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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 × 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 Reichstein et al. 2003; Burke 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 (Davidson et al. 1998; Irvine and Law 2002). 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

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

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 as hemlock-Sitka spruce in the fog belt of the Coast Range near Cascade Head Experimental Forest, Douglas-fir in the Cascade Mountains near HJ Andrews Experimental Forest, and ponderosa pine in the Metolius Basin on the dry east side of the Cascade Mountains (referred to here after as Coast Range, West Cascades, and East Cascades, respectively). The location of the study sites is shown in Figure 1 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 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 three approximately 90 s intervals. For a given day, plot-wide soil respiration was determined as the average of 12 point measurements regularly

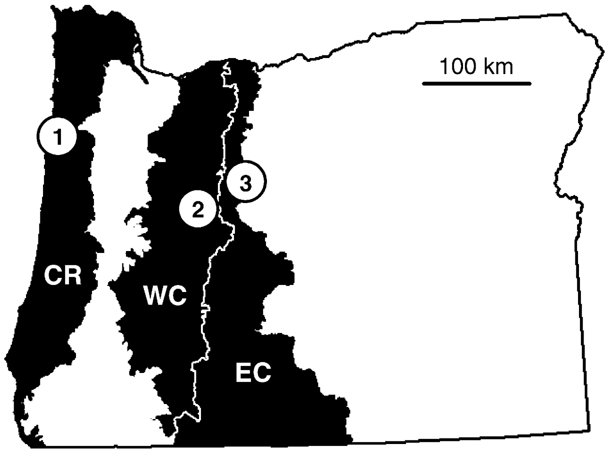

Figure 1. Geographic location of the study sites and the extent of the forest types they represent in western Oregon. Study sites are shown as 1–3. CR = Coast Range, WC = West Cascades, and EC = East Cascades.

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

stratified throughout the 1 ha plot. Measurements were taken at the same 12 points in each plot one day in May, July, September, November, 2001 and February, 2002.

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 30 cm using time domain refractometry (TDR, 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 et al. (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 Eq. (1), where R_{obs} is observed soil respiration (plot-wide averages measured periodically throughout the year), and T is the concurrently measured soil temperature (10 cm depth).

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

Soil respiration for each measurement date is then normalized to 10 °C using Eq. (2), where R_{10} is the soil respiration base rate (normalized to 10 °C), and β is the exponential coefficient fit in Eq. (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.

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

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

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

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

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 proportion 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 × age class interaction effects on annual soil respiration ($p < 0.05$) suggesting that both environmental gradients and disturbance patterns shape soil

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})	Min–max soil respiration (μmol C m^{-2} s^{-1})	Min–max base rate (μmol C m^{-2} s^{-1})	Mean temperature response (β)	Mean annual degree days ($\sum$ daily C°)
Coast Range					
Initiation	1.21 ± 0.12	1.8–4.1	2.3–4.0	0.06	3197
Young	1.09 ± 0.29	1.8–3.7	2.0–4.0	0.08	3015
Mature	1.08 ± 0.17	1.1–4.2	1.7–3.8	0.11	3156
Old	1.56 ± 0.22	1.3–6.3	2.0–5.7	0.11	3223
West Cascades					
Initiation	2.01 ± 0.24	0.8–11.7	2.2–6.3	0.11	2871
Young	1.48 ± 0.11	0.8–7.7	1.8–5.1	0.09	2850
Mature	2.07 ± 0.23	0.8–8.4	1.7–9.1	0.08	2796
Old	1.67 ± 0.26	0.8–8.4	1.8–5.8	0.09	2940
East Cascades					
Initiation	0.48 ± 0.02	0.5–3.1	0.7–2.3	0.04	3547
Young	0.59 ± 0.14	0.8–3.8	0.9–2.7	0.05	3086
Mature	0.87 ± 0.27	0.6–4.9	1.2–3.0	0.07	3181
Old	0.72 ± 0.08	0.5–4.0	1.1–2.1	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 10 cm. Annual soil respiration reported as the mean ± 1SD ($n = 3$ replicate plots). Min–max are the average rate for each site and age class combination during the period of minimum and maximum respiration, respectively.

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} in Eq. 2), and plot-specific temperature response curves (β in Eq. 1). Figure 2a illustrates the sensitivity of annual soil respiration to each of these parameters and Figure 2b 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. Variation among plots is driven primarily by differences in temperature-normalized base rates during the summer months.

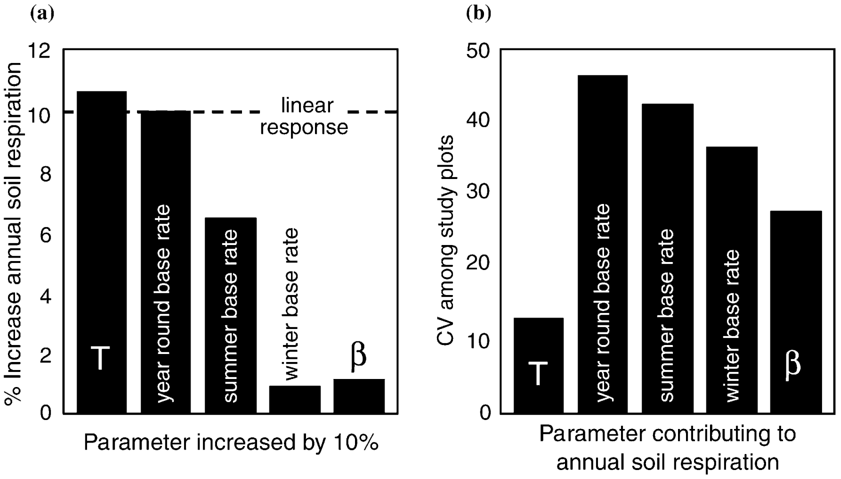

Figure 2. Sensitivity analysis (a) and regional variation (b) of the parameters used to compute annual soil respiration. T = cumulative annual soil temperature at 10 cm, base rates = seasonally variable temperature-normalized respiration rate, and β is the exponent coefficient relating respiration to temperature.

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 3, soil respiration in all plots of all age classes in both the Coast Range and the West Cascades reaches its 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, probably because of reduced 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 seasonal duration of soil activity is not the primary controlling factor of total 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 $m^3 m^{-3}$, 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

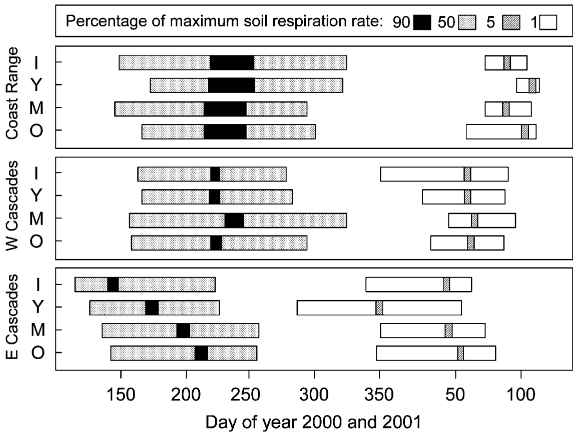

Figure 3. Seasonality of soil respiration for each of the four age classes in each of three forest types. I = initiation, Y = young, M = mature, and O = old.

the Coast Range or West Cascade forests (Figure 4). At the East Cascades site, however, soil respiration is more likely to be less than that predicted by temperature alone at times when soil moisture is below 50% of the seasonal maximum (Figure 4). A cross-forest relationship between soil moisture and soil respiration can explain 14% of the seasonal and regional variation in base respiration rates (Figure 5), although most of this relationship is made up of differences between measurements made at the East Cascades and those made at all other forests.

Scaling soil respiration by age class distribution

Figure 6 shows the observed variation in annual soil respiration across age classes for each of the three sites, and illustrates 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, coincidentally, equivalent to the influence of a disturbance event acting on an individual stand, and much less than the influence of the

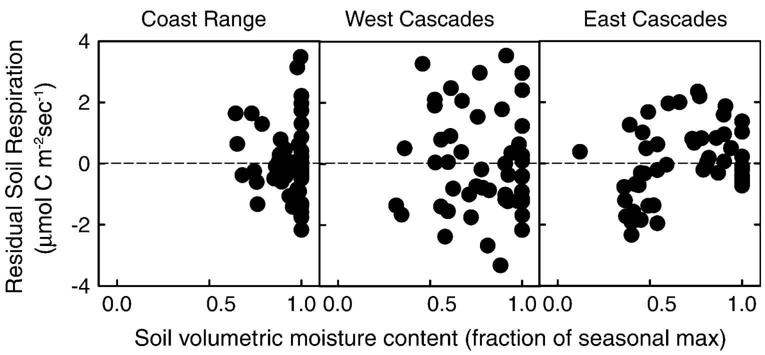

Figure 4. Temperature-normalized soil respiration plotted against the volumetric soil moisture as a fraction of the plot-specific maximum. Each point represents plot-wide averages (4 age classes × 3 replicate plots × 5 measurement periods = 60 separate points).

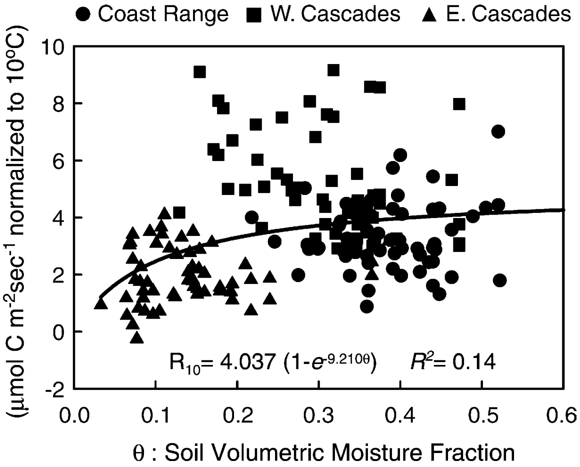

Figure 5. Cross-forest relationship between soil moisture and temperature- normalized soil respiration. Each point represents plot-wide averages (3 forest types × 4 age classes × 3 replicate plots × 5 measurement periods = 180 separate points).

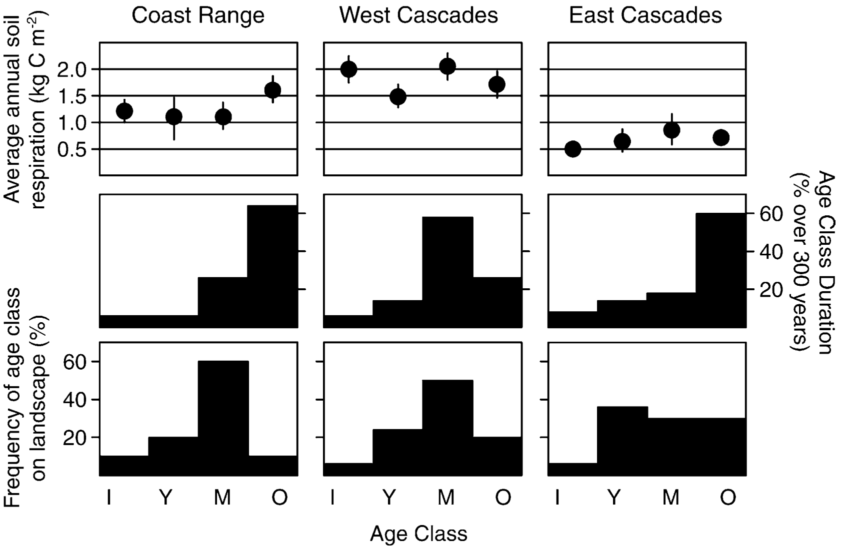

Figure 6. Age-related soil respiration for each forest type, approximate duration a stand may spend in each class, and the frequency of each age class on the landscape. Circles and error bars represent the average and SD of three replicate plots. Age classes represent roughly equivalent developmental stages between forest type. I = initiation, Y = young, M = mature, and O = old.

edaphoclimatic differences between forest types, suggesting that base rates are shaped more by edaphoclimatic differences between forest types than disturbance history.

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*

Discussion

Sources of variation in annual soil respiration

The first principles of carbon metabolism assume 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 7 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 et al. 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 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).

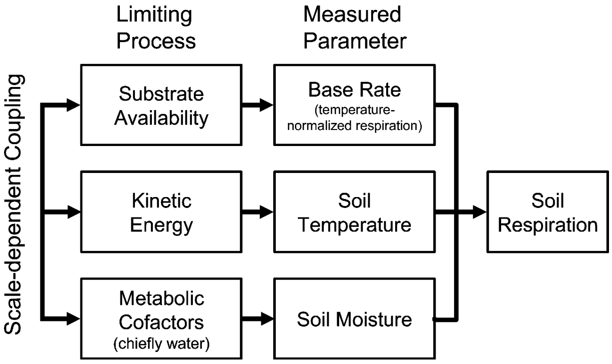

Figure 7. Scale-dependent coupling of processes affecting soil respiration. Soil respiration can be described as a function of substrate availability, temperature, and moisture. At small spatial-temporal scales, moisture and substrate availability may act as independent forces, while at larger scales, positive feedbacks between moisture and productivity may confound these drivers.

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 coupled 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 forests 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). Nevertheless, in sites where high temperatures are coincident with dry soils, measures of soil moisture improve the prediction of soil respiration beyond that predicted by temperature alone (Xu and Qi 2001; Irvine and Law 2002).

The only forests in this study where moisture appeared limiting were those of the semi-arid East Cascades. Here, soil respiration was lower than that predicted by soil temperature alone during periods of late season drought. 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 base respiration and soil moisture can be applied across all three forest types (Figure 5), 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. Overall, 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 are 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 respiration across Oregon's conifer forests is governed by substrate availability more than the direct physical constraints imposed by soil temperature or soil moisture. It is important to realize, however, that regional scale correlations, or lack there of, between soil respiration and potential drivers such as temperature and moisture do not necessarily imply an insensitivity of regional soil respiration to changes in these conditions over time. Moreover, the relatively low importance of soil temperature and moisture in shaping between-site variation in total soil respiration is not itself an indication that the metabolism of any individual carbon fractions (i.e. sugars by root cells, exudates in the rhisosphere, or detrital pools by decomposers) is not dictated by soil conditions.

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). Furthermore, work following that presented in this paper suggests that annual soil respiration among Oregon forests is correlated with fine root and foliage mass (Campbell et al. 2004). When applying 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 (where species composition changes characteristically over time), forest age and forest type become confounded. However, in forests of the Pacific Northwest pioneer species typically 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 of soil respiration is being shaped on this landscape by both environment and disturbance.

Successional trends in annual soil respiration are responsible for 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). These were followed by widespread timber harvesting in the 20th century, which 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 are 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" approach can be effectively used to assess the consequence of this pattern on the landscape. Nevertheless, 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 determinants 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 the extent to which age-related variation in soil respiration was influencing the overall patterns across the landscape. A paucity of initiation-aged stands across the region, and a paucity of old stands in the Coast Range, reduces 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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