AN ABSTRACT OF THE DISERTATION OF

John Campbell for the degree of Doctor of Philosophy in Forest Science

presented on November 24, 2003.

Title: Carbon Fluxes Across Three Climatically-distinct Forest

Chronosequences in Oregon.

Abstract approved:

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Beverly E. Law

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Warren B. Cohen

Biometric and gas exchange techniques were used to measure soil

respiration (soil surface CO_2 efflux) and NEP (Net Ecosystem Production)

across three climatically-distinct forest chronosequences in Oregon.

Results indicate significant forest type, age, and forest type x age

interaction effects on annual soil respiration. A regional age class

distribution skewed away from the youngest and oldest forests moderate regional variation in soil respiration. Sensitivity analysis suggests that the regional variation in annual soil respiration is most dependent on summer base rates (i.e. soil respiration normalized to a common temperature) and much less dependent on site-specific temperature response curve (to which annual rates are relatively insensitive) and soil degree-days (which vary only 10% among sites).

Across all plots, annual soil respiration was not correlated with aboveground net primary production (ANPP, R^2=0.06, p>0.1) but it was correlated with belowground net primary production (R^2=0.43, p<0.001). Despite the wide range in temperature and precipitation regimes experienced by these forests, all exhibited similar soil respiration per unit fine root biomass, (R^2=0.45, p<0.001). Forest floor mass and mineral soil carbon were only weakly coupled to soil respiration (R^2=0.14, and 0.12, respectively). Trends between soil respiration, production, and root mass among age classes within cover type were inconsistent and do not always reflect cross-site trends.

NEP was highly negative immediately following stand replacing disturbance in all forests and recovered to positive values by 10, 20, and 30 years of age for the mild and mesic Coast Range, West Cascades and East Cascades, respectively. The response of stand-level NEP to individual disturbance events is greater than that attributable to edaphoclimatic differences between forest type. However, when

successional trends in NEP are weighted by current age class distributions, the variability in landscape-level NEP attributable to whole disturbance regimes is equivalent to that attributable regional edaphoclimatic differences between forest types. Simulations of age class distribution under varying disturbance frequencies suggest that the sensitivity of landscape-level NEP to changes in disturbance regime varies among forest types and is linked to both remnant detritus and photosynthetic recovery rate that are partly a function of long-term edaphoclimatic differences.

Carbon Fluxes Across Three Climatically-distinct

Forest Chronosequences in Oregon

by

John Campbell

A DISSERTATION

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Head of the Department of Forest Science

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent

collection of Oregon State University libraries. My signature below

authorizes release of my dissertation to any reader upon request.

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John Campbell

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CONTRIBUTION OF AUTHORS

Dr. Osbert Sun assisted with the collection and processing of data. Dr.

Beverly Law was involved in the interpretation of data and assisted in the

editing of all three manuscripts

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General Introduction

Purpose

The sequestration of atmospheric C by terrestrial ecosystems can be described as the small difference between two large fluxes, namely, the flux of carbon into the ecosystem through primary production and the release of carbon from the ecosystem through the process of decomposition and autotrophic respiration. It has been estimated that the world's forests release 80 Pg of C into the atmosphere each year nearly balancing the 90 Pg of C that forests remove from the atmosphere. Forest respiration is approximately 20 times the total annual release of CO_2 from anthropogenic sources. Current concern over atmospheric CO_2 levels and subsequent climate change has brought the issue of forest carbon exchange to the forefront of earth science and challenged forest ecologists to quantify the impact of climate and disturbance on the carbon exchange, not only of individual forest stands, but across entire forested landscapes.

Over the last half century ecophysiologists have been very successful in providing a solid understanding of the forces that drive production and respiration at the leaf, plant, and, to some degree the stand level. However, as advances in earth science and terrestrial ecology bring these fields closer together, the search for drivers underlying forest

processes is being succeeded by a need to understand how forest processes manifest themselves over broader temporal and spatial domains.

Figure 1 illustrates how the regulation of carbon exchange between forest ecosystems can be manifest at various scales. Disturbance and edaphoclimatic forces operate to shape forest carbon exchange at the landscape and regional scale, yet the mechanisms through which these forces operate involve processes working at smaller scales. The overall objective of following three studies is to assess how landscape level forces are influencing regional carbon exchange between Oregon forests and the atmosphere.

Edaphoclimatic history disturbance

Figure 2 Illustrates the study design used in each of the following manuscripts. Considering that the forested landscape of Oregon is a mosaic of forest types (arranged along climatic gradient from the wet and cool Pacific coast to the semiarid plateau east of the Cascades) and age classes (succession following both natural and anthropogenic disturbances), the stratification of field measurements by these categories provides, at a minimum, an opportunity to quantify the variability in carbon fluxes across the region. More importantly, however, is the ability of this field design to separate out the relative influence of two fundamentally

Process = forest soil C-efflux
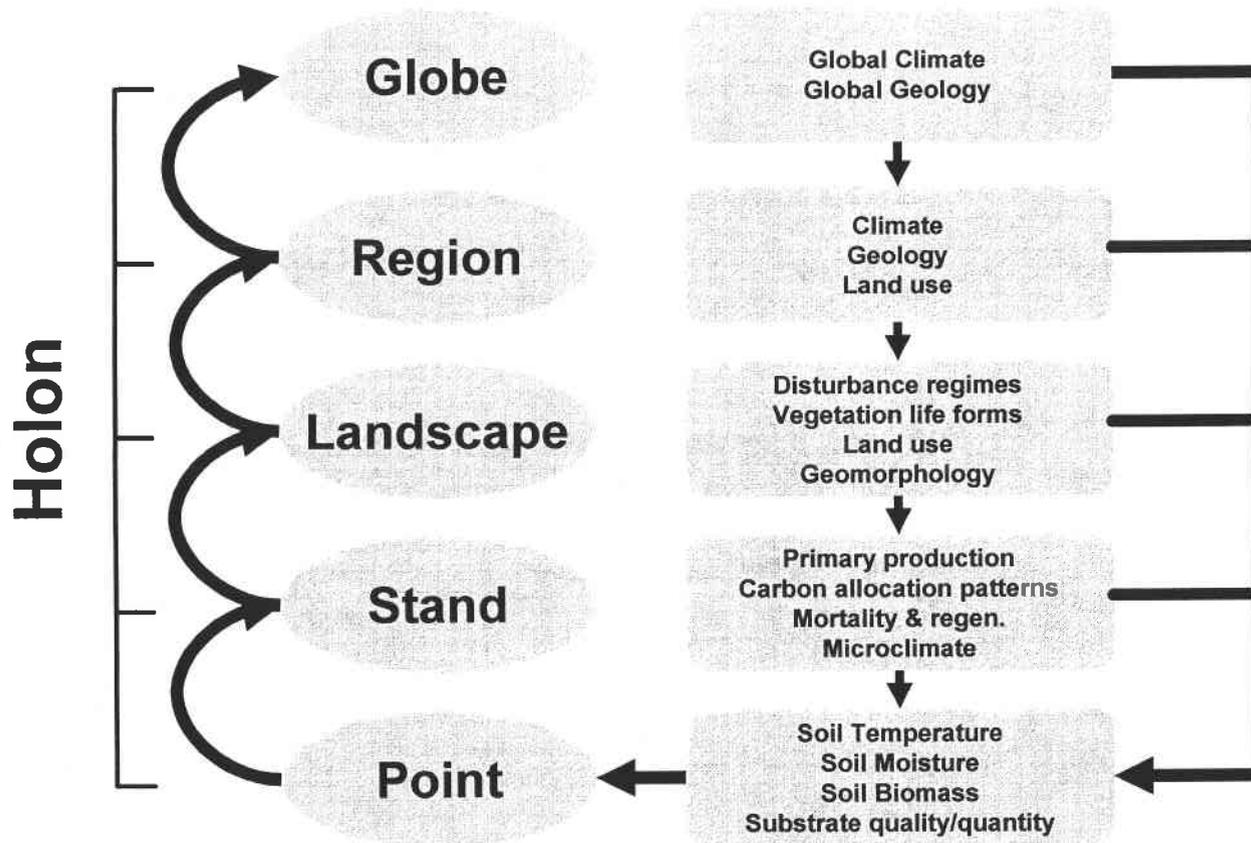
Figure 1. Forces influencing forest carbon exchange at multiple scales.
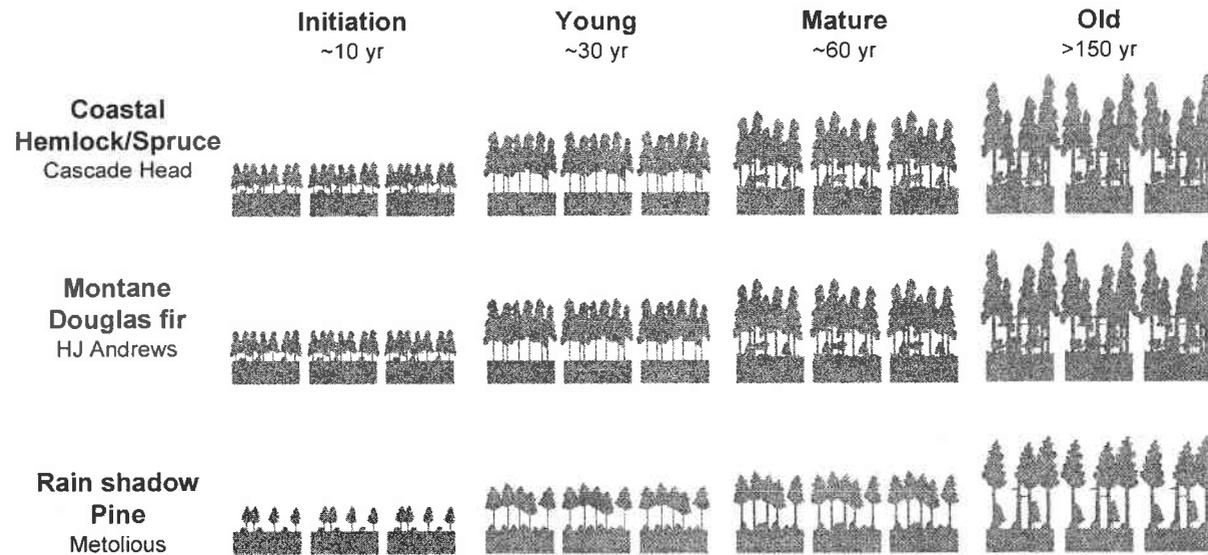
Figure 2. Replicated study design employed to assess carbon fluxes between the atmosphere and the forested landscape of Oregon.

different and opposing landscape forces on forest carbon fluxes, namely: edaphoclimatic history and disturbance.

The forested landscape of western Oregon is particularly suited to investigating the opposing influence of climate and disturbance. In the conifer forests of the Pacific Northwest, where the return interval for catastrophic disturbance ranges from 300-500 years and pioneer species typical retain dominance through the life of the stand, forest age and forest type serve as reliable and independent gauges of edaphoclimatic history and disturbance, respectively.

Specific goals

The first two manuscripts in this document deal specifically with forest soil respiration (soil surface CO_2 efflux) and the third addresses net ecosystem production (the net difference between all carbon gains and losses over a defined period of time). The emphasis on soil respiration and its regulation stems in part from the magnitude of this flux (it is estimated that more than half of the carbon absorbed by forests is released back to the atmosphere through the process of soil respiration) but also because our understanding of belowground processes has, and will continue to lag behind our understanding of aboveground processes. The emphasis on net ecosystem production in the third manuscript

addresses the larger issue of net carbon fluxes across landscapes and

how they are independently shaped by climate and disturbance history.

The specific goals of each manuscript are as follows:

Manuscript 1: Forest soil respiration across three climatically-distinct

chronosequences

1) Quantify annual soil respiration for a full range of age classes in each

of three edaphoclimatically-distinct forest types.

2) Determine which of the following variables typically used to predict soil

respiration at the plot level were the most important sources of regional

variation in soil respiration: base respiration rates, temperature

response coefficients, cumulative soil temperature, or soil moisture.

3) Weight age-related trends in soil respiration by the current age class

distribution to determine how much regional variation can be attributed

to disturbance history compared to the amount attributable to the

edaphoclimatic differences between forest types.

Manuscript 2: Supply-side controls on soil respiration among Oregon

forests

1) Determine how regional variation in soil respiration relates to plant

production and the subsequent allocation of carbon into various

ecosystem pools including leaves, coarse roots, and fine roots.

2) Compare the above relationships to that between soil respiration and the decomposition of dead organic matter in the forest floor and mineral soil.

Manuscript 3: disturbance and net ecosystem production across three climatically-distinct forest landscapes

1) Quantify the successional trends in net ecosystem production (NEP) that follow stand replacing disturbance in each of three edaphoclimatically-distinct forests types in Oregon.

2) Determine which component carbon fluxes were most responsible for the magnitude of NEP and which were most responsible for the trends in NEP.

3) Compare the relative importance of disturbance and edaphoclimatic controls on regulating NEP at both individual stands and across entire landscapes.

4) Assess the sensitivity of landscape level NEP to alterations in disturbance regimes and link this sensitivity to the production biology of each forest type.

In addition to these scientific objectives, the following manuscripts contain valuable and often novel methlogies including, but not limited to, the scaling of periodic soil respiration measurements to estimates of annual flux rates, the stochastic propagation of field measurement

uncertainty into uncertainty in the estimation of net ecosystem production, and the sensitivity analysis relating landscape level net ecosystem production to alterations in disturbance regimes.

Forest soil respiration across three climatically-distinct chronosequences in Oregon

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Abstract

To assess the relative influence of edaphoclimatic gradients and stand replacing disturbance on the soil respiration of Oregon forests, we measured annual soil respiration at 36 independent forest plots arranged as three replicates of four age classes in each of three climatically-distinct forest types.

Annual soil respiration for the year 2001 was computed by combining periodic chamber measurements with continuous soil temperature measurements, which were used along with site-specific temperature response curves to interpolate daily soil respiration between dates of direct measurement. Results indicate significant forest type, age, and type x age interaction effects on annual soil respiration. Average annual soil respiration was 1100-1600, 1500-2100, and 500-900 g C m^{-2} yr^{-1} for mesic spruce, montane Douglas-fir, and semi-arid pine forests respectively. Age related trends in annual soil respiration varied between forest types. The variation in annual soil respiration attributable to the climatic differences between forest types was 48%(CV). Once weighted by the age class distribution for each forest type, the variation in annual soil respiration attributable to stand replacing disturbance was 15%(CV). Sensitivity analysis suggests that the regional variation in annual soil respiration is most dependent on summer base rates (i.e. soil respiration normalized to a common temperature) and much less dependent on the

site-specific temperature response curves (to which annual rates are relatively insensitive) and soil degree-days (which vary only 10% among plots).

Introduction

The sequestration of atmospheric carbon into terrestrial ecosystems can be described as the small difference between two large fluxes, namely, the flux of carbon into the ecosystem through primary production and the release of carbon from the ecosystem through the processes of decomposition and autotrophic respiration. It has been estimated that the world's forests release 80 Pg of C into the atmosphere each year nearly balancing the 90 Pg of C that forests remove from the atmosphere and approximately 20 times the total annual release of CO_2 from anthropogenic sources (Schimel et al., 2000; Houghton, 2003). Given that 60-80% of all CO_2 released by forests emanates from the soil (Davidson et al., 1998; Law et al., 1999; Longdoz et al., 2000), it is clear that assessing the global carbon cycle demands an understanding of how forest soil respiration (also known as soil surface CO_2 efflux) is regulated not only at individual sites but over broad spatial and temporal scales.

A lot has been learned over the last two decades regarding the factors that regulate soil respiration in forests. Considering that soil respiration is driven by the cellular metabolism of belowground carbon, we

are not surprised to find it commonly influenced by temperature, moisture, and substrate quality and quantity. These underlying constraints are portrayed in many process models as a base respiration rate (representing either implicitly or explicitly a forest's belowground carbon supply) modified by various temperature and moisture response curves (see Burke et al., 2003 and Reichstein et al., 2003 for review of soil respiration models). Since we cannot reliably measure soil respiration over areas much larger than a hectare we depend on these models to estimate soil respiration over broad domains. However, proper parameterization is limited by a paucity of regional studies and a shift in parameter importance depending on the scale at which respiration is being assessed (Meentemeyer, 1984, Saunders et al., 2002).

At the stand level, where belowground carbon supply is relatively stable compared to seasonal and interannual fluctuations in soil temperature and moisture, these physical constraints surface as the dominant forces regulating soil respiration (Irvine and Law, 2002; Davidson et al., 1998). However, at the regional scale where patterns of disturbance and climate history are affecting forest production, the capacity of forests to supply carbon belowground may emerge as the dominant factor influencing soil respiration.

The forested landscape of western Oregon is a mosaic of forest types growing along a steep climatic gradient from the wet and cool

Pacific coast to the semiarid plateau east of the Cascades Mountains and age classes representing re-growth following both natural and anthropogenic disturbances. In this study, we took an empirical approach to better understand patterns of soil respiration across western Oregon. Our specific objectives were to:

4) Quantify annual soil respiration for a full range of age classes in each of three edaphoclimatically-distinct forest types.

5) Determine which of the following variables typically used to predict soil respiration at the plot level were the most important sources of regional variation in soil respiration: base respiration rates, temperature response coefficients, cumulative soil temperature, or soil moisture.

6) Weight age-related trends in soil respiration by the current age class distribution to determine how much regional variation can be attributed to disturbance history compared to the amount attributable to the edaphoclimatic differences between forest types.

Methods

Study design

To assess annual soil respiration across western Oregon, we selected 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 class and forest type. The three study sites are located along a wide precipitation and elevation gradient and are best described 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 here after as Coast Range, West Cascades, and East Cascades, respectively). The location of the study sites are shown in Figure 3 and the climatic, edaphic, and compositional characteristics of each forest type are given in Table 1. Age classes were selected such that they represented roughly equivalent developmental stages among across the different forest types and were subjectively classified as either initiation, young, mature or old.

Soil Respiration measurements

Soil respiration was measured using a portable infrared gas analyzer coupled to a soil respiration chamber (LI-COR model 6400 and 6400-09 respectively, LI-COR Biosciences, Lincoln, NE). 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. The permanent collars
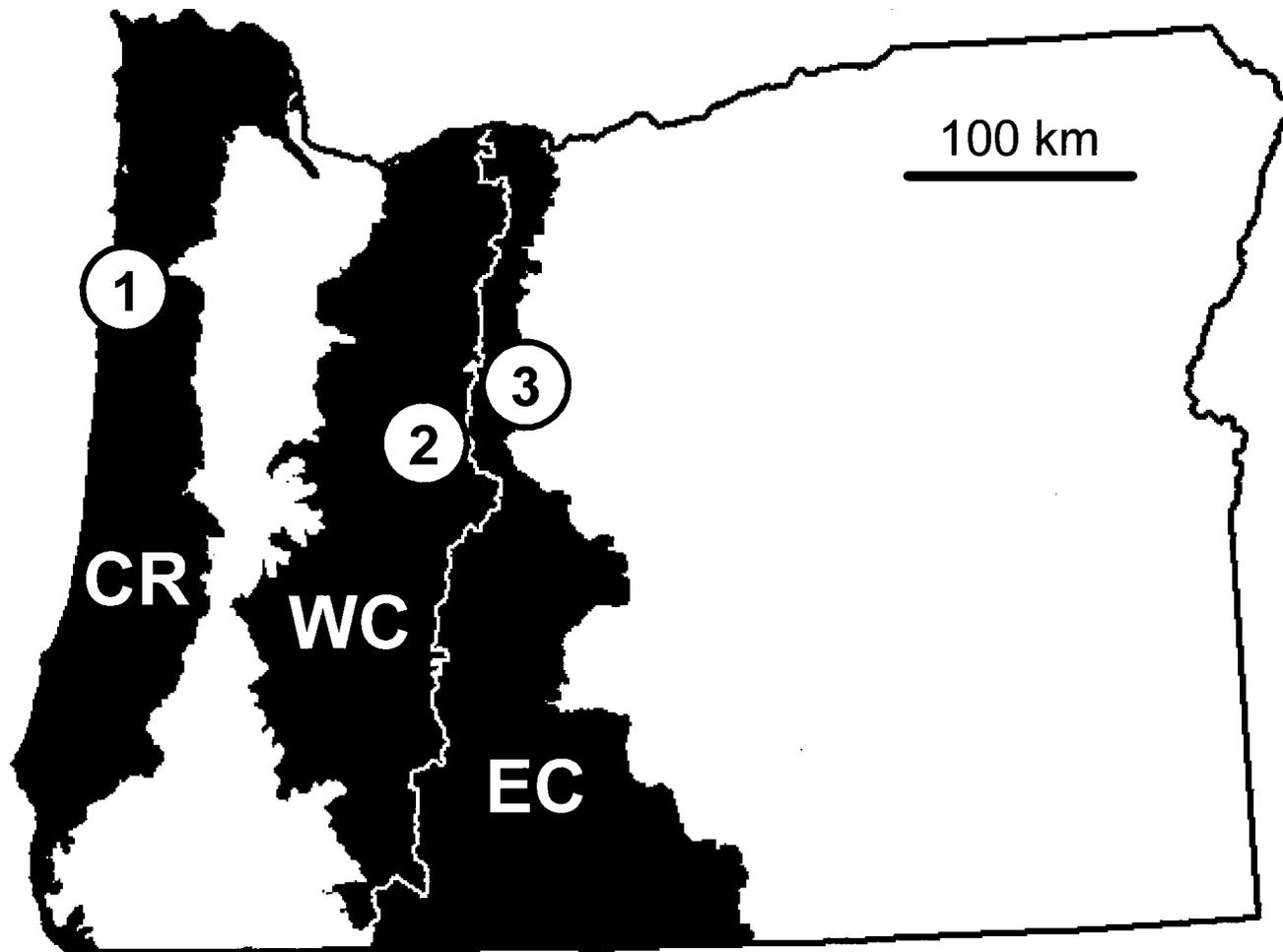
Figure 3. Geographic location of the study sites and the extent of the forest types they represent in western Oregon. Study sites are shown as 1-3. CR=Coast Range, WC=West Cascades, and EC= East Cascades.

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
Location of study sites	Salmon River drainage of Tillamook county Oregon	Blue River drainage of Linn county Oregon	upper Metolius River of Deschutes county Oregon
Precipitation (mm)	2800	2100	520
Number of frost free days	333	255	190
Soil Description	Basaltic colluvium forming well drained silt loams	Igneous colluvium and residuum forming well drained clay loams	Ash over colluvium forming well drained sandy loams
Age class boundries (90th percentile of plot-wide tree age distribution)	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

allow separation of effects of environmental change from within-plot

spatial variability on soil respiration. Each individual measurement covered

75 cm^2 of ground surface and measured soil respiration for approximately

90 sec. For a given day, plot-wide soil respiration was determined as the

average of 12 point measurements regularly stratified throughout the 1 ha

plot. Measurements were taken at the same 12 points in each plot five

times in a year including the 2001 growing season.

Soil temperature and moisture

      Soil temperature at a depth of 10 cm was measured coincident with

each individual soil respiration measurement next to the soil collar.

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).

Each time soil respiration measurements were made, plot-level soil

moisture content was determined to a depth of 30cm using TDR (time

domain refractometry, Tektronix, Portland, OR) at the same four regularly

stratified locations. Raw TDR output was converted to volumetric soil

moisture content using the generalized calibration equations of Ledieu

(1986).

Annual scaling

Annual soil respiration for the year 2001 was computed by combining the periodic chamber measurements with continuous soil temperature measurements, which were used along with plot-specific temperature response curves to interpolate daily soil respiration between dates of direct measurement. Following Ryan et al. (1997), the procedure begins by fitting to each plot a temperature response curve taking the form of equation 1, where R_{obs} is observed soil respiration (plot-wide averages measured periodically throughout the year), and T is the concurrently measured soil temperature (10cm depth).

$$R_{obs} = \alpha \, e^{(\beta T)} \tag{1}$$

Soil respiration for each measurement date is then normalized to 10 °C using equation 2, where R_{10} is the soil respiration base rate (normalized to 10 °C), and β is the exponential coefficient fit in equation 1. Note that $Q_{10}=e^{10\beta}$. A linear interpolation between each measurement date produces an estimated R_{10} for each day of the year.

$$R_{10} = R_{obs} \, e^{(\beta T-10)} \tag{2}$$

Finally, daily average soil respiration is estimated using equation 3, where R_{mod} is soil respiration modeled for each day of the year, and T is the daily average soil temperature (10cm depth, recorded by continuous loggers).

$$R_{mod} = R_{10} \, e^{(\beta T - 10)} \qquad (3)$$

Like other approaches used to interpolate soil respiration between periodic measurements (Pypker and Freedman, 2001; Brye et al., 2002; O'Connell et al., 2003) this procedure assumes that the slope of each temperature response curve (β in equation 1) is constant through out the year. Unique to this approach is that it replaces a fixed intercept (α in equation 1) with the seasonally variable (R_{10}). This accounts for the seasonal variation in R_{obs} that is not associated with T is accounted for. Seasonal variation in R_{10} (which may result from seasonality in soil moisture, soil biomass, or shifts between maintenance and growth respiration) ranged between plots in this study from 50 to 100%.

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 inter-measurement interval. As for the first concern, hourly

diel measurements (made at each forest age and type combination) give no indication of the sort of asymmetry in temperature and respiration that would lend bias to the hourly aggregation of temperature. As for the second concern, we were able to compare our estimates of annual soil respiration on two of the ponderosa pine plots to that calculated from continuous automated chamber measurements (Irvine and Law, 2002). The two approaches produced values that were within 17% of one another at one plot and within 1% at the other.

Age class distributions

For each forest type (Coast Range, West Cascades, East Cascades), the approximate percentage of land area falling into each of the four age classes (initiation, young, mature, and old) was determined from a combination of Forest Inventory Analysis (FIA) and Current Vegetation Survey (CVS) ground surveys (comprehensive USDA forest inventories of Forest Service and privately owned lands, respectively). For each of the 4500 survey plots, forest age was calculated as the 90th percentile of the tree age distribution (Spies and Franklin, 1991) and the breaks between age classes were assigned based on the mid point between the range of plot ages reported in Table 1.

Results

Annual respiration rates across forest age and type

The average annual soil respiration, temperature normalized base rates, and temperature response coefficients for each forest type and age class are shown in Table 2. ANOVA results indicate significant forest type, age class, and forest type x age class interaction effects on annual soil respiration ($p < 0.05$) suggesting that both environmental gradients and disturbance patterns shape soil respiration across Oregon's forests. Annual soil respiration was highest for the West Cascades, lowest for the East Cascades, and intermediate for the Coast Range. Trends with age class are not consistent between forest types. All age classes at Coast Range have similar rates except the old plots, which are significantly higher. In the West Cascades, the initiation and mature plots have the higher rates. In the East Cascades, rates are highest at the mature plots and lower in the older and younger plots.

Soil Temperature as a source of variation

The role soil temperature plays in regional variation in annual soil respiration is best examined through a computational sensitivity analysis. In this study, annual soil respiration values are computed using daily soil temperature, season patterns of temperature-normalized base rates (R_{10}

Table 2. Annual soil respiration by site and age class and the parameters used in computation.

site and age class	annual soil respiration (kg C m^{-2})	maximum base rate (g C m^{-2} sec^{-1})	minimum base rate (g C m^{-2} sec^{-1})	mean temperature response (β)	mean annual degree days (Σ daily C$^\circ$)
Coast Range					
Initiation	1.21 ±0.12	4.05	2.28	0.06	3197
Young	1.09 ±0.29	4.34	2.03	0.08	3015
Mature	1.08 ±0.17	3.89	1.54	0.11	3156
Old	1.56 ±0.22	5.97	2.04	0.11	3223
West Cascades					
Initiation	2.01 ±0.24	7.11	2.20	0.11	2871
Young	1.48 ±0.11	5.30	1.82	0.09	2850
Mature	2.07 ±0.23	9.07	1.65	0.08	2796
Old	1.67 ±0.26	5.83	1.82	0.09	2940
East Cascades					
Initiation	0.48 ±0.02	2.33	0.71	0.04	3547
Young	0.59 ±0.14	2.69	0.88	0.05	3086
Mature	0.87 ±0.27	3.25	1.13	0.07	3181
Old	0.72 ±0.08	2.37	1.07	0.07	3318

Annual soil respiration is calculated as the daily sum of a seasonally-variable base rate (soil respiration normalized to 10°C) multiplied by $e^{(\beta(T-10))}$ where T is soil temperature and β describes the seasonally-derived exponent relationship between soil temperature and respiration ($Q_{10}=e^{10\beta}$). All soil temperatures are at a depth of 10cm. Annual soil respiration reported as the mean ±1SD (n=3 replicate plots).

in equation 2), and plot-specific temperature response curves (β in

equation 1). Figure 4a illustrates the sensitivity of annual soil respiration to

each of these parameters and Figure 4b shows the variation in these

parameters among study plots. While both wintertime base rates (R_{10}) and

temperature response coefficients (β vary widely among study plots, a

10% increase in either results in only a 1% increase in annual soil

respiration. Daily soil temperature, to which annual soil respiration is

sensitive, varies little among study plots. While the magnitude of annual

soil respiration rates clearly depends on soil temperature, variation among

plots is driven primarily by differences in temperature-normalized base

rates during the summer months.

Season length as a source of variation

Because the period over which respiration is sustained could

influence cumulative annual soil respiration as much as the rates

themselves, we compared the relative seasonality of summer and

wintertime soil respiration for each forest type and age class combination.

As shown in Figure 5, soil respiration in all plots of all age classes in both

the Coast Range and the West Cascades reach their seasonal maximum

at about the same time, with plots in the Coast Range sustaining peak

rates longer than plots in the East Cascades. The peak rates in the East

Cascades occur earlier than in the other forests, likely because of reduced
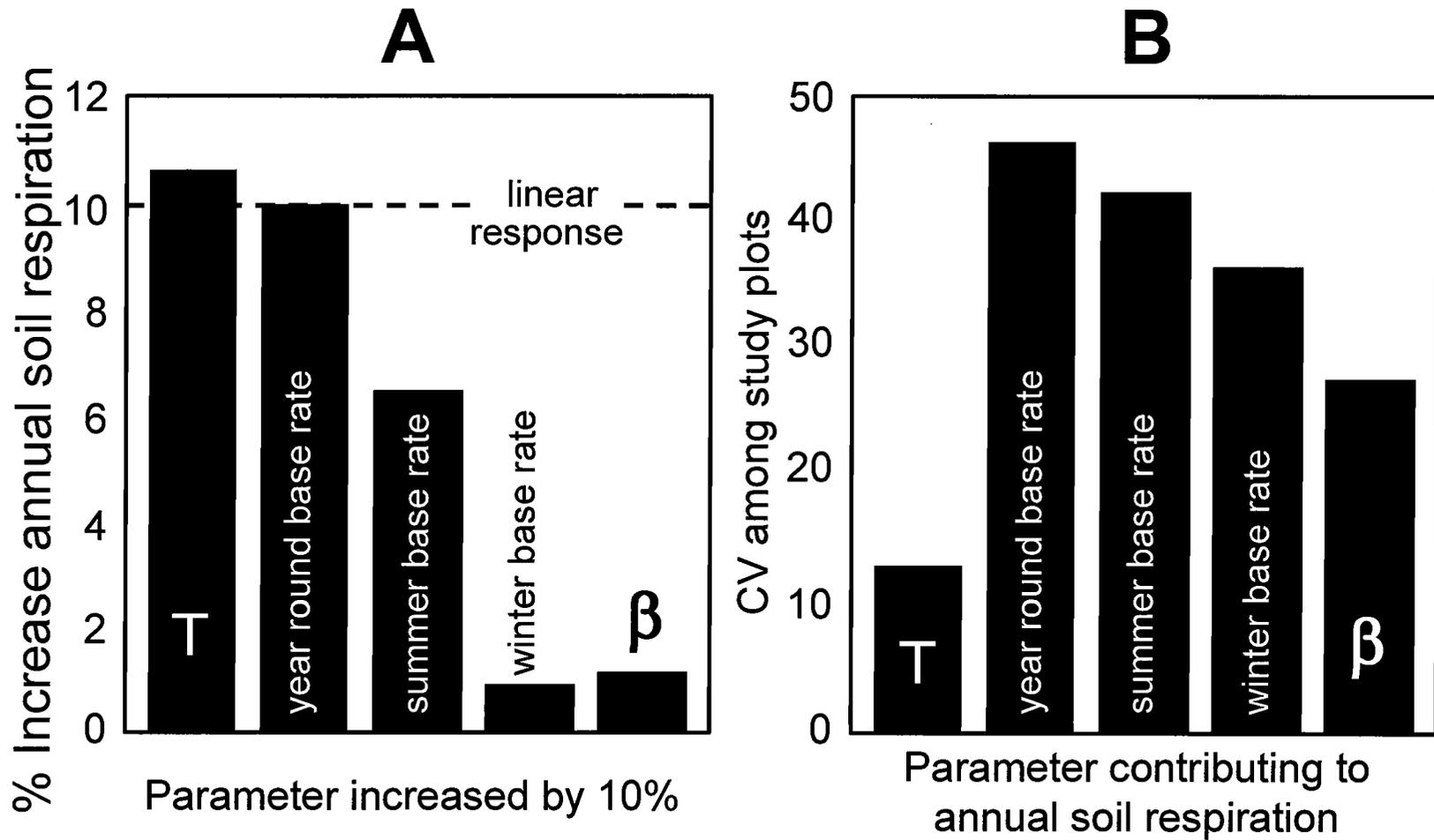
Figure 4. Sensitivity analysis (A) and regional variation (B) of the parameters used to compute annual soil respiration. T=cumulative annual soil temperature at 10 cm, base rates= seasonally variable temperature-normalized respiration rate, and β is the exponent coefficient relating respiration to temperature.
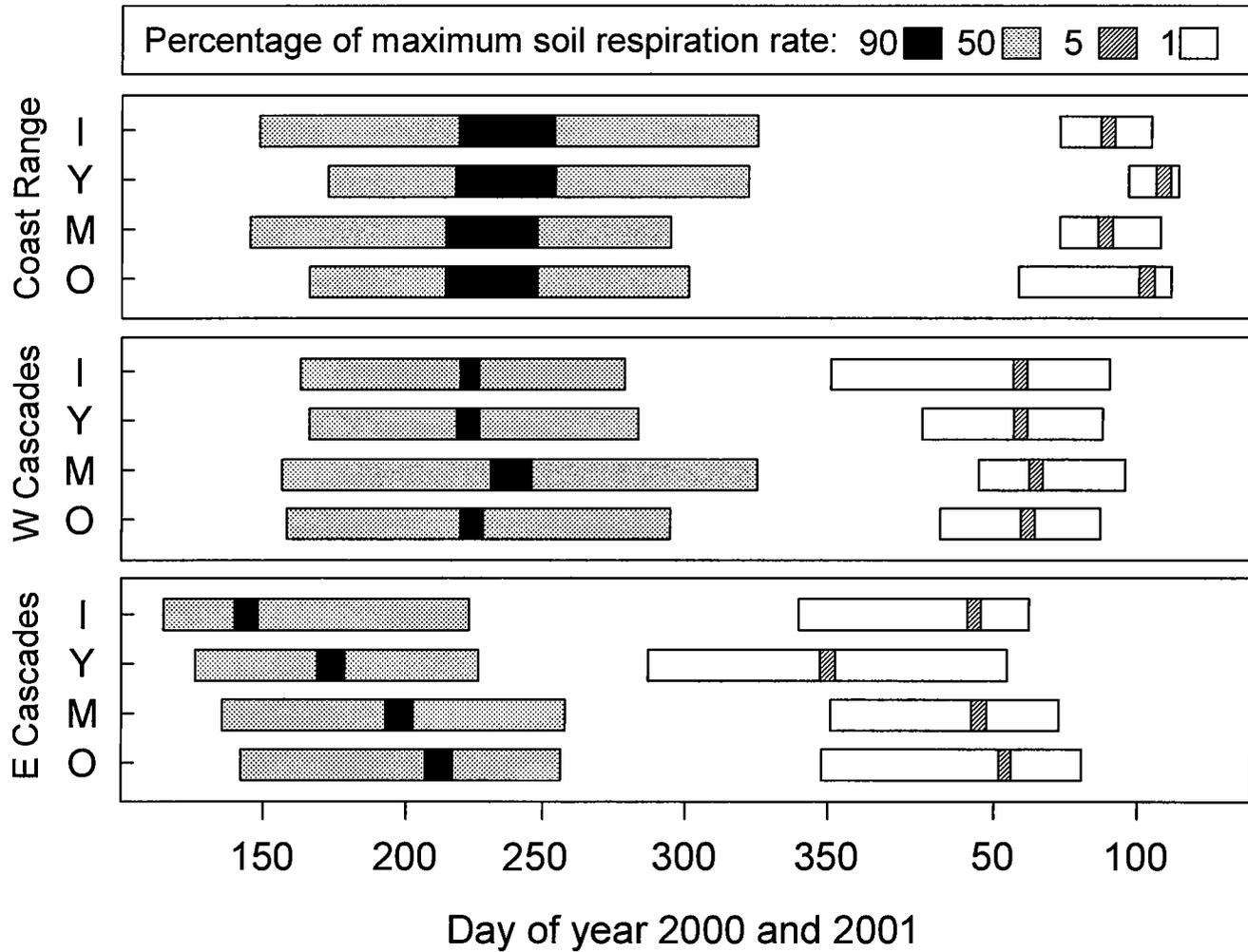
Figure 5. Seasonality of soil respiration for each of the four age classes in each of three forest types. I=initiation, Y=young, M=mature, and O=old.

rates during summer drought. Winter minimum rates are reached first in the East Cascades, then in the West Cascades, and latest in the Coast Range. The duration of minimum rates is similar for both the West and East Cascades, but much shorter for the milder winter climate of the Coast Range. Considering that the Coast Range has the longest period of maximum rates and the shortest period of minimum rates yet does not achieve the annual rates in the West Cascades indicates that the season duration of soil activity is not the primary controlling factor of annual soil respiration.

Soil Moisture as a source of variation

Volumetric soil moisture content during the periods of soil respiration measurement ranged from 0.22 to 0.52, 0.15 to 0.45, and 0.02 to 0.25 m^3m^{-3}, for the Coast Range, West Cascades, and East Cascades, respectively. The residuals of soil respiration, predicted by temperature alone, plotted against relative soil moisture at time of measurement, indicate no significant moisture limitation in the Coast Range or West Cascade forests (Figure 6). At the East Cascades, however, soil respiration is more likely to be less that that predicted by temperature alone at times when soil moisture is below 50% of the seasonal maximum (Figure 6). A cross-forest relationship between soil moisture and soil respiration can explain 14% of the seasonal and regional
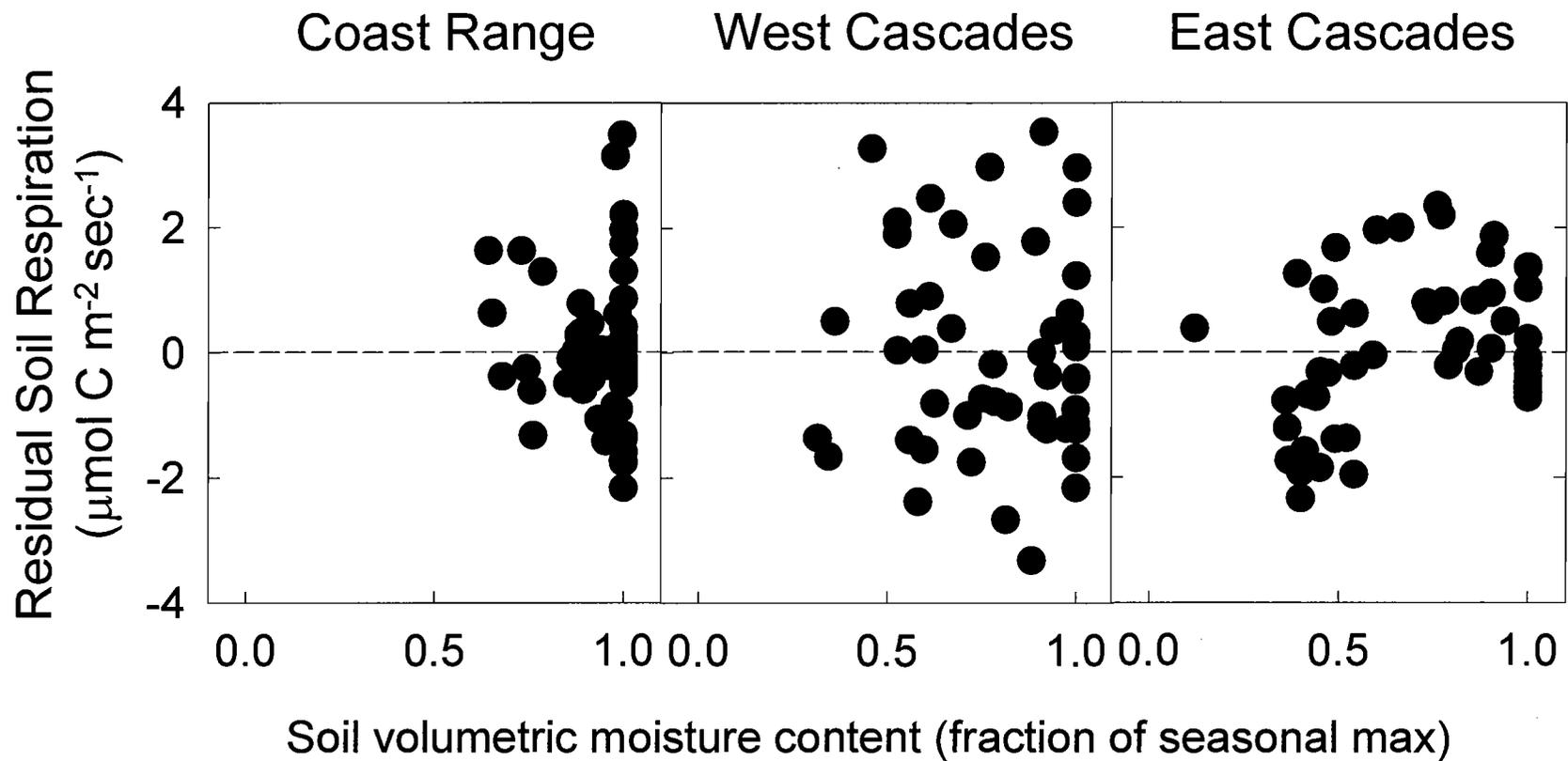
Figure 6. Temperature normalized soil respiration plotted against the volumetric soil moisture as a fraction of the plot-specific maximum. Each point represents plot-wide averages (4 age classes x 3 replicate plots x 5 measurement periods = 60 separate points).

variation in base respiration rates (Figure 7). Although most of this

relationship is made up differences between measurements made at the

East Cascades and those made at all other forests.

Scaling soil respiration by age class distribution

Figure 8 shows the observed variation in annual soil respiration

across age classes for each of the three sites and how these patterns are

weighted by both the approximate time a forest spends in each age class

and the relative frequency of each age class on the current landscape. By

weighting the observed age-related trends in soil respiration by these two

frequency distributions one can quantify the relative importance of

disturbance events acting on individual stands, disturbance history acting

on the entire landscape, and the edaphoclimatic history that separates the

three study forest types.

As shown in Table 3 the variation in annual soil respiration

observed among forests of the same age class growing under different

edaphoclimatic regimes is more than three times the variation observed

across age classes within the same edaphoclimatic regime whether

weighted by the temporal duration of each age class or by the frequency

of each age class on the landscape. In other words, the influence of the

prevailing disturbance history on landscape-level soil respiration is

coincidently equivalent to the influence of a disturbance event acting on an

The plot shows axes: y-axis labeled "R_{10}: Base Respiration Rate (μmol C m^{-2}sec^{-1} normalized to 10°C)" and x-axis labeled "θ: Soil Volumetric Moisture Fraction". Legend: ● Coast Range, ■ W. Cascades, ▲ E. Cascades.

$$R_{10} = 4.037\,(1-e^{-9.210\theta})\qquad R^2 = 0.14$$
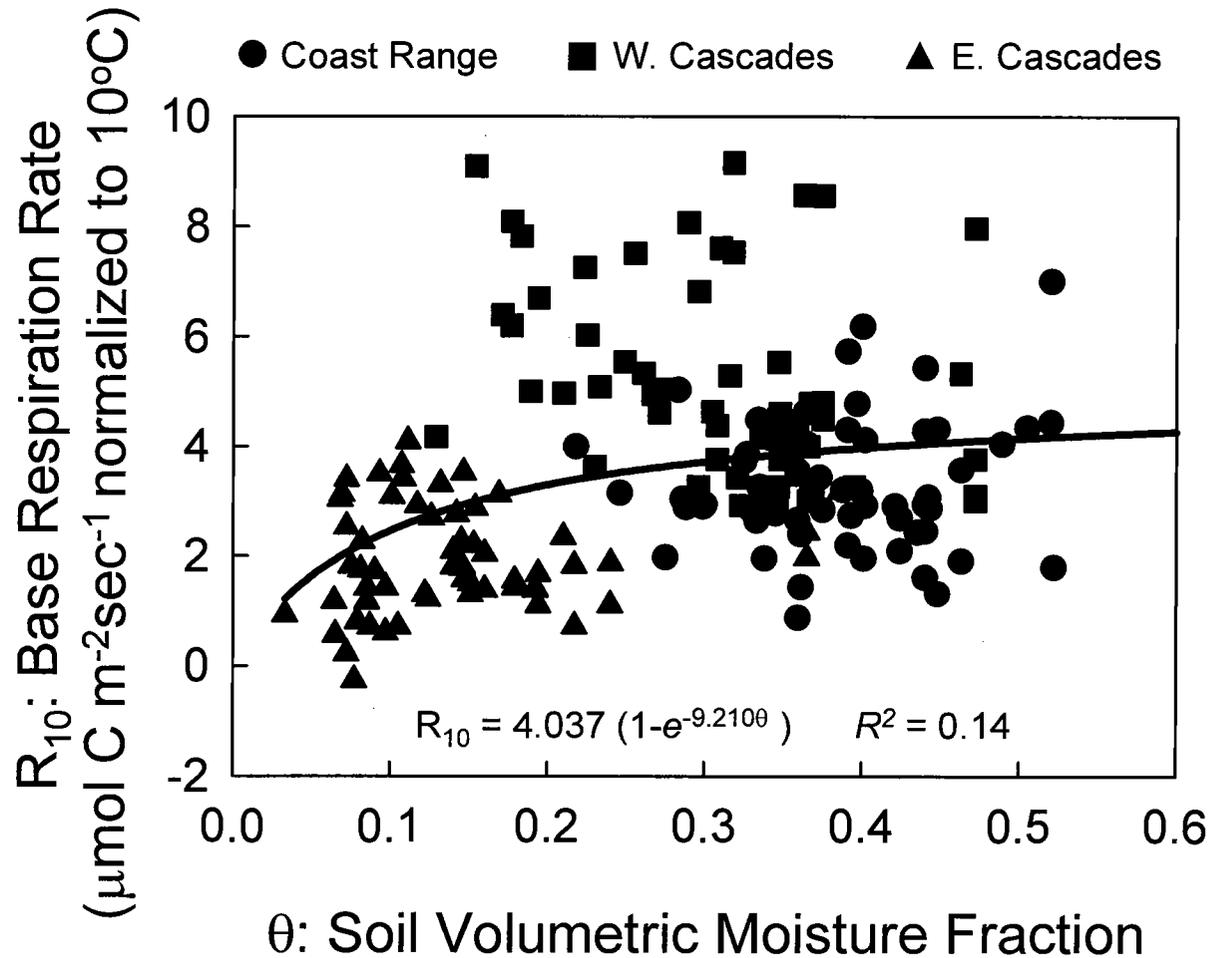
Figure 7. Cross-forest relationship between soil moisture and temperature normalized soil respiration. Each point represents plot-wide averages (3 forest types x 4 age classes x 3 replicate plots x 5 measurement periods = 180 separate points).
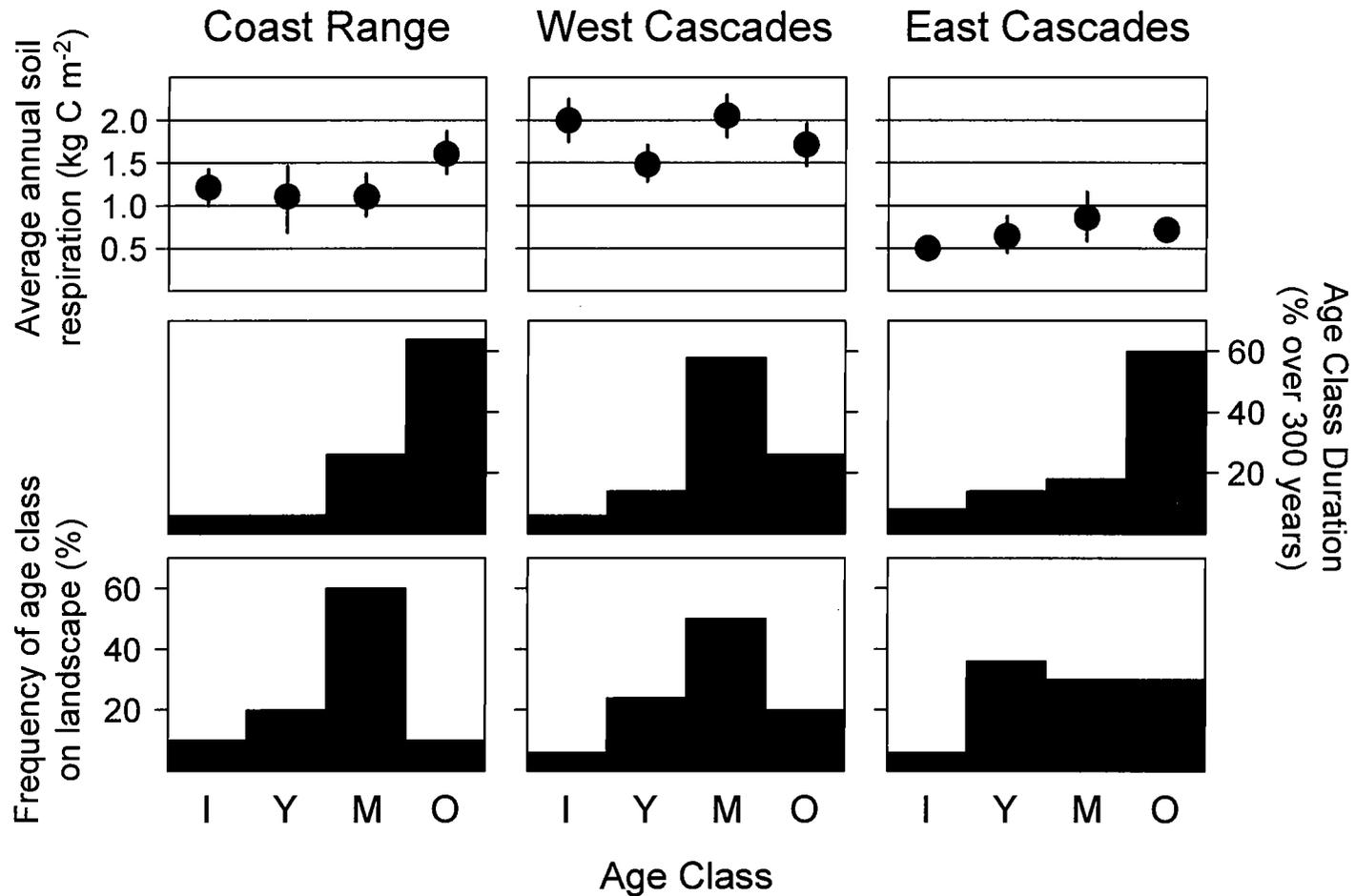
Figure 8. Age-related soil respiration for each forest type, approximate duration a stand may spend in each class, and the frequency of each age class on the landscape. Circles and error bars represent the average and SD of three replicate plots. Age classes represent roughly equivalent developmental stages between forest type. I=initiation, Y=young, M=mature, and O=old.

Table 3. Variation in annual soil respiration attributed to edaphoclimatic gradient, stand-level disturbance event, and landscape-level disturbance history.

Source of variation	Average annual Soil Respiration (kg C m-2)	Standard Deviation	Coefficient of Variation
Across sites within age class			
Initiation	1.23	0.76	0.62
Young	1.05	0.44	0.42
Mature	1.34	0.64	0.48
Old	1.31	0.52	0.40
Variation resulting from edaphoclimatic difference between sites:			*0.48*
Across age class within site (weighted by the duration of each age class over 300 years)			
Coast Range	1.40	0.23	0.16
W. Cascades	1.90	0.24	0.13
E. Cascades	0.71	0.11	0.16
Variation resulting from disturbance events acting on a single stand:			*0.15*
Across age class within site (weighted frequency of each age class on landscape)			
Coast Range	1.14	0.15	0.13
W. Cascades	1.84	0.26	0.14
E. Cascades	0.71	0.13	0.18
Variation resulting from disturbance history acting on whole landscape:			*0.15*

individual stand and much less than the influence of the edaphoclimatic differences between forest types, suggesting that base rates are shaped more by edaphoclimatic differences between forest types than disturbance history.

Discussion

Sources of variation in annual soil respiration

The first principles of carbon metabolism assure that soil respiration is ultimately governed by the availability of suitable carbon substrates, kinetic energy, and various metabolic co-factors such as nutrients and water. Understanding how soil respiration behaves over broad spatial and temporal scales is, in essence, a matter of understanding how these limiting factors vary and co-vary in space and time. Figure 9 illustrates how the process of soil respiration can be described as a function of respiration base rate, soil temperature, and soil moisture and the potential for these parameters to become confounded with one another depending on the scale of interest. For instance, in among-biome comparisons where temperature and production are strongly coupled, soil temperature serves as an integrator of all three parameters regulating soil respiration (Kicklighter, 1994). In plot-level studies, where the focus is typically on temporal variation in soil respiration (e.g. those associated eddy flux tower sites), temperature again becomes the chief index of respiration both
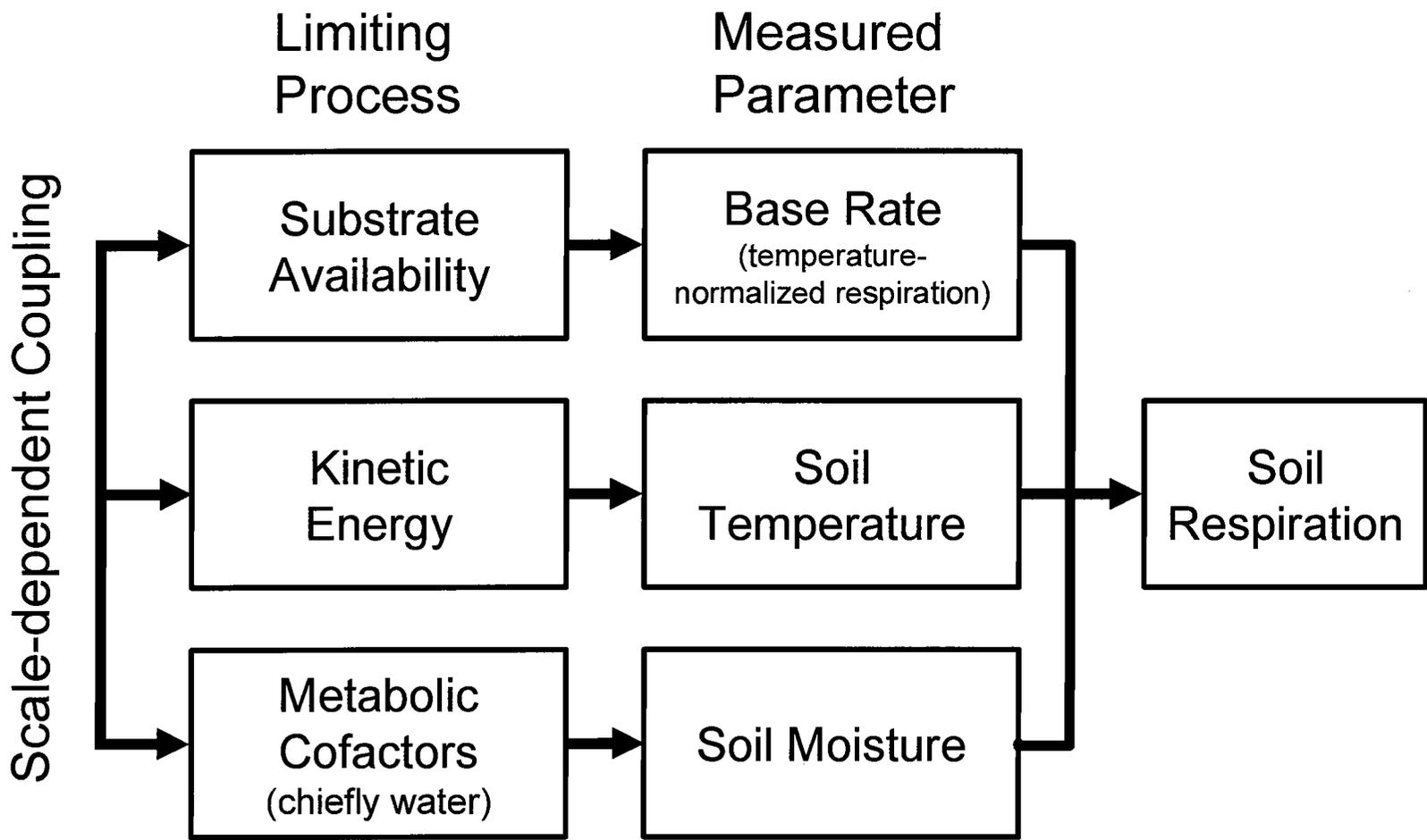
Figure 9. Scale-dependent coupling of processes affecting soil respiration.

because of its direct regulation of daily metabolism and its indirect connection to seasonal patterns of substrate availability. Here again moisture can become important in situations where soils become saturated and anaerobic or where late season drought limits metabolism in spite of high temperature and sufficient substrate availability (Irvine and Law, 2002).

In the regional-scale study presented here, we demonstrate that annual soil respiration represents a substantial release of carbon to the atmosphere and varies by a factor of four among conifer forests of western Oregon. Soil temperature, while strongly linked to seasonal patterns of soil respiration at all plots, explains very little of the regional variation in annual soil respiration. Similarly, soil moisture is linked to seasonal patterns of soil respiration at forest in the East Cascades but explains very little of the regional variation in annual soil respiration. Instead, variations in temperature-normalized base rates explain more of the regional variation in annual soil respiration.

The degree to which temperature and moisture co-vary in the field limit our ability separate them as independent factors affecting soil respiration (Davidson et al., 1998). Never the less, in sites where high temperatures are coincident with dry soils, measures of soil moisture improve the prediction of soil respiration beyond that predicted with temperature alone (Irvine and Law 2002; Xu and Qi, 2001).

The only forests in this study where moisture appeared limiting were those of the semi-arid East Cascades where late-season drought correlated with periods when soil respiration was lower than that predicted by soil temperature alone. However, for modeling purposes it may be desirable to apply a single moisture response curve across the entire region (Reichstin, et al., 2003). While a single hyperbolic relationship between soil moisture and base respiration can be applied across all three forest types (Figure 7), it is unclear whether soil respiration in West Cascades or Coast Range would respond to moisture limitation in the same manner observed in the East Cascades simply because soil moisture in these forests rarely dropped below the response threshold of 0.15 volumetric content or 0.5 the seasonal maximum. In other words, a common regional relationship between soil moisture and base respiration rate may empirically explain 14% of the regional variation but may not represent any true physiological response to moisture in the two mesic forest types.

The use of soil moisture to improve cross-site prediction of soil respiration is further complicated by the multiple scales at which water availability may influence respiration. For instance, a history of low precipitation in the East Cascades can limit the amount of carbon made available to belowground metabolism while at the same time short-term drought affects metabolism itself. Over all, the seasonal patterns of soil

moisture and respiration within forests combined with the precipitation history between forests suggest that direct effects of soil moisture on regional soil respiration is minor while the historical effects of soil moisture underlie the overwhelming disparity in soil respiration between the semi-arid East Cascades and the more mesic forests west of the Cascades.

Empirically linking regional variation in annual soil respiration to growing-season base respiration rates, largely independent of soil moisture, soil temperature or the slope of the temperature response curve, suggests that variation in annual soil across Oregon's conifer forests is governed by substrate availability more than the direct physical constraints imposed by soil temperature or soil moisture.

These results are consistent with a growing appreciation of the importance of supply-side controls on soil respiration over that of the soil physical environment (Hogberg et al., 2001; Janssens et al., 2001; Litton et al., 2003). When distributing soil respiration models across western Oregon it may be more important to accurately characterize variation in substrate quality and quantity and belowground allocation than variation in either temperature response curves or even the seasonal patterns in soil temperature itself.

Regional consequences of patterns in soil respiration

The forested landscape of western Oregon is particularly suited to investigating the separate influence of climate and disturbance. For instance, in systems where relay succession prevails, forest age and forest type become confounded. However, in forests of the Pacific Northwest pioneer species typical retain dominance through the life of the stand, forest age and forest type serve as reliable and independent gauges of disturbance and environment, respectively. Wimberley and Spies (2001) demonstrated this situation by showing that forest structure along the Oregon coast was determined chiefly by disturbance history while forest composition was dependent almost entirely on a site's physical environment. In the current study we show that the process soil respiration is being shaped on this landscape by both environment and disturbance.

Successional trends in annual soil respiration results in only one third the variation in annual soil respiration attributable to the edaphoclimatic differences between forest types. This is the case whether successional trends are amortized for one stand over 300 years to represent the effect of a disturbance event acting on a stand or weighted by the relative abundance of each age class to represent the history of disturbance acting on the landscape.

Exactly how age class distributions are affecting regional soil respiration differs between the three forest types. The Coast Range forests of Oregon experienced a series of extensive stand replacing fires between 1880 and 1910 (Miller, 1982) This followed by widespread timber harvesting in the 20th century has reduced the number of stands defined as old in this study (>150 years) to less than 10% of the land area. If, as suggested by this study, soil respiration is the same among all but the oldest stands in the Coast Range, stand-replacing disturbance during the last century has had little influence on patterns of soil respiration. However, substantial reductions in timber harvest that began in the 1990's have lead to an overall aging of forests in the Coast Range (Spies, et al., 2003). Should this trend continue, a shift in age structure toward old forests might eventually lead to higher regional soil respiration.

The consequences of age related soil respiration among forests of the West Cascades is especially difficult to assess. Here, soil respiration rates were significantly higher in the initiation and mature age classes than in the young and old age classes. This apparently complex relationship between age and soil respiration requires more investigation before a simple measure and multiply technique can be effectively used to assess the consequence of this pattern on the landscape. Never-the-less, we can acknowledge that soil respiration varies up to 34% as a function of age in the West Cascades and that disturbance regimes resulting in the current

distribution of age classes are influencing patterns of respiration among these forests. The consequences of age-related soil respiration are most important in the pine forests of the East Cascades. Among these forests, soil respiration increases with forest development up to the mature age class (60-80 years old in this study) and declines thereafter. This follows trends in net primary production reported by Law et al. (2003). The history of disturbance on this landscape is such that young, mature, and old forest are represented nearly equally. As a consequence age-related trends in soil respiration are the most pronounced on the landscape of the East Cascades.

Summary

In this study we measured annual soil respiration across three climatically distinct forest chronosequences. The first objective was to determine how annual soil respiration varies across the conifer forests of western OR. Our results demonstrate that both the disturbance regimes that result in a diversity of forest age and the edaphoclimatic forces that result in a diversity of forest type are affecting soil respiration on this landscape and that the latter is responsible for more variation than the former.

Our second objective was to determine if the variation in annual soil respiration associated with either forest age or type could be accounted

for by the same variables commonly used to predict soil respiration at individual sites. Our results suggest that temperature and moisture are of minimal importance in defining regional variation in soil respiration and that base respiration rates measured during the summer months appear to be the primary determinant of regional variation in soil respiration. This study highlights the importance of belowground carbon allocation over soil environment in shaping regional patterns of soil respiration.

Our final objective was to consider the distribution of age classes for each of the forest types and determine how much age related variation soil respiration was likely being manifest on the landscape. A paucity of initiation-aged stands across the region, and a paucity of old stands in the Coast Range reduce the regional variation in soil respiration attributable to disturbance to a value three times less than that attributable to the edaphoclimatic differences between forest types.

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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 to net primary production and the subsequent allocation of carbon to various ecosystem pools including, leaves, fine roots, forests 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 (ANPP, R^2=0.06, p>0.1) but it was strongly correlated with belowground net primary production (R^2=0.43, p<0.001). Despite the wide range in temperature and precipitation regimes experienced by these forests, all exhibited similar soil respiration per unit fine live root biomass, with about five grams of carbon respired each year per one gram 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 mass 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 short term-supply of

carbohydrates to roots and the rhizosphere, and that the regional patterns of soil respiration may depend more on belowground carbon allocation than abiotic soil factors, which at regional scales are often confounded with plant production.

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; Law et al., 2002). Considering the importance of forests in sequestering atmospheric carbon, it is clear that assessing 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 whether this has more to do with direct constraints on belowground metabolism or indirect controls 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 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. (2002), who found that measures of vegetation productivity were necessary to reliably model large scale patterns of soil respiration and Litton et al. (2002) who found that soil respiration in a chronosequence of lodgepole pine was correlated with measures of biomass rather than abiotic variables.

In another study (Campbell and Law, in review.), 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 mountians, 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, 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 are located along a large precipitation and elevation gradient and are best described 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 here after 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 location of the study sites are shown in Figure 10. The climatic, edaphic, and compositional qualities of each forest type are given in Table 4 while the structural qualities of each age class are given in Table 5.

Annual Soil Respiration

Soil respiration (soil surface CO_2 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 cm^2 of ground surface and soil respiration was measured for approximately 90 sec. 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 five to six times during 2001. 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
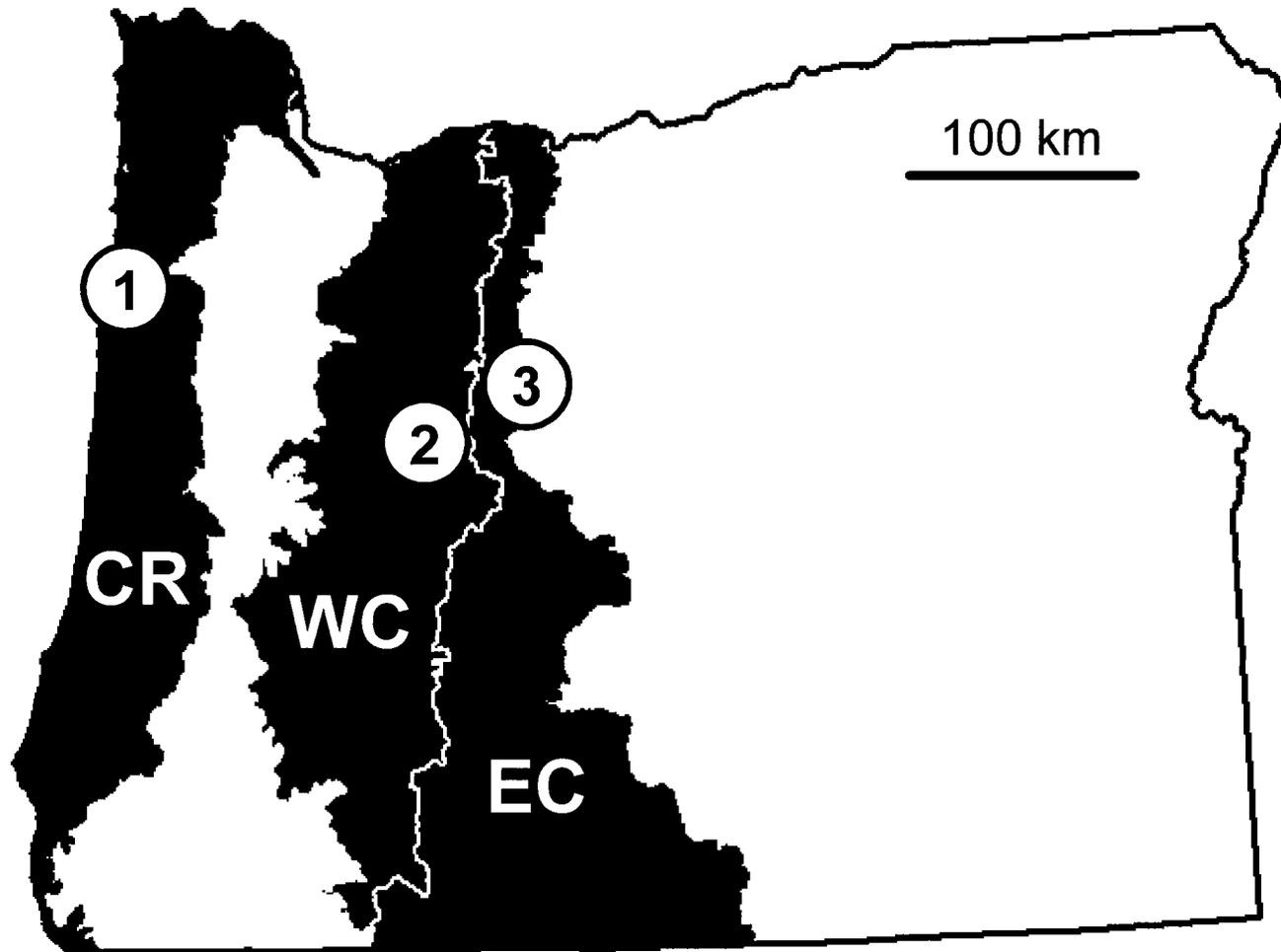
Figure 10. Geographic location of the study sites and the extent of the forest types they represent in western Oregon. Study sites are shown as 1-3. CR=Coast Range, WC=West Cascades, and EC= East Cascades.

Table 4. 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 5. Structural qualities of each age-class averaged across three replicate stands

	stand age	stem diam. (cm)	stem density (m^{-2})	canopy height (m)	ontogeny
Coast Range					
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 reestablishing
old	170-190	51	340	51	multi-story canopy, gap formation, well developed understory
West Cascades					
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	multi-story canopy, gap formation, well developed understory
East Cascades					
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 multi-story canopy, understory often burned.

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

logger buried at a depth of 10 cm in the center of each plot (Hobo

temperature logger, Onset Computer Corporation, Warner, NH, USA).

Following Ryan (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 then using soil temperature to model annual

soil respiration. Specifically, daily average soil respiration was computed

according to equation 1.

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

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=a $e^{\beta x}$ (where y= soil

respiration and x=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. The specifics of this interpolation procedure are given in

Campbell and Law (in review).

Biomass measurements

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

The mass 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 mass 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 used for understory species were acquired from the BIOPACK data base (Means et al., 1994). The allometric equations used for trees came from a variety of sources and are described in VanTuyl (2003).

The mass of tree foliage was calculated as overstory leaf area multiplied 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, Lincoln, NE, USA). Leaf mass per unit area was measured directly on at least six foliage samples per plot (more for multi species stands) and scaled to the entire plot using an average weighted by species composition.

The mass of live fine roots (<2.0mm diam.) was determined by manually separating live fine roots from 5cm diameter soil cores. From each plot In July 2001, twelve cores were taken from 0-20 cm, six from 20-50cm and six from 50-100cm. Rarely were roots found at a depth of 100cm (Sun et al., in press).

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 sub sample 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 five 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 site-specific estimates of fine root turnover. Fine root turnover was assumed to be 0.66 yr^{-1} for plots in the Coast Range and West Cascades based on the average of measurements compiled by Santantonio (1985) and 0.60 yr^{-1} for plots in the East Cascades based on minirhizotron measurements made by C. Anderson (unpublished data) at several sites of varying age (Law et al., 2001).

Soil carbon measurements

Forest floor (soil O-horizon) mass was measured at eight 75 cm^2 locations regularly stratified through out 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 through out each study 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. (in press). 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 6 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 are 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 are undetectable, due in part to high variation within each forest type age class combination.

Soil carbon and nitrogen content in the top 20 cm of mineral soil are shown in Table 7. Total soil carbon is approximately 12, 6, and 3 kg C m^{-2} for the Coast Range, West Cascades, and East Cascades, respectively. However, due to a higher proportion of light-fraction carbon in the West Cascades, the total amount of light-fraction carbon is equivalent between the Coast Range and West Cascades. Soil nitrogen concentration and content are, on average, four times higher in the Coast Range than in the West Cascades and East Cascades.

Estimates of ANPP, BNPP, and annual soil respiration across each of the three chronosequences are shown in Table 8. Average ANPP decreased from about 700 g C m^{-2} yr^{-1} for forests in the Coast Range to

Table 6. 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})	
Coast Range								
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)
West Cascades								
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)
East Cascades								
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 parenthesis are the among-plot uncertainty (1 SD of the mean of 3 replicate plots).

Table 7. 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})	
Coast Range										
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	
West Cascades										
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	
East Cascades										
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 parenthesis are 1 SD of the mean of 3 replicate plots, except for the light C fraction values which are the SD of 12 measurements made in a single plot. See methods for description of density fractionation.

Table 8. 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})	
Cascade Head						
initiation	1205	(116,380)	793	(83,22)	273	(83,95)
young	1086	(288,415)	801	(26,48)	259	(99,73)
mature	1081	(166,387)	657	(44,59)	202	(22,70)
old	1557	(219,384)	486	(145,49)	217	(68,81)
average	1232		684		238	
HJ Andrews						
initiation	2007	(235,623)	315	(24,34)	252	(52,118)
young	1478	(114,458)	476	(127,31)	234	(45,66)
mature	2067	(227,620)	478	(103,40)	274	(74,99)
old	1669	(263,395)	318	(53,56)	218	(34,128)
average	1805		397		245	
Metolius						
initiation	482	(19,117)	114	(42,8)	72	(24,43)
young	593	(136,175)	231	(27,19)	141	(30,43)
mature	872	(272,218)	323	(151,36)	162	(75,62)
old	717	(76,191)	180	(71,27)	133	(38,45)
average	666		212		127	

The first value in parenthesis is the experimental uncertainty (1 SD of the mean of 3 replicate plots). The second value in parenthesis, following the coma, 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 and Law (2003).

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, follows a different pattern, with rates approaching 250 g C $m^{-2}yr^{-1}$ in both the Coast Range and West Cascades, and 130 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 Figure 11, soil respiration among all 36 plots is coupled to BNPP (R^2=0.43; 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 (Figure 12). Annual soil respiration which was poorly correlated to total biomass was strongly coupled to fine root mass. Figure 13 shows that approximately five grams of carbon are released each year for every gram of fine root carbon (R^2=0.45, p<0.001).

Annual soil respiration is also linearly related to total foliage mass (with approximately five grams of carbon released each year for each four grams 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 is that positive outliers are plots with particularly high understory fractions
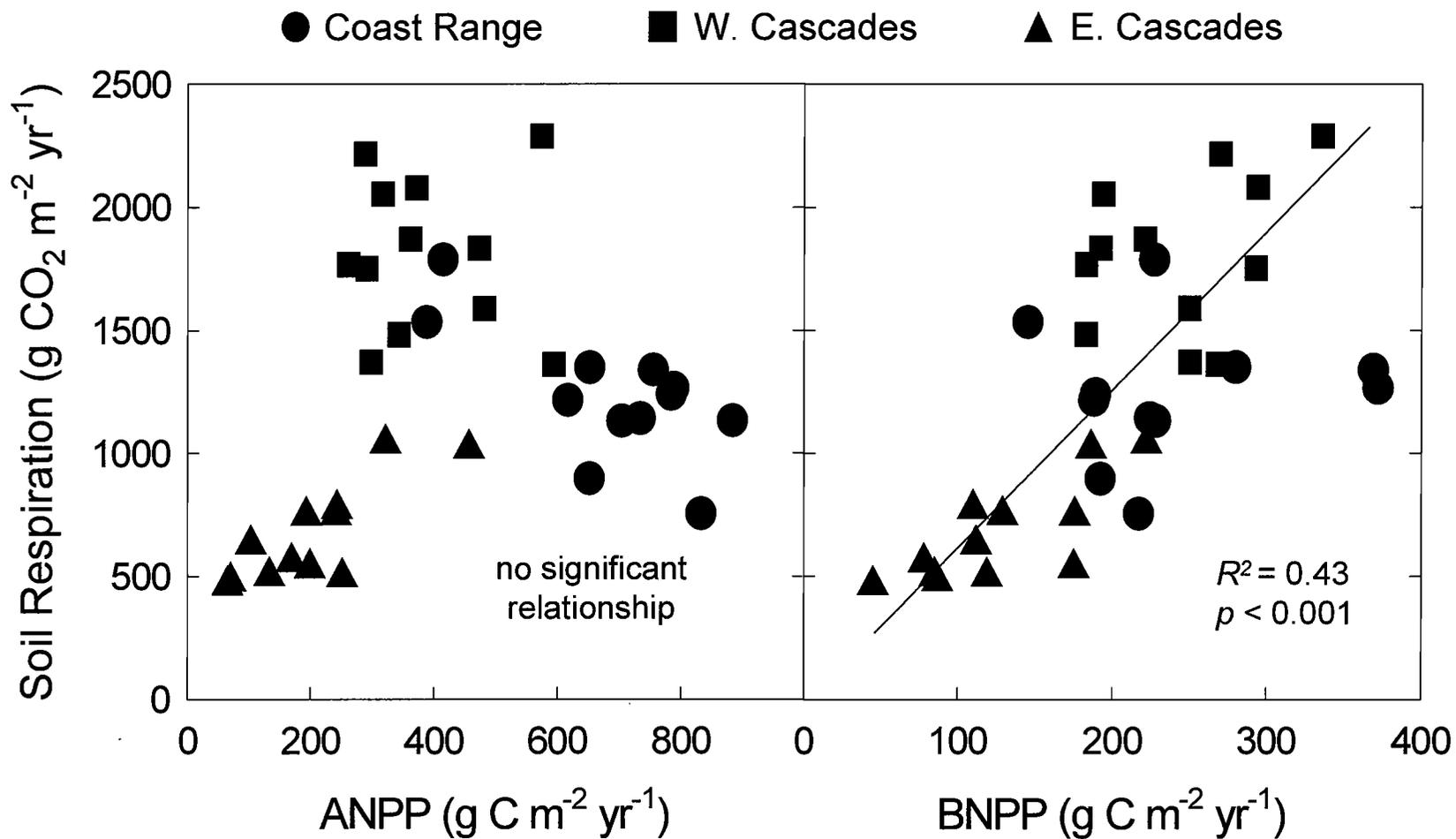
Figure 11. Cross-site relationships between annual soil respiration and aboveground net primary production (ANPP) and belowground net primary production (BNPP).
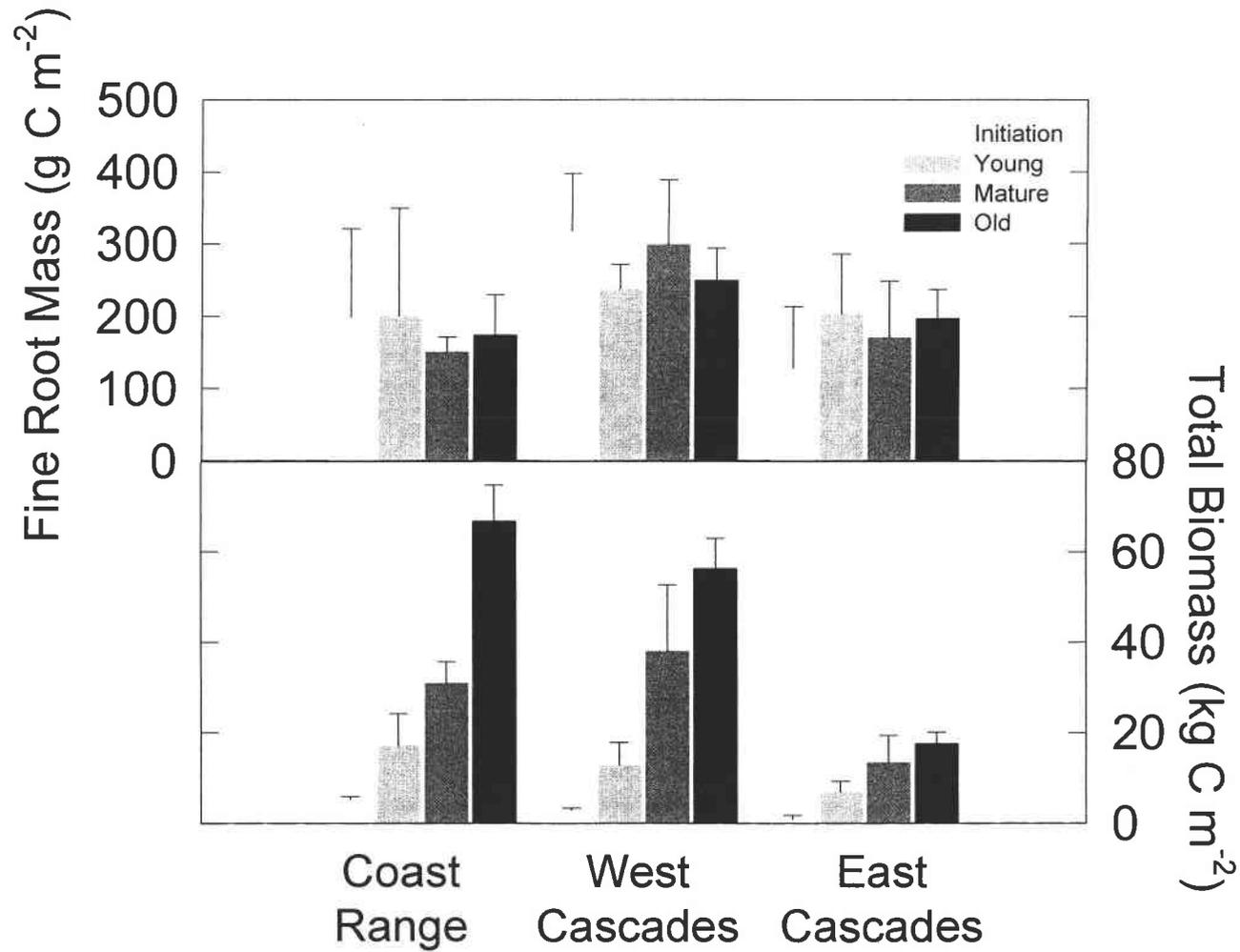
Figure 12. Successional trends in fine root and total biomass for each of three climatically-distinct forest types. Values are the average and standard deviation of three replicate study plots.
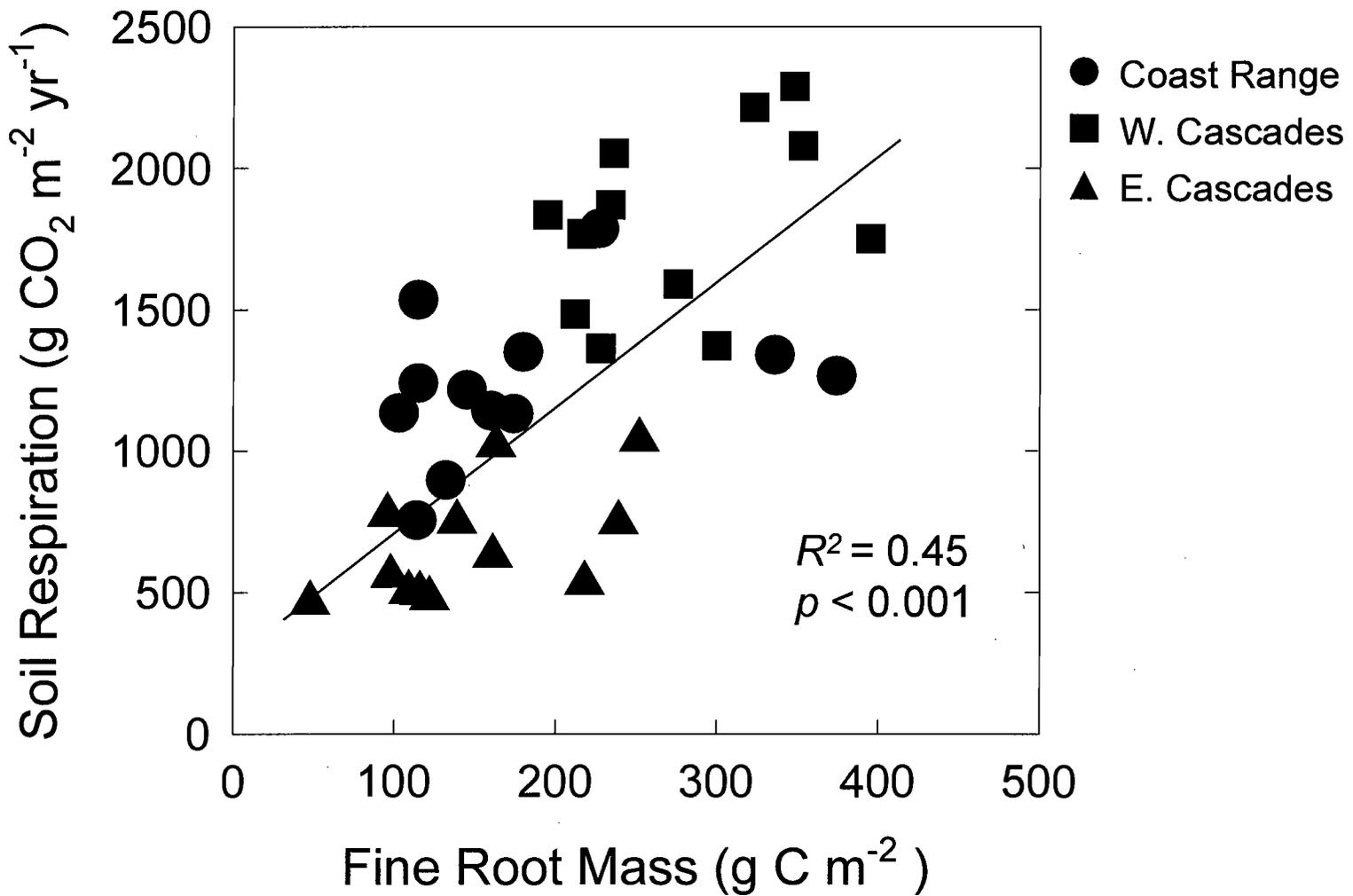
Figure 13. Cross-site relationships between annual soil respiration and fine root mass.

while negative outliers are plots with particularly low understory fractions (see Figure 14). 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 show in Table 9. Unlike live fine root and foliage mass, the size of detritus pools such as forest floor and dead root mass are poorly correlated to soil respiration across the 36 plots. Soil carbon and nitrogen properties also show little or no correlation with annual soil respiration. It is apparent that the factors most coupled to annual soil respiration within forest type are different that those related to variation between forest type. While mineral soil carbon is not correlated to annual soil respiration across forest types, this variable explains over 60% of the variation in annual soil respiration among Coast Range plots. Among plots at the East Cascades annual soil respiration is strongly coupled nearly all measures of biomass production including ANPP. Among plots at in the West Cascades, annual soil respiration is not correlated to any measure of biomass, production, or detritus.
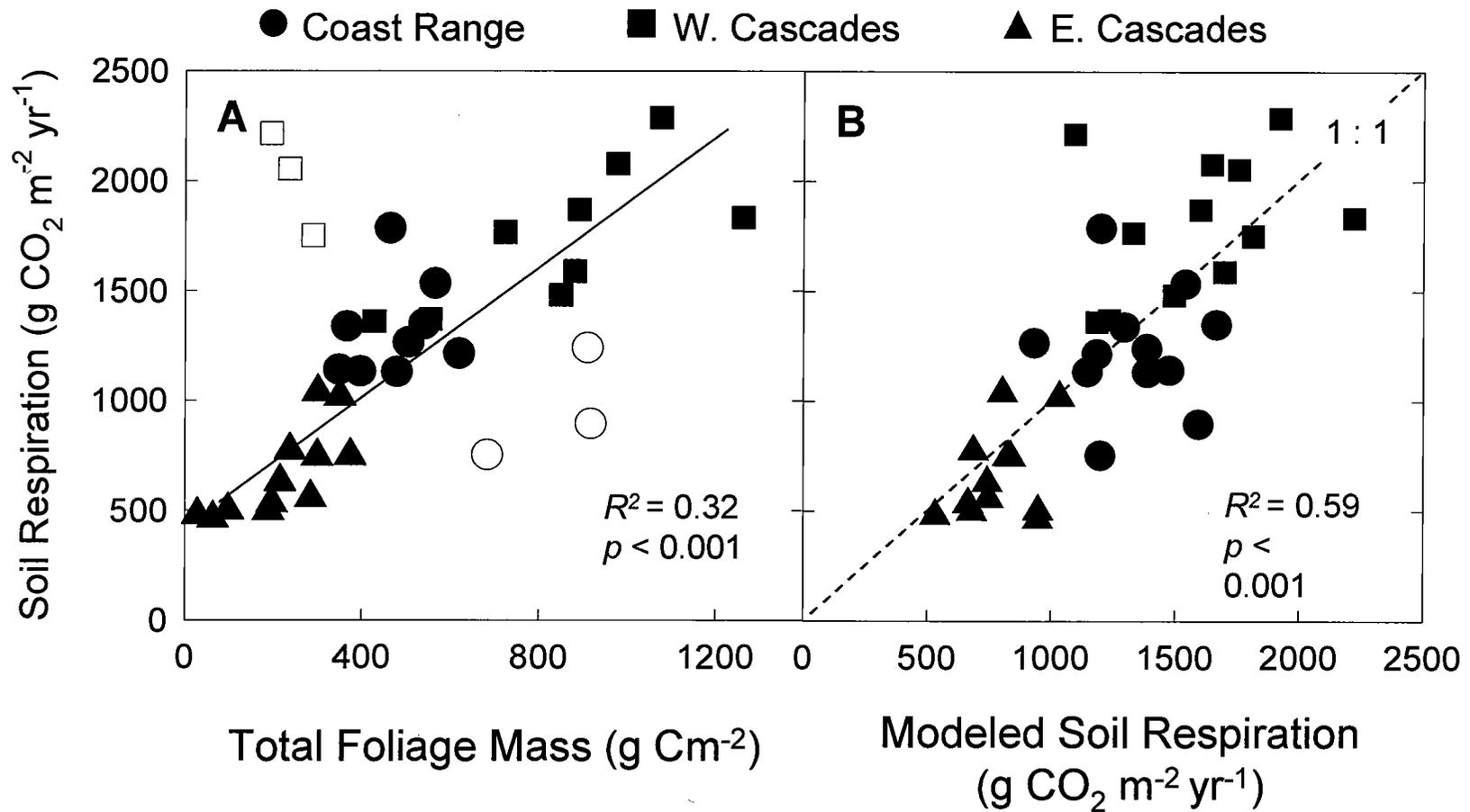
Figure 14. A) Cross-site relationship between measured soil respiration and total foliage mass; open squares represent plots with notably high fraction of understory and open circles represent plots with notably low fraction of understory. B) Soil respiration as modeled by least squares regression allowing understory foliage mass to be weighted separately from overstory foliage: Annual soil respiration = 435 + 1.0 x (overstory foliage mass) + 11.2 x (understory foliage mass).

Table 9. 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	
Biomass and Production							
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	**
Aboveground Biomass							
aboveground foliage mass	0.47		0.13	0.75	**	0.59	**
aboveground woody mass	0.63	*	0.05	0.77	**	0.44	**
Belowground Biomass							
fine root mass	0.33		0.38	0.53		0.67	**
small root mass	0.32		0.27	0.85	**	0.50	**
coarse root mass	0.59	*	0.05	0.76	**	0.44	**
total root mass	0.59	*	0.06	0.80	**	0.46	**
Soil Pools							
forest floor mass	0.28		0.01	0.53		-0.38	*
total soil C (0-20cm)	0.79	**	0.07	0.02		0.35	*
total soil C (0-100cm)	0.46		0.45	0.13		0.22	
light fraction soil C (0-20cm)	0.61		0.12	0.27		0.19	
total soil N (0-20cm)	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. ** = $p<0.001$, * = $p<0.05$.

Discussion

Considering the first principles of enzymatic metabolism, we should not be surprised to find soil respiration to be positively correlated with soil temperature (for reviews see Singh and Gupta, 1977; Reich and Schlesinger, 1992; Lloyd and Taylor, 1994), soil moisture (Orchard et al., 1992; Davidson et al., 1998; Burton et al., 1998; Irvine and Law, 2002), soil aeration (McGroddy and Silver 2000; Savage and Davidson, 2001), substrate quality (Minderman, 1967; Aber et al., 1990; Edmonds 1984, Patron et al., 1993; Berg and Tamm, 1994), substrate quantity (Myrold, 1989), and the biomass of metabolizing tissue (microbial biomass: Zak et al., 1999; root biomass: Dornbush and 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, are not the major factors driving variation in annual rates observed among forest types when the data are pooled (Irvine and Law, 2002; Campbell and Law, in review). 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 emphasize a conservation of function across varied environments. That is, despite widely different temperature and moisture regimes, all three forest types examined in this study exhibit similar soil respiration per unit fine root biomass and belowground production.

Fine root and allocation

Among the forests studied, successional trends in live fine root biomass do not follow that of total biomass or even foliage mass. Instead, fine root biomass varies 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 is reached at ages younger than those investigated in this study and much earlier than maximum foliage mass.

The greatest fractional allocation to fine roots occurs 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 review see Landsburg and Gower 1995 p.148). Our data supports this hypothesis and go on to imply that a relatively high allocation of carbon below ground maintains soil respiration at rates higher than would be predicted by total

biomass alone. Similarly, Dornbush and Raich (in review) found that soil respiration among various grassland ecosystems was governed more by belowground carbon allocation than above ground production. Allocation patterns are also important in defining fine root mass and subsequently soil respiration between the two mesic forest types west of the Cascades, however patterns can not be explained as a simple tradeoff between above and belowground allocation. Rather, forests at the West Cascades simultaneously support greater fine root and foliage mass per unit total biomass than the forests in the Coast Range.

Foliage mass

The connection between foliage mass and soil respiration is especially notable, not only because it can explain nearly 60% 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 represents 11-20% of instantaneous soil respiration rates (Law, 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 and 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., 2002) 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 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 (Figure 14). 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 and Schmidt, 2003; E. Sulzman, per. com.), it is difficult to account for the ten-fold factor implied by this study. More work needs to be done 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 mater

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, shows 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 fine roots and mineral soil

contribute nearly equal to instantaneous soil respiration rates (Law et al., 2001). However, considering that soil carbon pools are the dynamic balance between inputs and minerialization, we should expect to see strong relationships between soil carbon pools and respiration in very limited circumstances. For instance, when comparing systems with similar soil inputs and contrasting decomposition (such as oxygen limited soils: O'Connell et al., 2003; McGroddy and Silver, 2000; Savage and Davidson, 2001) or when comparing systems with disparate inputs and similar decomposition rates (such as till and no-till agriculture: Wagai, 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

There exists a variety of supporting evidence for a large belowground carbon allocation in western Oregon. Previous work by Fogel and 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 mycorrhizal hyphae has recently been demonstrated by Staddon et al. (2003). Evidence for more C allocation to belowground fine roots of

Douglas-fir stands growing on a drier and less fertile site relative to a more fertile one was shown by Keyes and Grier (1982). Their work supports observations in this paper of more belowground C allocation observed in the West Cascades 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., 2003). Among the pine forests, soil respiration is strongly coupled to almost all measures of biomass and production while soil C is the strongest predictor of soil respiration among the Coast Range plots, and soil respiration varies independently of all measured parameters among the West Cascades plots. The fact that foliage and fine root biomass is a reasonable predictor of variation in soil respiration between forest types, but not within forest types could be partly due to 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 that 100 years of development. By nesting replicated chronosequences within multiple, edaphoclimatically-distinct forest types, this study is among the most extensive and inclusive to address landscape patterns of soil respiration. As of yet, the most promising opportunity to deduce regional values of soil respiration comes from simulation models that can be run contiguously over large spatial domains (Rastetter et al., 2003; Law 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, 2003 for review of soil respiration models). However, as emphasized by the works of Högberg et al. (2001) and Bhupinderpal-Singh et al. (2003), 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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Disturbance and net ecosystem production across three climatically-distinct forest landscapes

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Abstract

Biometric techniques were used to measure NEP (Net Ecosystem

Production) across three climatically-distinct forest chronosequences in

Oregon. NEP was highly negative immediately following stand replacing

disturbance in all forests and recovered to positive values by 10, 20, and

30 years of age for the mild and mesic Coast Range, mesic West

Cascades and semi-arid East Cascades, respectively. The response of

stand-level NEP to individual disturbance events is greater than that

attributable to edaphoclimatic differences between forest type. However,

when successional trends in NEP are weighted by current age class

distributions, the variability in landscape-level NEP attributable to whole

disturbance regimes is equivalent to that attributable regional

edaphoclimatic differences between forest types. Simulations of age class

distribution under varying disturbance frequencies suggest that the

sensitivity of landscape-level NEP to changes in disturbance regime varies

among forest types and is linked to both remnant detritus and

photosynthetic recovery rate that are partly a function of long-term

edaphoclimatic differences.

Introduction

Net Ecosystem Production (NEP) can be defined as the difference

between gross primary production and ecosystem respiration. Forests

exhibiting negative NEP are acting as sources of atmospheric carbon while forests exhibiting positive NEP are acting as sinks. Current concern over atmospheric CO_2 levels and subsequent global warming has brought the issue of forest NEP to the forefront of earth science and challenged forest ecologists to quantify the impact of climate and disturbance on NEP, not only of individual forest stands but across entire forest landscapes. Climate is known to affect forest NEP by directly controlling the physiology of production and decomposition of organic matter (Woodwell and Whittaker, 1968; Jarvis, 1995). Much less is known about how disturbance affects the balance between the two fluxes.

Conventional theory regarding the successional trends in NEP following disturbance is based on assumptions about relative proportions of growing and decomposing tissue (Odum, 1969; Sprugel, 1985; Harmon et al., 1990). According to this theory (Figure 15, top), forests experience a pulse of negative NEP following catastrophic disturbances such as crown fire or clear-cutting, as these events both drastically reduce the amount of photosynthetic tissue and generate new pools of respiring detritus. As living vegetation recovers and detrital pools decay, NEP becomes more positive reaching a peak when detrital pools are near their lowest and production is near its highest. A subsequent decline in NEP occurs as inter-disturbance mortality re-stocks detrital pools, which may or may not be compounded by declines in gross primary production.
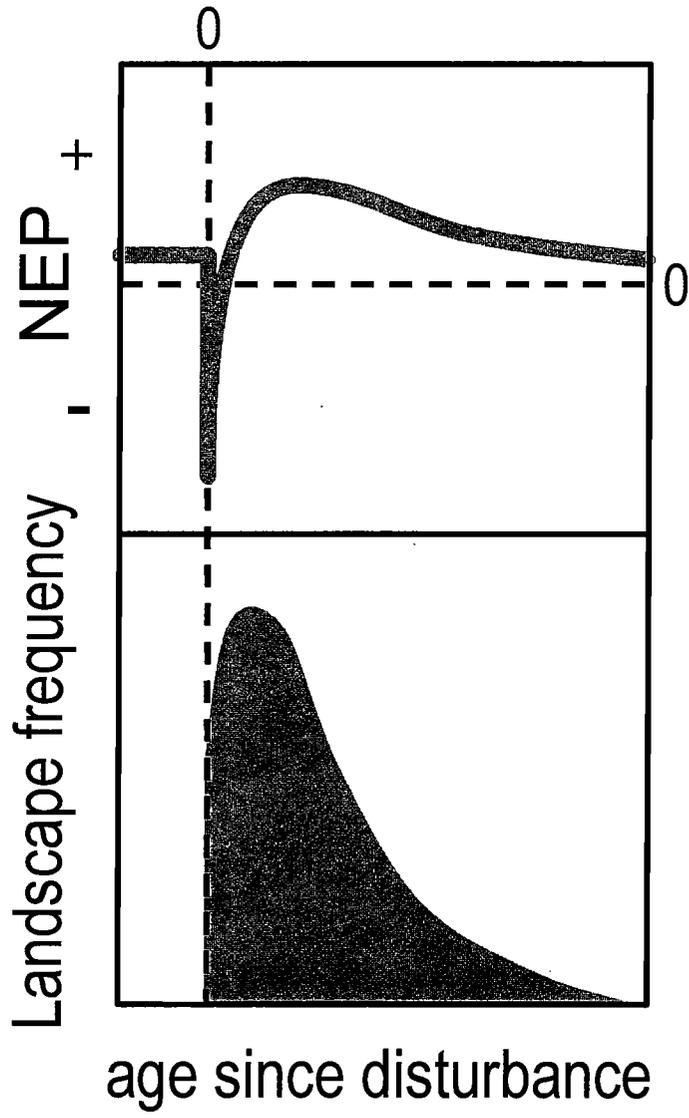
Figure 15. Theorized successional patterns in forest NEP following a stand replacing disturbance. Disturbance regimes affect landscape-level NEP by defining the relative frequency of forest age classes.

Recent studies suggest that the changes in stand-level NEP that occur as a result of disturbance, even without accounting for losses incurred during the disturbance event, may well exceed that attributable to either interannual variation in climate (Thornton et al., 2002) or among-biome variation in climate (Chapin et al., 2002). However, when considering landscapes comprised of stands in varying stages of re-growth, it is not immediately apparent how much variability in overall NEP is being caused by disturbance or how sensitive landscape NEP is to changes in the frequency of disturbance.

As implied in Figure 15, the NEP of any forested landscape is constrained both by the successional trends in NEP and the age class distribution created by the prevailing disturbance regime, and perhaps more important than the overall weighting of NEP by age class frequency is just how the amplitude and recovery rate of NEP renders a landscape more or less sensitive to alterations in age class distribution brought on by changes in disturbance regimes. After all, depending on the exact shape of the NEP curve in Figure 15, we would expect there to be age ranges where shifts in relative abundance would have little effect on landscape NEP as well as age ranges where shifts in relative abundance would profoundly alter landscape NEP.

The robust chronosequence studies necessary to quantify the influence of age class distribution on regional NEP are only now appearing

in the literature. Wirth et al. (1999), Bond-Lamberty et al. (2003), Howard et al. (2003), and Litvak et al. (2003) have all quantified age-related trends in NEP for boreal forests, while Smith and Resh (1999), Janisch and Harmon (2002) and Law et al. (2003) have reported age related trends in temperate systems. Together these studies help refine theories regarding successional trends in forest carbon exchange and provide valuable information regarding the response of stand-level NEP to disturbance. In this study (the first we know of its kind) we present values for NEP measured across multiple, replicated, edaphoclimatically-distinct, forest chronosequences and assess for each the capacity of disturbance to influence landscape-level NEP through current and alternative age class distributions. Specifically, our goals were to:

1. Quantify the successional trends in NEP that following stand replacing disturbance in each of three edaphoclimatically-distinct conifer forests types in Oregon.

2. Determine which component carbon fluxes were most responsible for the magnitude of NEP and which were most responsible for the trends in NEP.

3. Compare the relative importance of disturbance and edaphoclimatic controls on regulating NEP at both individual stands and across entire landscapes.

4. Assess the sensitivity of landscape level NEP to alterations in disturbance regimes and link this sensitivity to the production biology of each forest type.

Methods

Study design

To assess successional trends in NEP across western Oregon, we selected 36 independent forest plots arranged as three replicates of four age classes in each of three climatically-distinct forest types. Each study plot encompassed 1 ha of structurally homogenous forest determined to be representative of its age and compositional type. The three forest types are located along a wide precipitation and elevation gradient and are best described as hemlock-Sitka spruce in the fog belt of Coast Range near Cascade Head Experimental Forest, Douglas fir in the West Cascade Mountains near HJ Andrews Experimental Forest, and ponderosa pine in the Metolius basin on the dry east side of the Cascade Mountains. The location of the study sites are shown in Figure 16 and the climatic, edaphic, and compositional characteristics of each site are given in Table 10. Forest ages range from 10 to 800 years and are subjectively classified as either initiation, young, mature or old. Structural qualities of these age classes are described in Table 11.
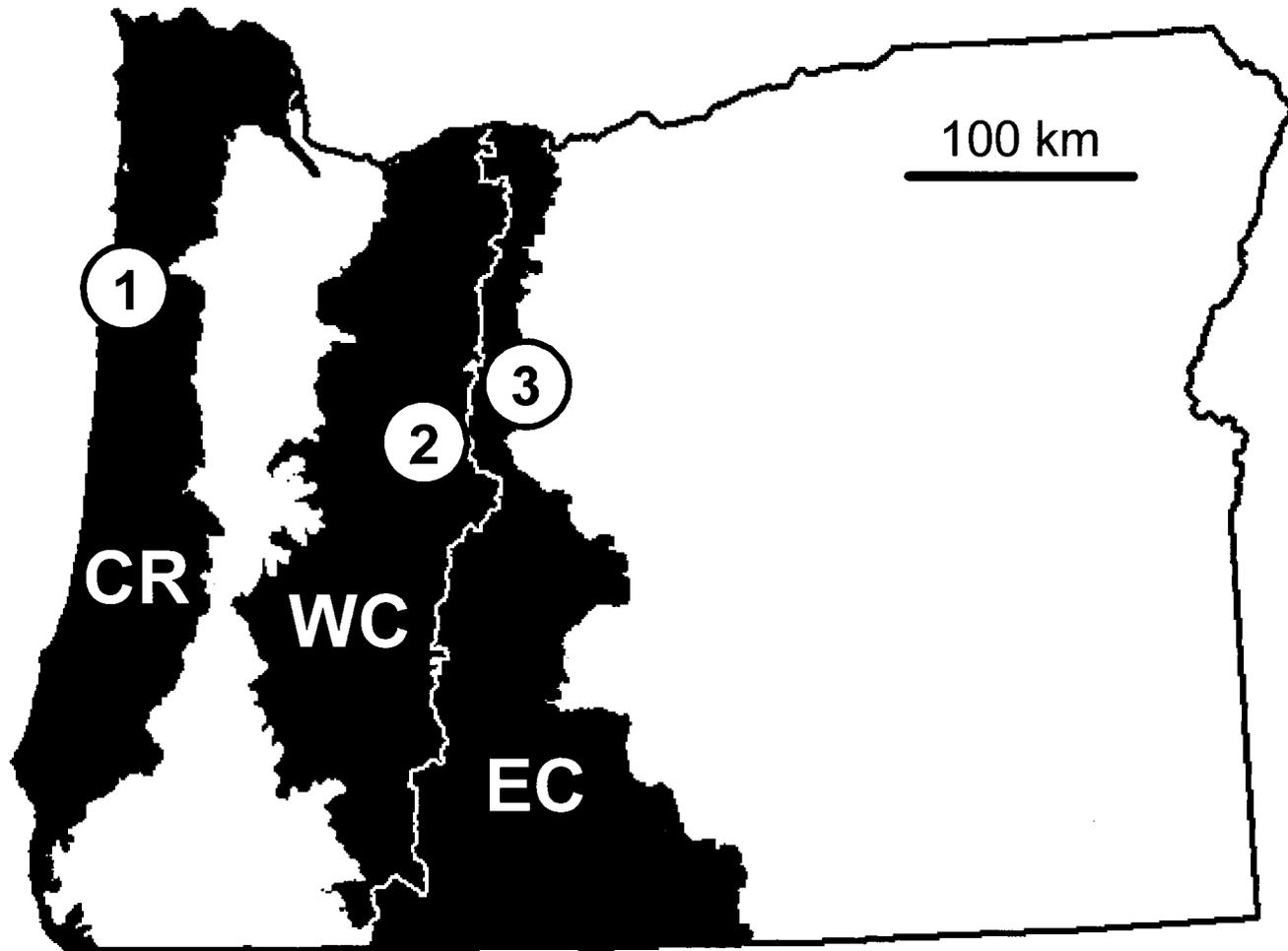
Figure 16. Geographic location of the study sites and the extent of the forest types they represent in western Oregon. Study sites are shown as 1-3. CR=Coast Range, WC=West Cascades, and EC= East Cascades.

Table 10. 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, green leaf 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
Map coordinates	45.1°N 123.9°W	44.2°N 122.2°W	44.4°N 121.7°W
Elevation (m)	120-300	710-860	890-1230
Precipitation (long-term average mm yr^{-1})	2800	2100	500
Mean Summer air temp (long-term average C°)	14.5	14.1	14.5
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 clay loams	Ash over colluvium forming well drained sandy to gravelly loams

Table 11. Structural qualities of each age-class averaged across three replicate stands.

	age	stem diam. (cm)	stem density (m^{-2})	canopy height (m)	ontogeny
Coast Range					
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 reestablishing
old	170-190	51	340	51	multi-story canopy, gap formation, well developed understory
West Cascades					
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	multi-story canopy, gap formation, well developed understory
East Cascades					
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 multi-story canopy, understory often burned.

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

Estimating NEP

The mass balance approach for estimating NEP from field measurements begins in this study by separating the flow of gross photosynthate into three carbon allocation paths represented by equations 1 through 3.

$$NEP_{foliage} = NPP_{foliage} - Litterfall \qquad (1)$$

Where $NPP_{foliage}$ is the Net Primary Production of tree, shrub, and herb foliage and litterfall is assumed to approximate the heterotrophic decomposition of dead leaves.

$$NEP_{wood} = NPP_{wood} - RH_{woody\ debris} \qquad (2)$$

Where NPP_{wood} is the net primary production of the bole branches and bark of trees and shrubs, and $RH_{woody\ debris}$ is the heterotrophic respiration from fine and coarse woody debris.

$$NEP_{root} = \Delta coarse\ root + \Delta fine\ root - \Delta soil\ C \qquad (3)$$

Where $\Delta coarse\ root$, $\Delta fine\ root$, and $\Delta soil\ C$ are the changes in each of these carbon pools over time, respectively. Total plot-level NEP is then calculated as:

$$NEP_{total} = NEP_{foliage} + NEP_{wood} + NEP_{root} \hspace{2cm} (4)$$

Vegetation surveys

All forest vegetation was divided into three classes: Trees (woody plants having a stem diameter >5cm at a height of 1.24m), understory (woody shrubs and saplings having a stem diameter <5cm at a height of 1.24m) and herbs (grasses, forbs, and bryophytes). Vegetation surveys were conducted inside four subplots regularly stratified throughout each of the 1 ha study plots. Subplot sizes ranged from 75-700 m^2 for trees, 5-75 m^2 for understory, and $2m^2$ for herbs, depending on the density and homogeneity of the vegetation. The frequency and dimensions of trees and understory in each subplot were converted to tissue mass or volume per unit area using species and site-specific allometric equations obtained from the BIOPAC data base (Means, 1994; VanTuyl, 2003). Herb mass per unit area was determined thorough the harvest, drying and weighing all aboveground tissue. All foliage and woody tissue mass were converted to carbon mass by multiplying by 0.50 and 0.45 respectively.

Wood production

Tree wood production was determined for each plot by subtracting estimates of current wood mass from that estimated five years prior. For

each tree in a subplot, the frequency, species, and DBH (stem diameter at 1.34m) were recorded. For every fifth tree encountered total height was recorded and two increment cores were taken to determine the average radial growth during the past five years. Plot-specific regressions relating height and radial increment to DBH allowed us to estimate the probable height and growth of trees from which no cores were taken. DBH and height were combined with site and species-specific allometric equations to determine the past and present volume of stemwood, branches, and bark for each tree. Wood volume was converted to mass using site and species-specific wood densities determined from the increment core samples. Understory wood production was not directly measured, rather we assumed it to approximate 0.06 of the estimated understory wood mass.

Foliage production

Overstory foliage production was calculated as the product of total overstory leaf mass and the canopy-average leaf retention time. Total overstory leaf mass was calculated as the product of LAI (Leaf Area Index: expressed as hemispherical leaf area per unit ground area) and canopy-wide estimate of leaf mass per unit area). LAI for each plot was determined optically using a LAI2000 plant canopy analyzer (LICOR, Lincoln, NE) as the average of 30 sample points per plot. Corrections for

crown clumping were obtained using a TRAC crown gap analyzer (3rd

Wave Engineering, Canada), while corrections for shoot clumping and

wood interception were made as in Law et al. (2001a). Canopy-wide leaf

retention time and SLM were determined by weighting plot and species-

specific values by the frequency of overstory species in each plot, which

were determined form 7-20 representative shoot samples collected in

each plot. Understory foliage production was calculated as the understory

foliage mass divided by leaf retention time which varied from 1 year for

deciduous species to 6 years for certain evergreen shrubs. Herbaceous

production was assumed to be all foliage and equal to the above ground

biomass.

Respiration from woody debris

The volume, species, and decay class (one of five) of woody debris

in each study plot was estimated using line intercept transects (four 100m

transects for woody debris >10cm diameter and four 25m transects for

woody debris <10 and >2cm diameter). For each piece of debris

encountered in the surveys, diameter was converted to volume per unit

area (using probabilistic geometry) then to mass per unit area (using a

species-specific density) then to mass loss per unit time (using site,

species, or diameter-specific decay constants) and finally to carbon loss

per unit time (assuming 0.50g C/g debris). Scaling constants were

provided by M. Harmon (personal communication) and the details

regarding the scaling of woody debris transects are given in Harmon and

Sexton (1996).

Δ Coarse root

The annual change in coarse root (roots >2cm diameter) was

calculated as the difference between live coarse root growth minus the

decomposition of dead roots attached to stumps and snags. Live coarse

root growth was estimated from tree radial increment, a single region-wide

allometric equation relating coarse root volume to tree diameter and

species specific wood density values (Santantonio, 1985 and VanTuyl,

2003, respectively). The decomposition of dead coarse roots was

computed as volume of coarse roots attached to stumps and snags

(determined, using the same allometric equations used for live trees)

multiplied by decay class-specific densities and site and species-specific

decomposition constants (Janisch and Harmon, 2002).

Δ fine root and soil carbon

Measurement inaccuracies make it very difficult to directly assess a

single year's change in either fine root mass or mineral soil carbon.

Consequently we used the relative size of these carbon pools across the

chronosequence to estimate how much these pools may change over the

course of a single year. Using this approach, nether the change in fine

root mass or mineral soil carbon was discernibly different from zero.

Especially notable was fine root mass that was no higher in mature forests

than in the youngest age classes. Recognizing that this conclusion is

subject to type II statistical error (Davidson et al., 2000) we assigned an

uncertainty to these zero values based on the site-wide range of pool size

(see Table 12).

Ecosystem heterotrophic respiration

Because we are more confident in our ability to estimate the

components of NEP contained in equations 1 though 4 than our ability to

estimate belowground heterotrophic respiration we made estimates of

HR_{total} (total ecosystem heterotrophic respiration) by subtraction according

to equation 5.

$$HR_{total} = NPP_{total} - NEP_{total} \qquad (5)$$

Where NPP_{total} is the sum of NPP of foliage wood and roots. HR_{total} was

then further partitioned into fluxes from mineral soil, forest floor, and

woody debris based on the relative magnitude of these fluxes estimated

independently on each plot. Heterotrophic respiration from the mineral soil

and forest floor were approximated by multiplying estimates of annual soil

Table 12. Measurement errors associated with each component of NEP.

Component of NEP	Source of largest measurement error	Average standard error ($gCm^{-2}y^{-1}$)	Average coefficient of variation (%)	Average resulting error in NEP (%)
Tree wood production	Prediction of radial growth based on stem diameter for the portion of trees from which no increment cores were taken.	58	20	20
Tree foliage production	Spatial sampling error associated with optical estimates of leaf area within each plot	36	26	16
Understory wood production	Predicting mass from stem diameter using non site-specific allometry	20	317	7
Understory foliage production	Uncertainty in estimates of leaf retention	8	35	2
Woody debris decomposition	Spatial sampling error in field estimates of debris volume	17	25	5
Litterfall	Spatial sampling error in field estimates of litterfall mass	45	33	18
Δ Coarse roots	Prediction of radial growth based on stem diameter for the portion of trees from which no increment cores were taken.	33	57	13
Δ Fine roots	Standard error of a linear the slope (not different from zero) fit to the change in fine root mass across the chronosequence	<1	NA	<1
Δ Soil carbon	Standard error of a linear the slope (not different from zero) fit to the change in soil carbon across the chronosequence	<1	NA	<1

Average SE and CV computed across all 36 plots. In the case of Δ fine root and Δ soil C, mean values were zero therefore a CV is not computable.

respiration on each study plot (Campbell and Law, in review.) by forest type-specific fractions representing the portion of soil respiration attributable to live roots, mineral soil, and forest floor based on *insitu* root separation measurements (Law, unpublished data, methods in Law et al. 2001b).

Back-calculated C losses

An equation describing annual NEP as a function of age must include a zero point representing carbon lost to the atmosphere during the initiation disturbance if it is to be applied to a population of stands, some of which may experience such disturbances in the NEP measurement interval. Accordingly, estimates of carbon combusted during harvest and site preparation were back-calculated for the youngest stands in each forest type. Without specific knowledge of what percentage of post-harvest debris was combusted in site preparation and believing that among-site variation in debris combustion is more a function of detritus volume than the fraction combusted, we assumed that 80% of harvest debris was combusted in each plot (M. Harmon, per. com.) Consequently NEP at age zero (NEP_0) was computed as 0.80 of the pre-harvest carbon stocks in foliage, tree branch, and understory wood, which in turn was estimated from stump inventories and site specific allometric relationships between basal area and biomass pools.

Another NEP, reflecting the heterotrophic losses occurring immediately following disturbance but prior to the re-establishment of vegetation (NEP_1) was also back-calculated for each of the youngest stands. Maximum NEP_1 at this stage was estimated as the sum of woody debris decomposition (set equal to that of the initiation stand) and soil heterotrophic respiration (set equal to the average of total soil respiration among old stands on the site). Minimum NEP_1 was estimated as the sum of respiration from woody debris decomposition (recalculated from the initiation stand as if all volume was of the freshest decay class) and soil heterotrophic respiration (equal to the total soil respiration measured on the initiation stand multiplied by the site-wide fraction attributable to heterotrophic sources). The methods and values for soil respiration and separation of heterotrophic fraction are given in (Campbell and Law, in review and Law et al., 2001b, respectively). NEP_0 was located on the chronosequence at year zero while NEP_1 was located on the chronosequence at the end of the first year following disturbance.

By not including the export and fate of carbon as forest products, we limit our definition of NEP to the on-site exchange of carbon between the forest and atmosphere apart from a regional mass balance.

Uncertainty propagation

We recognize that there is a great deal of uncertainty associated with each of the above mentioned field measurements. In reporting field estimates of NEP, we believe it is more important to define the range of possible NEP values than to report a single "best estimate". When quantifying the behavior exhibited by a certain condition class (forest type and age in this study), the most useful measure of uncertainty is the variance among condition replicates. We refer to this as experimental uncertainty and calculate it for all measured parameters, including NEP, as the standard deviation among each of the three plot replicates. It is important to realize that computing this experimental uncertainty is possible only when there is true plot replication (Hurlbert, 1984).

When quantifying the structure of an individual study plot, the most useful measure of uncertainty is that stemming from measurement inaccuracy. We refer to this as measurement uncertainty. The measurement uncertainty associated with each component of the NEP equation was propagated through to NEP, using a Monte Carlo stochastic uncertainty estimation (M. Harmon, http://carbon-model.forestry.oregonstate.edu). In this approach, values for each component of NEP are randomly selected from a probability distribution defined by the mean and uncertainty of that component as well as the estimated covariance among components. We simulated NEP in this manner 1000 times for each plot and reported

measurement uncertainty as the range in which 90% of the outcomes occurred. The sources of error assigned to each component of NEP are shown in Table 11. While these are not the sole sources of error for each parameter, our experience suggests that they dominate the uncertainty of each parameter estimate.

Regional age class distribution

To assess the importance of age class distribution in weighting landscape level NEP, equations of the following form were fit to each chronosequence:

$$y = y_o + a \cdot \exp(-0.5(\ln(x/x_o)/b)^2) \qquad (6)$$

where y = NEP and x= age since stand replacing disturbance. This three parameter log normal function was the simplest equation that captured the biologically relevant trends in NEP and produced an R^2 of greater than 0.94 for each chronosequence. Current age class distributions for each of the forest types are shown in Figure 17 and were determined from a combination of Forest Inventory Analysis (FIA) and Current Vegetation Survey (CVS) field surveys (comprehensive USDA forest inventories of Forest Service and privately owned lands, respectively). For each of the 4500 survey locations, forest age was calculated as the 90th percentile of the distribution of tree ages (Spies and Franklin, 1991).
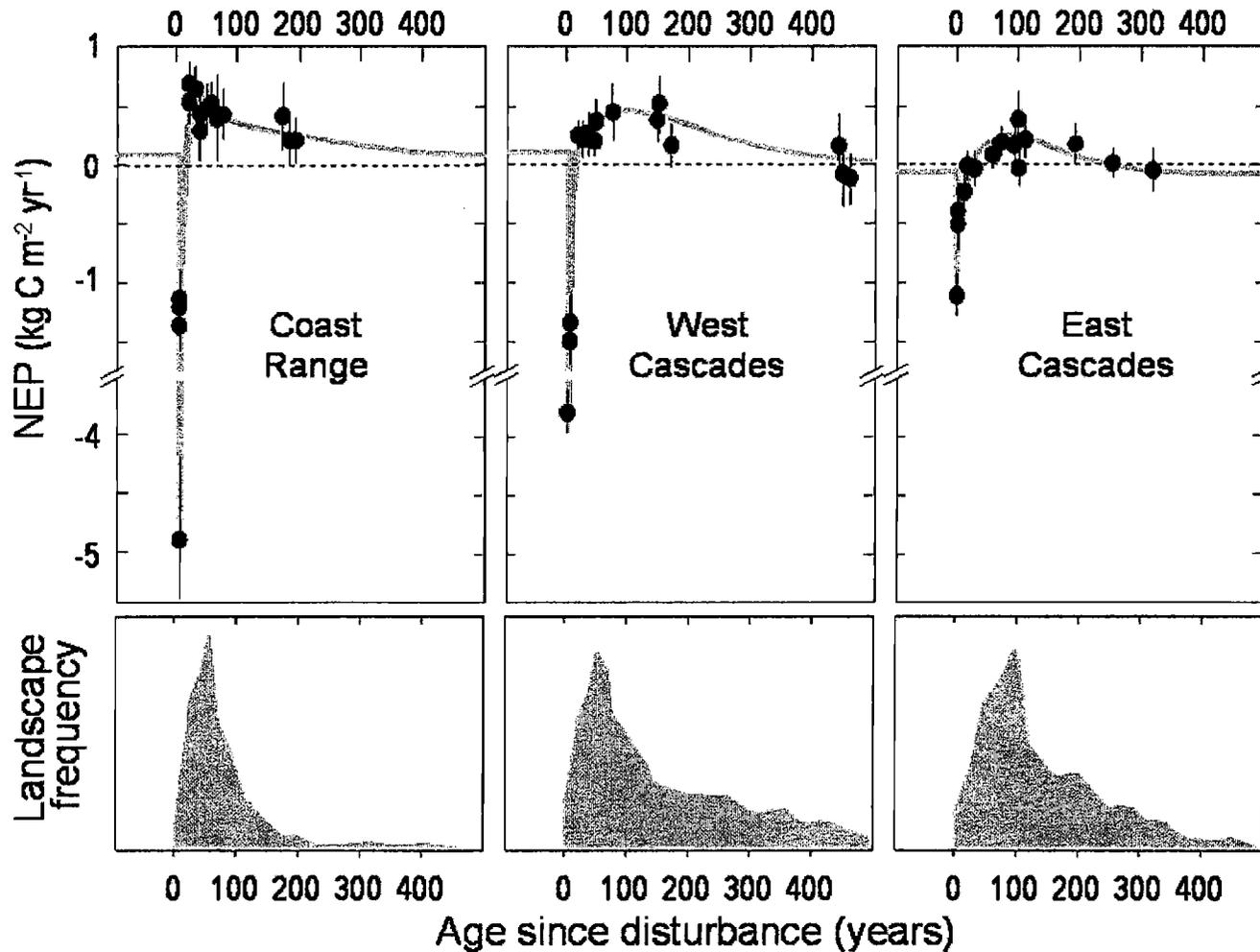
Figure 17. Successional trends in NEP measured in three climatically-distinct forest types in Oregon and the current distribution of forest ages in forest type. Error bars represent measurement error expressed as 90 percent confidence intervals.

The landscape-level variability in NEP resulting from a given age class distribution was determined by counting the NEP predicted for each one-year age class as many times as that age class would probabilistically occur in a 1000-cell landscape and then computing the standard deviation among all counts. The same approach was used to determine the variability in NEP experienced in the life of a single stand following a disturbance event, except in this case, all age classes were counted evenly since a single stand spends an even amount of time at each age.

Results and Discussion

Successional trends in NEP

As shown in the top panels of Figure 17, successional patterns in NEP are remarkably similar to that theorized by Odem (1969). That is, disturbance initiates a large spike of negative NEP (driven in this case by the combustion of harvest residue) followed by a recovery to positive, then maximum NEP with some decline there after.

In the Coast Range, positive NEP is reached in less than 10 years following disturbance. In the West Cascades, positive NEP is achieved as early as 20 years following disturbance. The ponderosa pine forests growing in the East Cascades first attain positive NEP about 30 years following disturbance, which is similar to values reported for jack pine

forests in Saskatchewan (Howard et al., 2003) and lodgepole pine forests in Colorado (Smith and Resh, 1999).

Generally speaking, maximum NEP corresponds to the time when stands first reach the maximum leaf area for the site. That is, about 10, 60, and 90 years following disturbance for the Coast Range, West Cascades, and East Cascades respectively (Sun et al., in press).

Component fluxes of NEP

To understand which factors are most important in driving successional trends in NEP it is necessary to consider the component fluxes separately. NEP immediately following disturbance is driven almost entirely by the mass of combusted or decomposing detritus, which in turn reflects the biomass of the site prior to harvest. The subsequent trajectory in NEP includes also the contribution of plant production. In Figure 18, the NEP for each age class is broken first into total net primary production and heterotrophic respiration and further into carbon accumulation by wood, foliage, coarse roots, and fine roots as well as carbon release by woody debris, forest floor, and mineral soil.

The decline in NEP with age at the Coast Range is the result of a decline in NPP balanced against substantial yet relatively stable heterotrophic respiration. The production of foliage and fine roots remain surprisingly consistent across all age classes in the Coast Range such
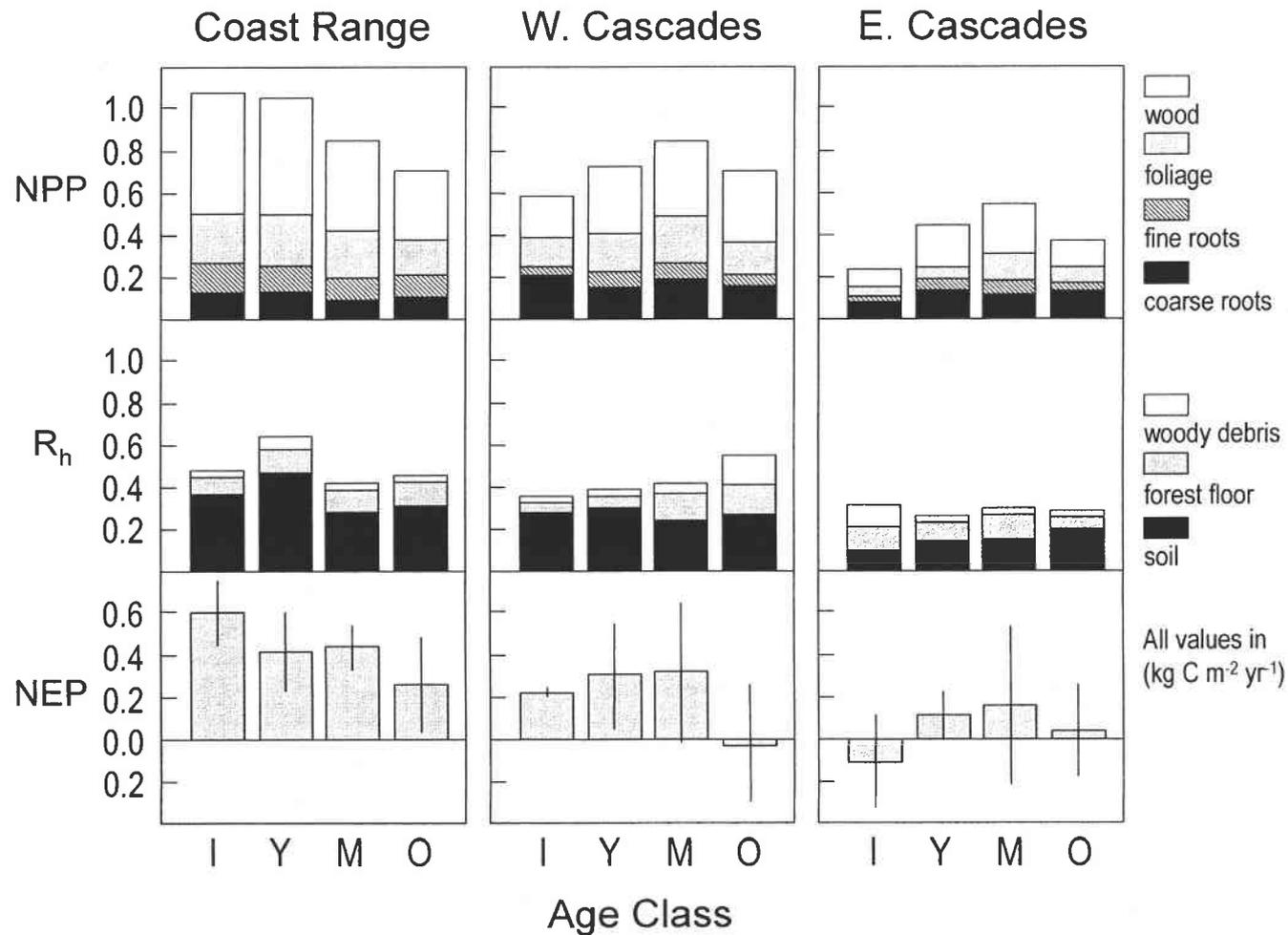
Figure 18. Component fluxes of NEP by age class and forest type. NPP=net primary production, R_h=heterotrophic respiration. Values represent the average of three replicate stands in each age class (I=initiation, Y=young, M= Mature, and O=Old). Error bars are the SD among the three replicate stands.

that the age related decline in total production among these forests can be attributed almost entirely to declines in wood and coarse root production. Substantial rates of heterotrophic respiration in all age classes offset nearly half of the net production but do not appear to contribute as much as NPP to successional trends in NEP. Because the Coast Range forests recover more quickly from stand replacing disturbance and we did not have stands less than 10 years of age, we missed the pattern of increasing NPP and NEP soon after disturbance, which is seen at the other sites.

Age related trends in wood and coarse root production are largely responsible for successional trends in NEP in the West Cascades too. In these forests, however, maximum production is not reached until the mature age classes (~100-200 years following disturbance). Furthermore an increase in respiration from woody debris and the forest floor in the oldest age class compounds the effects of late successional decline in production and plays an key role in lower NEP in these old forests.

The most pronounced successional trends in NPP occur at the East Cascade site where wood, coarse root, and foliage all contribute to a doubling of NPP between the initiation and mature age classes. At this site, a decline in woody debris respiration over time is somewhat compensated by an increase in soil and forest floor respiration leaving total heterotrophic respiration remarkably consistent across the entire

chronosequence such that the trend in NPP is the primary driver of the trend in NEP.

Excluding detritus combusted as a result of disturbance itself, above and below ground wood production and the heterotrophic respiration of mineral soil are the fluxes that contribute most to magnitude of NEP in all three forests. However, due to the lack of consistent trends in heterotrophic respiration over the chronosequences it appears that successional trends in NEP across all sites are driven chiefly by the net production of wood. Generally speaking, the age class at which NEP first declines corresponds to the age class at which wood production first declines. The decline in stand-level wood production following crown closure is a nearly universal phenomena (Ryan et al., 2004). This pattern was original attributed to age- and or size-related increases in autotrophic respiration (Odum, 1956; Yoda, 1965). Subsequent studies on individual trees, however, suggest decreases in gross primary production as the cause, brought on by either height-related hydraulic constraints (Yoder et al., 1994, Magnani et al. 2000) or by nutrient immobilization (Gower et al., 1996). We may never identify a single physiological explanation for age-related declined in wood NPP that can be applied across sites (Weiner et al. 2001) but even empirical relationships between tree height, canopy position, and resource-use efficiency can be useful in describing the changes in stand-level production that occur over stand development

(Binkley, 2004). The NEP of old forests in this study is influenced by a

decrease in wood production relative to younger forests in all three sites.

Unfortunately, the decline in wood production observed after age 40 in the

Coast Range, after age 200 in the West Cascades, and after age 100 in

the East Cascades does not consistently correspond to either changes in

canopy height or the dominance structure of the stand (see Table 11).

Consequently, we can not rule out any of the above mentioned hypothesis

regarding the declining wood production. Declining NPP with stand age

should not be ignored when considering age related change in annual

rates of NEP.

Disturbance events and stand level NEP

Assessing the relative importance of disturbance and

edaphoclimatic variability on stand-level NEP can be done by comparing

the successional variability in NEP within a forest type to the variability in

NEP among forest types of the same age. This exercise is somewhat

complicated by the fact that successional variability in NEP is dependent

on the number of years over which NEP is amortized. However, as shown

in Figure 19, the variability in stand-level NEP attributable to forest

succession is typically one to ten times higher than the variability among

forest types of the same age, regardless of the period over which NEP is

amortized. The one exception to this is the East Cascades where low

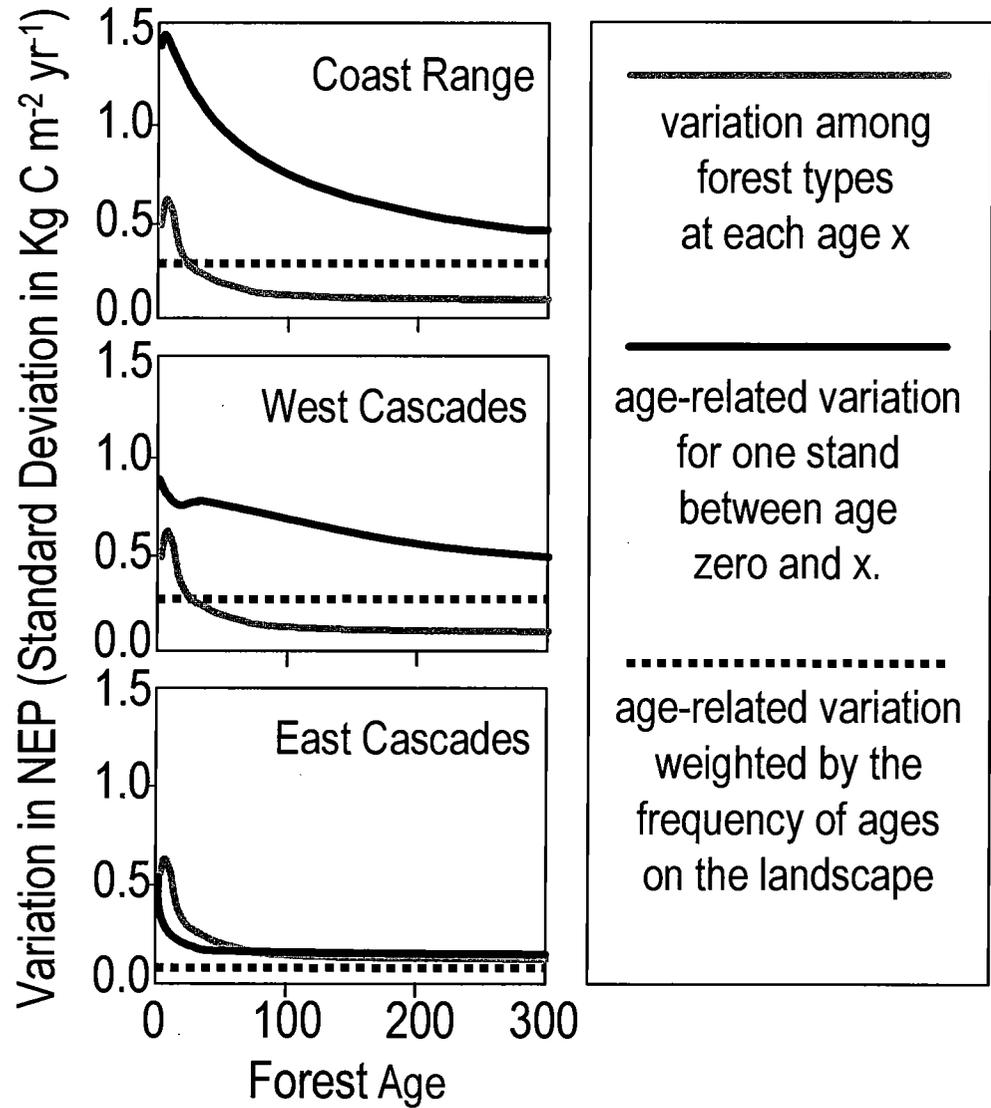**Figure 19.** A comparison of the variation in NEP attributable to: 1) the edaphoclimatic differences among forest types (variation among forest types at each age x), 2) disturbance events acting on a single stand (age related variation amortized up to age x), and 3) disturbance regimes acting on the whole landscape (age related variation weighted by the frequency of stand ages on the landscape).

total biomass minimizes the amount of carbon lost following disturbance and reduces the successional variability in NEP to levels equivalent to the variability observed among forest types. In other words, where the potential to gain and therefore loose carbon is high (e.g. the Coast Range and West Cascades) a stand-replacing disturbance has more influence on NEP than does Oregon's edaphoclimatic gradient, even when amortize over 300 years. However, where the potential to gain and therefore loose carbon is low (e.g. the East Cascades) the influence of a stand-replacing disturbance on NEP is equivalent to that of Oregon's edaphoclimatic gradient.

Disturbance regimes and landscape NEP

When comparing the relative influence of disturbance and edaphoclimatic controls on forest NEP, it is important to realize that the impact of a disturbance event acting on a single stand can be very different from the impact of a disturbance regime acting on an entire landscape (Harmon, 2001). It is clear from Figure 17 that disturbance history of western Oregon has produced an age class distribution skewed towards younger stands. However, despite this skewness, the return to positive NEP values following disturbance is so rapid (10-30 years) that only a small fraction of the landscape is likely experiencing highly negative NEP. Even as the NEP recovery time increases from the Coast Range to

the West Cascades to the East Cascades, a corresponding shift in age class distribution among these landscapes minimizes the number of stands in the recovery phase. Moreover, a relative paucity of very old stands in all three forest types is further acting to minimize the proportion of the landscape experiencing negative or near neutral NEP. As a result, the spatial variability in NEP across these landscapes is greatly moderated. Figure 19 shows that once the effect of stand age on NEP is weighted by the distribution of age classes in each landscape, its influence on NEP becomes one half to one fifth less than the effect of age on a single stand. In other words, Oregon's edaphoclimatic gradient has less influence on NEP than does a stand replacing disturbance event acting on a single forest but a comparable influence on NEP from the current disturbance regimes acting on the whole landscape.

The sensitivity of landscape NEP to disturbance

Because disturbance histories and resulting age class distributions are functioning to shape current NEP across the landscape, we are interested in how sensitive landscape-level NEP is to alterations in the current disturbance regime. It is clear from Figure 17 that because NEP is relatively consistent between the age of 50 and 150 years in all three forest types, the age class distribution could move a considerable amount toward older stands in all three study locations with a minimum effect on

landscape NEP. However, even a small change in the number of stands in the early, steep portion of the NEP curve (0-10 years) could greatly increase both the magnitude and spatial variability of landscape NEP. For example, the shortening of rotation cycles on Oregon's privately owned land may have substantial effects on landscape level NEP.

Figure 20 shows the results of a sensitivity analysis where landscape NEP was calculated by weighting age-dependent NEP by various hypothetical age class distributions simulated by allowing the current age class distribution to advance 20 years into the future recruiting new stands at frequencies ranging from 0 (no stand replacing disturbances) to 0.01 (approximately 10 times the current disturbance frequency).

For all forest types, an increase in disturbance frequency leads to a decrease in landscape NEP as a larger number of stands experience very negative NEP. The relatively flat response of East Cascades forests suggests that these forests are the least sensitive to changes in disturbance frequency in terms of the absolute amount of carbon uptake relative to the other forest types. The landscape NEP of the West Cascades is by comparison very sensitive to alterations in disturbance frequency. The response of Coast Range forests suggests an intermediate sensitivity to disturbance regime changes.

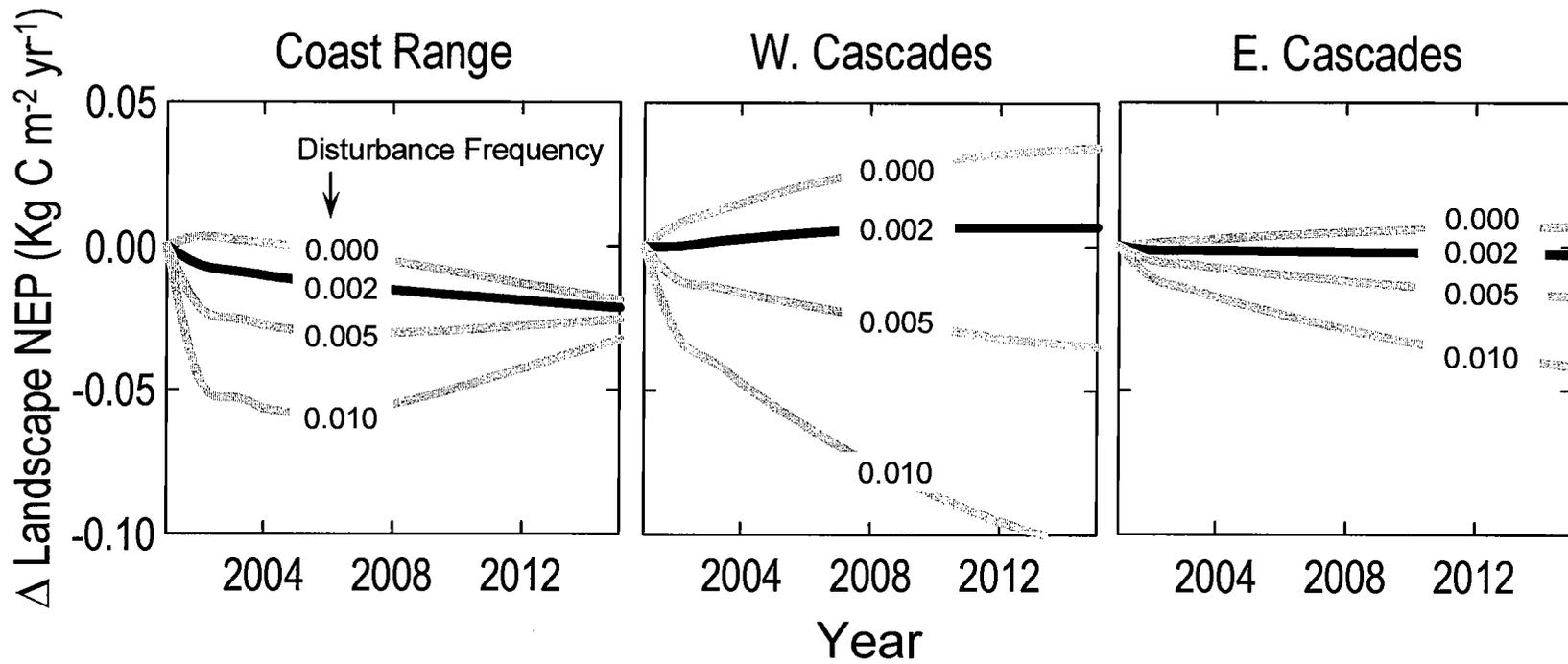**Figure 20**. The sensitivity of Landscape NEP to short-term changes in disturbance frequency. Grey lines represent either an increase or decrease in disturbance frequency. The black line approximates current disturbance frequency. The steepness of the curves represents the relative sensitivity of each forest type to shifts in the age class distributions resulting from changes in disturbance frequency.

The different sensitivity these landscapes exhibit towards various disturbance regimes can be traced directly to the successional trends in NEP reported in Figure 17. The 20 years required for NEP to level out in the West Cascades is just long enough that increases in the skewness of age class distributions can easily capture and express this condition on the landscape. The response of landscape NEP to disturbance in the West Cascades is further compounded by the magnitude of the negative NEP spike which results from the ability of these forests to accumulate large biomass pools that become respiring detritus following disturbance. The forests in the Coast Range are left with similarly large detritus pools following disturbance, however high early production rates shorten the number of age classes contributing to negative NEP. In this simulation sensitivity to short-term changes in disturbance regime is determined by the ratio of recovery rate to harvest residue and is highest in the West Cascades, lowest in the East Cascades and intermediate in the Coast Range.

Because these simulations contain no feedback between harvest intensity and any pre-harvest conditions such as biomass or nutrient status, they are not useful in predicting long-term responses to various disturbance regimes. Never-the-less, they do illustrate how differences in growth rate and biomass potential among Oregon forest types influence

the sensitivity of landscape-level NEP to decadal-scale alterations in disturbance frequencies, all else being equal.

Conclusions

From the results reported in this and other studies it is clear that forest NEP varies widely and characteristically as a function of age since disturbance. It is also clear that the distribution of forest ages is playing a key role in defining landscape-level NEP. By weighting forest type-specific successional patterns in NEP by the distribution of age classes in that that forest type, we made two notable discoveries about how disturbance regimes are shaping NEP across Oregon forests.

Firstly, by concentrating the age class distribution into a range where NEP is relatively stable over time, regional disturbance histories in Oregon are functioning to moderate the spatial variation in NEP attributable to disturbance to levels equal to or less than that attributable to Oregon's edaphoclimatic gradient, despite the fact that an individual stand experiences more variation in NEP as a result of disturbance than that observed among similar aged forests growing in different edaphoclimatic regions in Oregon. These results emphasize the difference between a disturbance event acting on a given forest stand and a disturbance regime acting on a forest landscape. Secondly, the site-specific biology of Oregon

forests renders them differently sensitive to short term changes in disturbance regimes.

In the last decade, concerns over biodiversity and wildfire in western forests has led to a shift in management objectives on federal forest land from fiber production to fuel reduction and the creation of structural habitat. Lower harvest intensity has already led to a shift in age class distribution toward older stands (Spies et al., 2003). By increasing the regional biomass these changes in disturbance regime will lead to increased carbon storage on the landscape (Harmon et al., 1990). However, considering that the median stand age in each of the three forest types already lies past the sensitive portion of the NEP-age curve the rates at which this landscape draws carbon from the atmosphere is not likely to increase substantially beyond current levels.

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General Conclusions

Study 1

In the first study annual soil respiration was measured across three climatically distinct forest chronosequences. The first objective of this study was to determine if annual soil respiration varied across Oregon forests as a function of either forest type or forest age. Our results demonstrate that both the disturbance regimes that result in a diversity of forest age and the edaphoclimatic forces that result in a diversity of forest type are acting to shape soil respiration on this landscape and that factors associated with the latter are responsible for more variation than the former.

The second objective study 1 was to consider the distribution of age classes for each of the forest types and determine how much age related variation soil respiration was actually being manifest on the landscape. Despite the regularity of forest harvest, fast regeneration rates among all three forest types considered in this study result in a region wide paucity of initiation class stands. Consequently respiration rates in these youngest stands make only a slight contribution to regional variability. Since soil respiration was similar among all but the oldest age

class in the Coast Range, a scarcity of old stands here results in nearly homogenous rates throughout the coastal forests. Conversely the relatively even distribution of age classes in the East and West Cascades maximizes the influence of age on regional soil respiration.

The final objective of study 1 was to determine if the variation in annual soil respiration associated with either forest age or type could be accounted for by the same variables commonly used to predict soil respiration at individual sites. Our results suggest that differences in annual soil respiration among forest types were not the result of differences among site-specific soil degree days or site-specific temperature response curves ($Q_{10}s$) and the direct effect of soil moisture was limited to only the driest forest type. This study points to the importance of belowground carbon allocation over soil environment in shaping landscape-level patterns of soil respiration.

Study 2

Results from study 2 indicates the importance of belowground production and fine root biomass in shaping annual rates of soil respiration across forests of western Oregon. Between-site patterns of fine root mass are dictated both by total forest biomass and belowground carbon 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 cover types than with the structural changes that occur in more that 100 years of development following stand replacing disturbance. Despite the wide range in temperature and precipitation regimes experienced by these forests, all exhibited similar soil respiration per unit fine live root biomass.

As our attention moves up in scale from forest stands to forest landscapes, the range of belowground production becomes larger and confounded with measures of the soil environment. Therefore we were not surprised to find plant production and carbon allocation emerges as the primary driver of soil respiration at the regional scale.

Study 3

From the results reported in study 3 it is clear that forest NEP varies widely and characteristically as a function of age since disturbance. It is also clear that the distribution of forest ages is playing a key role in defining landscape-level NEP.

Results indicate that a stand replacing disturbance event acting on a single forest has more influence on forest NEP than edaphoclimatic forces even when amortized over 200 years. However, once NEP is weighted by the frequency of stands existing in each age class, variation is similar to that among similar aged forest across the three study sites. In

other words, Oregon's edaphoclimatic gradient has less influence on NEP than does a stand replacing disturbance event acting on a single forest but a comparable influence on NEP than the current disturbance regimes acting on the whole landscape. These results emphasize the difference between a disturbance event acting on a given forest stand and a disturbance regime acting on a forest landscape.

Examination of component fluxes of NEP, suggest no clear trend heterotrophic respiration across age classes. As such, successional trends in NEP in these sites were driven primarily by net primary production and in particular, above and belowground wood production.

Simulations of age class distribution under varying disturbance frequencies indicate that the sensitivity of landscape-level NEP to short-term changes in disturbance regime is determined by the ratio of recovery rate to harvest residue and is highest in the West Cascades, lowest in the East Cascades and intermediate in the Coast Range.

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