMA was measured directly on at least six shoot samples per plot (more for multispecies stands) and scaled to the entire plot using an average weighted by species composition. To increase the probability that these shoot samples were representative of the whole canopy, shoot samples were collected by shotgun from either the east or west side of the middle third of the tree crown.

The standing crop of live fine roots (<2.0 mm diameter) for each plot was determined as the average of measurements taken in May and again in October of 2001. Without specific knowledge of root phenology at all sites, we feel that this was the best approach to capture between-site differences. Fine root sampling involved manually separating live fine roots from 5 cm diameter soil cores. From each plot, 12 cores were taken from 0–20 cm, six from 20–50 cm and six from 50–100 cm. Rarely were roots found at a depth of 100 cm (Sun *et al.*, 2004).

Production estimates

Aboveground net primary production (ANPP) was calculated as the sum of tree woody production, tree foliage production, understory production, and herb production. Belowground net primary production (BNPP) was calculated as the sum of coarse root production and fine root production. To compute aboveground woody and coarse root production, stem increment cores were collected from a representative subsample of trees on each plot (every fifth tree). From these increment cores and the above-mentioned

allometrics, we were able to estimate wood and coarse root mass for dates prior to sampling, which were then used to compute the mean annual increase in these pools over the last 5 years. Tree foliage production was computed as tree foliage mass divided by estimates of foliage retention (which were measured for each species on each plot and scaled to the whole canopy based on the contribution to basal area by each species). Details regarding these computations are given in Law *et al.* (1999). Fine root production was computed as fine root biomass multiplied by a generalized estimate of fine root turnover index (turnover expressed as a fraction of standing crop). Twenty years after the original fine root studies were conducted in the Pacific North-west, facts regarding turnover rates in the region remain limited. While there exists some evidence that absolute fine root turnover varies as a function of resource availability (Santantonio & Hermann, 1985), it appears that most of the variability in turnover is driven by variation in standing crop. That is, fine root turnover index may be fairly conserved between sites (Keyes & Grier, 1981). Considering this, we assumed the fine root turnover index to equal 1.2 year^{-1} , determined as the average of several values reported by Keyes & Grier (1981) and C. Anderson (personal communication) throughout the region.

Soil carbon measurements

Forest floor (soil O-horizon) mass was measured at eight 75 cm^2 locations regularly stratified throughout each forest plot. Mineral soil carbon in the top 20 cm was determined as the average of 12 soil cores collected

at regularly stratified points throughout each plot. After the removal of roots, the mineral soil was separated into two density fractions. This fractionation was based on a modified polytungstate suction method of Strickland and Sollins (1987) and is described in detail by Sun *et al.* (2004). Our hope was that the lighter of these two fractions represented a more labile pool of carbon. The carbon concentration of the forest floor, mineral soil, and light fraction of mineral soil was determined using a Carlo-Erba C-N-S analyzer (Central Analytical Lab, Oregon State University).

Results

Table 3 shows estimates of total biomass, foliage biomass, fine root biomass, and forest floor mass, across each of the three chronosequences. Foliage and fine root mass were highest in the West Cascades, lowest in the East Cascades, and intermediate in the Coast Range. Successional trends in fine root mass within each forest type were undetectable, due in part to high variation within each forest type and age class combination.

Soil carbon and nitrogen content in the top 20 cm of mineral soil are shown in Table 4. Total soil carbon was approximately 12, 6, and 3 kg C m^{-2} for the Coast Range, West Cascades, and East Cascades, respectively. However, because of a higher proportion of light-fraction carbon in the West Cascades, the total amount of light-fraction carbon was equivalent between the Coast Range and West Cascades. Soil nitrogen concentration and content were, on average, four times higher in the Coast Range than in the West Cascades and East Cascades.

Table 3 Mean estimates of biomass, for each age class and cover type represented by the chronosequence plots

	Total biomass (kg C m^{-2})	Foliage biomass (kg C m^{-2})	Fine root biomass (kg C m^{-2})	Forest floor mass (kg C m^{-2})
<i>Coast Range</i>				
Initiation	5.3 (0.6)	0.883 (0.100)	0.199 (0.122)	389 (0.078)
Young	17.2 (7.0)	0.700 (0.203)	0.201 (0.149)	522 (0.143)
Mature	30.9 (4.9)	0.672 (0.224)	0.151 (0.021)	520 (0.130)
Old	66.8 (8.0)	0.523 (0.53)	0.174 (0.056)	560 (0.299)
<i>West Cascades</i>				
Initiation	2.9 (4.6)	0.386 (0.152)	0.318 (0.080)	540 (0.063)
Young	12.9 (5.0)	0.720 (0.253)	0.239 (0.033)	589 (0.133)
Mature	38.0 (14.7)	1.105 (0.144)	0.299 (0.090)	974 (0.236)
Old	56.3 (7.8)	0.723 (0.168)	0.250 (0.044)	999 (0.312)
<i>East Cascades</i>				
Initiation	0.9 (7.9)	0.083 (0.055)	0.129 (0.085)	1230 (0.433)
Young	7.0 (2.3)	0.254 (0.105)	0.204 (0.082)	994 (0.226)
Mature	13.4 (6.0)	0.312 (0.034)	0.171 (0.078)	1981 (0.157)
Old	17.6 (2.5)	0.251 (0.043)	0.197 (0.040)	1425 (0.459)

Values in parentheses are the among-plot uncertainty (1 SD of the mean of three replicate plots).

Table 4 Carbon and nitrogen content of the top 20 cm of mineral soil for each forest type and age class combination

	Total soil carbon (kg C m ⁻²)	Light fraction soil carbon (% of total)	Light fraction soil carbon (kg C m ⁻²)	Soil N concentration (%)	Soil N content (kg N m ⁻²)
<i>Coast Range</i>					
Initiation	10.6 (2.1)	25 (6)	2.2 (0.8)	0.65 (0.25)	0.56 (0.09)
Young	11.1 (2.3)	na	na	0.65 (0.19)	0.52 (0.12)
Mature	10.9 (2.2)	31 (16)	2.6 (1.7)	0.59 (0.09)	0.63 (0.14)
Old	13.5 (3.8)	24 (12)	2.4 (1.3)	0.71 (0.02)	0.63 (0.11)
Average	11.5	27	2.4	0.65	0.59
<i>West Cascades</i>					
Initiation	6.9 (1.8)	52 (9)	2.6 (0.8)	0.17 (0.04)	0.21 (0.07)
Young	5.7 (0.6)	na	na	0.14 (0.03)	0.19 (0.02)
Mature	5.2 (1.3)	42 (9)	2.7 (1.2)	0.21 (0.02)	0.14 (0.05)
Old	6.5 (1.6)	35 (6)	1.7 (0.4)	0.16 (0.04)	0.22 (0.05)
Average	6.1	43	2.4	0.17	0.19
<i>East Cascades</i>					
Initiation	4.1 (0.9)	38 (8)	1.4 (0.5)	0.06 (0.01)	0.12 (0.03)
Young	2.8 (1.4)	36 (9)	1.5 (0.5)	0.06 (0.01)	0.10 (0.04)
Mature	3.3 (0.5)	na	na	0.06 (0.01)	0.09 (0.09)
Old	2.8 (0.8)	34 (7)	0.9 (0.4)	0.05 (0.01)	0.08 (0.08)
Average	3.2	36	1.3	0.06	0.10

Values in parentheses are 1 SD of the mean of three replicate plots, except for the light C fraction values, which are the SD of 12 measurements made in a single plot. See methods for a description of density fractionation.

Estimates of ANPP, BNPP, and annual soil respiration across each of the three chronosequences are shown in Table 5. Average ANPP decreased from about 700 g C m⁻² yr⁻¹ for forests in the Coast Range to about 400 g C m⁻² yr⁻¹ for forests of the West Cascades to about 200 g C m⁻² yr⁻¹ for forests of the East Cascades. BNPP, on the other hand, followed a different pattern, with rates approaching 500 g C m⁻² yr⁻¹ in both the Coast Range and West Cascades, and 250 g C m⁻² yr⁻¹ in forests of the East Cascades. Annual soil respiration averaged about 1200, 1800, and 700 g C m⁻² yr⁻¹ in the Coast Range, West Cascades, and East Cascades forests, respectively.

As illustrated in Fig. 2, soil respiration among all 36 plots was coupled to BNPP ($R^2 = 0.46$; $P < 0.001$) and not to ANPP ($R^2 = 0.06$; $P > 0.1$). Fine root mass was generally highest among the West Cascades plots, intermediate among the Coast Range plots, and lowest among the dry East Cascade plots. There was no consistent trend in fine root mass with age, unlike total biomass which increased with age (Fig. 3). Annual soil respiration, which was poorly correlated to total biomass, was moderately coupled to fine root mass. Figure 4 shows that approximately 5 g of carbon was released each year for every gram of fine root carbon ($R^2 = 0.45$, $P < 0.001$).

Annual soil respiration was also linearly related to total foliage mass (with approximately 5 g of carbon

released each year for each 4 g of leaf carbon; $R^2 = 0.32$, $P < 0.001$). Perhaps more notable than the overall fit of this relationship between foliage mass and soil respiration was that positive outliers were plots with particularly high understory fractions, while negative outliers were plots with particularly low understory fractions (see Fig. 5). This suggests that understory foliage may have a disproportional influence on soil respiration. A regression model including overstory and understory foliage mass separately explains nearly 60% of the variation in soil respiration and weights understory foliage 10 times that of overstory foliage.

Correlation coefficients (r) between annual soil respiration and all measures of ecosystem carbon pools and fluxes are shown in Table 6. Unlike live fine root and foliage mass, the size of detritus pools such as forest floor and dead root mass were poorly correlated to soil respiration across the 36 plots. Soil carbon and nitrogen properties also showed little or no correlation with annual soil respiration. It is apparent that the factors most coupled to annual soil respiration within forest type were different from those related to variation between forest type. While mineral soil carbon is not correlated to annual soil respiration across forest types, this variable explained over 60% of the variation in annual soil respiration among Coast Range plots. Among plots at the East Cascades, annual soil respiration was coupled to nearly all measures of biomass

Table 5 Means, experimental uncertainties, and measurement uncertainties for field estimates of aboveground net primary production (ANPP), belowground net primary production (BNPP), and annual soil respiration, for each age class and cover type represented by the chronosequence plots

	Soil respiration* (g C m ⁻² yr ⁻¹)	ANPP (g C m ⁻² yr ⁻¹)	BNPP (g C m ⁻² yr ⁻¹)
<i>Coast Range</i>			
Initiation	1205 (116, 380)	793 (83, 22)	546 (166, 190)
Young	1086 (288, 415)	801 (26, 48)	518 (198, 146)
Mature	1081 (166, 387)	657 (44, 59)	404 (44, 140)
Old	1557 (219, 384)	486 (145, 49)	434 (136, 162)
Average	1232	684	476
<i>West Cascades</i>			
Initiation	2007 (235, 623)	315 (24, 34)	504 (104, 236)
Young	1478 (114, 458)	476 (127, 31)	468 (90, 132)
Mature	2067 (227, 620)	478 (103, 40)	548 (148, 198)
Old	1669 (263, 395)	318 (53, 56)	436 (68, 256)
Average	1805	397	490
<i>East Cascades</i>			
Initiation	482 (19, 117)	114 (42, 8)	131 (44, 78)
Young	593 (136, 175)	231 (27, 19)	256 (55, 78)
Mature	872 (272, 218)	323 (151, 36)	295 (136, 113)
Old	717 (76, 191)	180 (71, 27)	242 (69, 82)
Average	666	212	231

The first value in parentheses is the experimental uncertainty (1 SD of the mean of three replicate plots). The second value in parentheses, following the comma, is the average measurement uncertainty calculated for each site-age combination (measurement uncertainty determined for each plot by Monte Carlo simulation as 1 SD of 300 standard normal iterations, accounting for covariance among equation components).

*From Campbell & Law (2003).

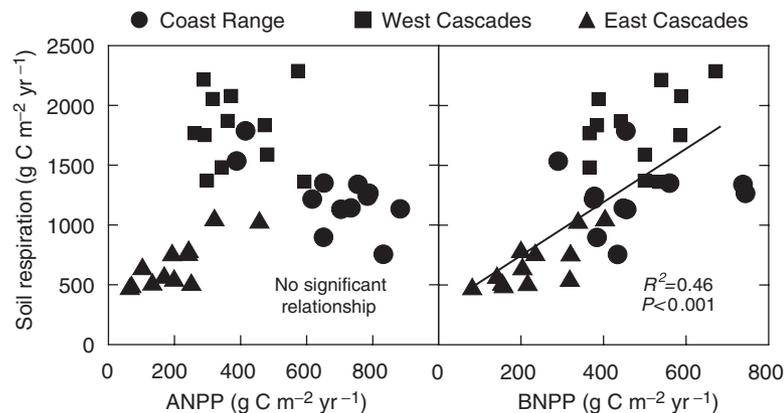


Fig. 2 Cross-site relationships between annual soil respiration and aboveground net primary production (ANPP) and belowground net primary production (BNPP).

production including ANPP. Among plots in the West Cascades, annual soil respiration was not correlated to any measure of biomass, production, or detritus.

Discussion

Considering the first principles of enzymatic metabolism, we should not be surprised to find soil respiration

positively correlated with soil temperature (for reviews see Singh & Gupta, 1977; Raich & Schlesinger, 1992; Lloyd & Taylor, 1994), soil moisture (Orchard *et al.*, 1992; Burton *et al.*, 1998; Davidson *et al.*, 1998; Irvine & Law, 2002), soil aeration (McGroddy & Silver, 2000; Savage & Davidson, 2001), substrate quality (Minderman, 1967; Edmonds, 1984; Aber *et al.*, 1990; Parton *et al.*, 1993; Berg & Tamm, 1994), substrate quantity

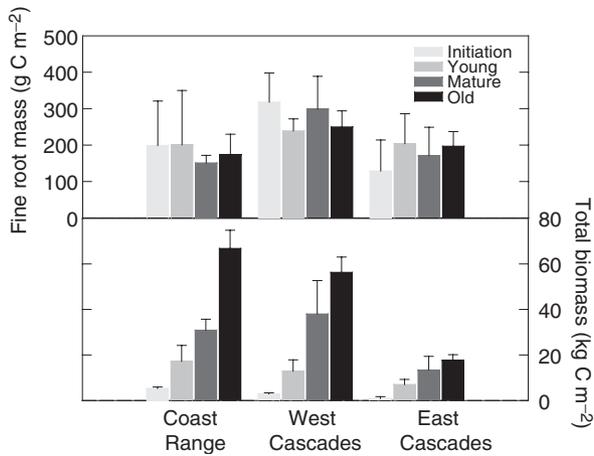


Fig. 3 Successional trends in fine root and total biomass for each of three climatically distinct forest types. Values are the average and standard deviation of three replicate study plots.

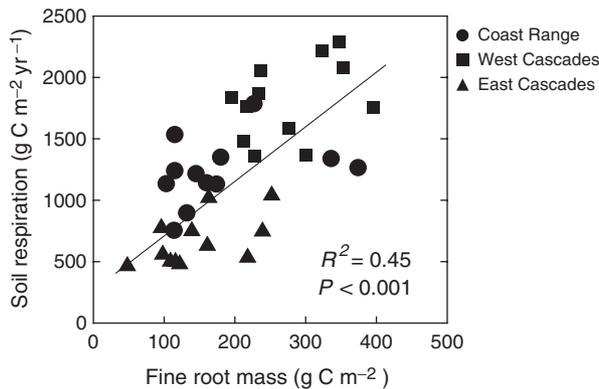


Fig. 4 Cross-site relationships between annual soil respiration and fine root mass.

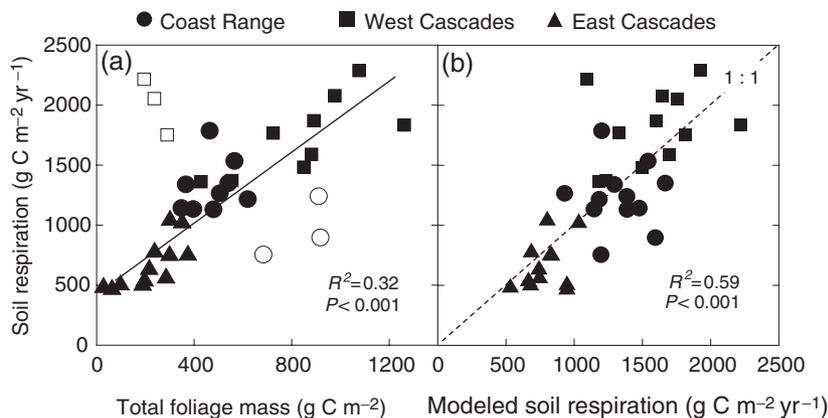


Fig. 5 (a) Cross-site relationship between measured soil respiration and total foliage mass; open squares represent plots with a notably high fraction of understory and open circles represent plots with a notably low fraction of understory. (b) Soil respiration as modeled by least-squares regression allowing understory foliage mass to be weighted separately from overstory foliage: Annual soil respiration = $435 + 1.0 \times (\text{overstory foliage mass}) + 11.2 \times (\text{understory foliage mass})$.

(Myrold *et al.*, 1989), and the biomass of metabolizing tissue (microbial biomass: Zak *et al.*, (1999); root biomass: Dornbush & Raich, in review). We are keenly aware of the factors that regulate soil respiration; unfortunately, our ability to use this knowledge to assess soil respiration at landscape and regional scales remains very limited.

Previous analysis of soil respiration across Oregon forests suggests that soil temperature and moisture, while clearly important in shaping plot-level daily respiration rates, were not the major factors driving variation in annual rates observed among forest types when the data are pooled (Irvine & Law, 2002; Campbell & Law, 2004). Based on these observations, we hypothesized that total ecosystem production and particularly the amount of carbon allocated to roots was the dominant factor influencing cross-site variation in soil respiration. Results of the current study support this hypothesis and suggest a conservation of function across varied environments. That is, despite widely different temperature and moisture regimes, all three forest types examined in this study exhibited similar soil respiration per unit fine root biomass.

Fine roots and BNPP

Among the forests studied, successional trends in live fine root biomass did not follow that of total biomass or even foliage mass. Instead, fine root biomass varied within forest type independent of age class, with the youngest forests often containing as much fine root mass as mature forests. These results suggest that maximum fine root mass was reached at ages younger than those investigated in this study and much earlier than maximum foliage mass.

Table 6 Linear correlation coefficients between annual soil respiration and various stand-level measures of biomass and production

Ecosystem parameter	Among Coast Range plots	Among West Cascades plots	Among East Cascades plots	Among all plots
<i>Biomass and production</i>				
Aboveground NPP	-0.70*	0.05	0.82**	0.24
Belowground NPP	0.09	0.33	0.77**	0.65**
Total biomass	0.62*	0.06	0.78**	0.46**
<i>Aboveground biomass</i>				
Aboveground foliage mass	0.47	0.13	0.75**	0.59**
Aboveground woody mass	0.63*	0.05	0.77**	0.44**
<i>Belowground biomass</i>				
Fine root mass (<2 mm)	0.33	0.38	0.53	0.67**
Small root mass (<2 cm)	0.32	0.27	0.85**	0.50**
Coarse root mass (>2 cm)	0.59*	0.05	0.76**	0.44**
Total root mass	0.59*	0.06	0.80**	0.46**
<i>Soil pools</i>				
Forest floor mass	0.28	0.01	0.53	-0.38*
Total soil C (0–20 cm)	0.79**	0.07	0.02	0.35*
Total soil C (0–100 cm)	0.46	0.45	0.13	0.22
Light fraction soil C (0–20 cm)	0.61	0.12	0.27	0.19
Total soil N (0–20 cm)	0.59	0.53	0.42	0.63

$n = 12$ for regressions among Coast Range, West Cascades, and East Cascades plots except for light fraction soil C, where $n = 3$. $n = 36$ for regressions among all plots.

* $P < 0.05$; ** $P < 0.001$.

Fine root mass relative to the mass of coarse roots, foliage, and woody tissue was highest in the pine forests growing in the East Cascades where coarse textured soils and low annual precipitation lead to a relative scarcity of belowground resources. It is commonly believed that forests respond to belowground resource limitation by allocating a higher fraction of carbon to roots (for a review see Landsberg & Gower, 1997, p. 148). Our data support this hypothesis and go on to imply that a relatively high allocation of carbon belowground maintains soil respiration at rates higher than would be predicted by total biomass alone. Similarly, Dornbush & Raich (in review) found that soil respiration among various grassland ecosystems was governed more by belowground carbon allocation than aboveground production. It is notable, however, that most of the East Cascades plots lie on or below the regression line describing soil respiration as a function of fine root mass (Fig. 4), suggesting that root activity per unit mass was slightly lower than that for other sites. Allocation patterns were also important in defining fine root mass and subsequently soil respiration between the two mesic forest types west of the Cascades, however patterns cannot be explained as a simple tradeoff between- above- and belowground allocation. Rather, forests at the West Cascades simultaneously supported greater fine root and foliage mass per unit total biomass than the forests in the Coast Range.

The positive linear relationship between BNPP and annual soil respiration reported in this study is predicated largely on our assumption that fine root turnover index is conserved across sites (see methods). One can easily imagine scenarios wherein forests had similar standing crops of fine root but differed in their rates of turnover or maintenance respiration. Under these conditions, we would expect poor correlations between soil respiration and fine root biomass. However, the fact that annual soil respiration in this study related linearly to fine root mass across sites is itself consistent with a conservation of turnover among Oregon forest types. A more broadly applicable relationship between BNPP and soil respiration will come only when we have better estimates of fine root turnover or independent measurements of total belowground allocation. Until then, recognizing that cross-site variation soil respiration can be reasonably coupled to BNPP while not at all coupled to ANPP or detrital carbon pools implicates root allocation as the dominant factor driving annual soil respiratory fluxes across the region.

Foliage mass

The connection between foliage mass and soil respiration is especially notable, not only because it can explain nearly 60% (see Fig. 5b) of the overall variation in soil respiration among Oregon forests but because it

implies that the integrative significance of foliage mass extends beyond the canopy to belowground processes. Biologically, foliage mass is linked to soil respiration through both litterfall and the interdependence of roots and leaves. While decomposing leaf litter at these sites represents 11–20% of instantaneous soil respiration rates (Law *et al.*, 2001b), neither annual litterfall nor forest floor mass were good indicators of soil respiration in this study. Consequently, we believe that the connection between root and leaf metabolism is what maintains a strong cross-site relationship between foliage mass and soil respiration.

The utility of linking foliage metrics to soil respiration depends on the particular spatial–temporal domain over which one is assessing respiration. For instance, seasonal fluctuations in conifer leaf mass are typically so small as to render them useless in predicting soil respiration for time periods any smaller than a year. Foliage mass could potentially predict monthly soil respiration rates in deciduous forests but this would require site-specific knowledge regarding the temporal lags between root and foliar activity (see Kuhns *et al.*, 1985; Hendrick & Pregitzer, 1993; Pregitzer *et al.*, 2000). The greatest value in linking soil respiration to foliage mass would be to distribute estimates of annual rates across entire landscapes and describe the patterns of soil respiration induced by large-scale drivers such as land form, mesoclimate, and disturbance histories. Leaf area was used successfully to describe cross-site patterns of soil respiration among 17 forests in Europe and North America (Reichstein *et al.*, 2003), and foliage production was used successfully to explain age-related patterns of soil respiration among lodgepole pine forests. However, we did not see a good correlation between annual soil respiration and leaf area index, which would have permitted the use of remote-sensed leaf area index to map soil respiration across regions.

Any attempt to model soil respiration across Oregon forests using foliage mass is complicated by the apparent disproportional contribution to soil respiration by understory species (Fig. 5). While there is some local evidence that understory species may sustain higher rates of root metabolism than their overstory associates (Law *et al.*, 2001b; Tashe & Schmidt, 2003; E. Sulzman, personal communication), it is difficult to account for the ten-fold factor implied by this study. More work needs to be carried out on the unique behavior of understory species, particularly the N-fixers and grasses that make up much of the understory in these forests. In general, the consideration of growth forms separately is an underutilized yet potentially powerful approach to modeling plot-level carbon dynamics (Grime, 2001).

Soil organic matter

Despite a wide range of forest floor mass, soil C content, and dead coarse root mass (60%, 60%, and 80%, respectively), annual rates of soil respiration across this landscape are not well correlated with these sources of heterotrophic respiration. Even the light-density fraction of soil carbon, which we presume represents the more labile portion of soil carbon, showed no significant correlation with annual soil respiration. This observation is surprising in light of root separation experiments conducted on the same pine study plots, which suggest that fine roots and mineral soil contributed nearly equal to instantaneous soil respiration rates (Law *et al.*, 2001a). However, considering that soil carbon pools are the dynamic balance between inputs and mineralization, we should expect to see strong relationships between soil carbon pools and respiration in only very limited circumstances, for instance, when comparing systems with similar soil inputs and contrasting decomposition (such as oxygen-limited soils: McGroddy & Silver, 2000; Savage & Davidson, 2001; O'Connell *et al.*, 2003) or when comparing systems with disparate inputs and similar decomposition rates (such as till and no-till agriculture: Wagai *et al.*, 1997). Our results suggest that in the conifer forests of Oregon, carbon storage and fluxes from the soil are governed independently.

Litterfall and total root allocation

Global comparisons suggest that forest soil respiration is typically about three times the carbon inputs through canopy litterfall (Raich & Nadelhoffer, 1989; Davidson *et al.*, 2002). By assuming belowground C pools to be in near steady state, this relationship has been used to set upper limits on the amount of carbon allocated belowground. In cases where total annual soil respiration exceeds three times annual litterfall, it is believed that one of two situations apply: (a) long-term changes in root, soil, or litter stocks of carbon are substantially negative relative to the annual soil respiration, or (b) site conditions and plant responses are such that the annual carbon allocation to roots proportional to litter inputs exceeds the global average.

In this study, annual soil respiration exceeded three times litterfall inputs at all 36 study plots and exceeded ten times litterfall inputs in each of the West Cascade plots. Notwithstanding type II statistical error (Davidson *et al.*, 2000), the lack of discernable trends in root, soil, or litter carbon stocks, across even the early portions of each chronosequence, are consistent with the attribution of these high soil respiration values to carbon metabolism by roots and their heterotrophic

associates. Furthermore, the high soil respiration observed among the West Cascades plots, relative to the other sites, can be accounted for by the relatively high fine root mass present at this site. There exists a variety of supporting evidence for this apparently large belowground carbon allocation. Previous work by Fogel & Hunt (1983) in a western Oregon 35–50-year-old Douglas-fir stand found that nearly 70% of total NPP was invested in growth and maintenance of roots and mycorrhizae. Most of the annual turnover in the root zone would be accounted for by ectomycorrhizae on fine root tips and in soil-colonizing mycorrhizal rhizomorphs and hyphae. Rapid turnover of VA (Vesicular Arbuscular) mycorrhizal hyphae has recently been demonstrated by Staddon *et al.* (2003). Evidence for greater C allocation to belowground fine roots by Douglas-fir stands growing on a drier and less fertile site relative to a more fertile one was shown by Keyes & Grier (1981). Their work supports observations in this paper of greater belowground C allocation observed for West Cascades site relative to the Coast Range.

Within-site patterns

Attempts to develop general principles that can be applied to carbon metabolism across forest type and age are complicated by the fact that factors relevant at one scale may be relatively unimportant at others (Meentemeyer, 1984; Turner, 1990; Saunders *et al.*, 2002). Among the pine forests, soil respiration was strongly coupled to almost all measures of biomass and production, while soil C was the strongest predictor of soil respiration among the Coast Range plots, and soil respiration varied independent of all measured parameters among the West Cascades plots. The fact that foliage and fine root biomass was a reasonable predictor of variation in soil respiration between forest types, but not within forest types could be partly because of type II experimental error. That is, the variation in fine root mass exhibited within forest type is not broad enough to detect a trend that is apparent between forest type.

Conclusions

Results from this study point to the importance of belowground production and fine root biomass in shaping annual rates of soil respiration across forests of western Oregon. Among-site patterns of fine root mass are dictated both by total forest biomass and belowground allocation patterns. An apparent conservation of fine root biomass throughout forest development leads fine root mass (and subsequently soil respiration) to vary more between forest types than

with the structural changes that occur in more than 100 years of development. By nesting replicated chronosequences within multiple, edaphoclimatically distinct forest types, this study addresses landscape patterns of soil respiration. As of now, the most promising opportunity to deduce regional values of soil respiration comes from simulation models that can be run contiguously over large spatial domains (Law *et al.*, 2003; Rastetter *et al.*, 2003). While the logic describing soil respiration varies from model to model, attention has typically focused on the controls imposed by soil temperature and moisture (see Burke *et al.*, 2003 for a review of soil respiration models). However, as emphasized by the works of Hogberg *et al.* (2001) and Bhupinderpal-Singh *et al.* (2003), soil respiration can be tightly coupled to the immediate supply of root carbon and it seems increasingly evident that supply-side controls are equally if not more important in explaining variation in soil respiration.

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