

Water limitations to carbon exchange in old-growth and young ponderosa pine stands

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Summary We investigated the impact of seasonal soil water deficit on the processes driving net ecosystem exchange of carbon (NEE) in old-growth and recently regenerating ponderosa pine (*Pinus ponderosa* Doug. ex Laws.) stands in Oregon. We measured seasonal patterns of transpiration, canopy conductance and NEE, as well as soil water, soil temperature and soil respiration. The old-growth stand (*O*) included two primary age classes (50 and 250 years), had a leaf area index (LAI) of 2.1 and had never been logged. The recently regenerating stand (*Y*) consisted predominantly of 14-year-old ponderosa pine with an LAI of 1.0. Both stands experienced similar meteorological conditions with moderately cold wet winters and hot dry summers. By August, soil volumetric water content within the upper 30 cm had declined to a seasonal minimum of 0.07 at both sites. Between April and June, both stands showed similar rates of transpiration peaking at 0.96 mm day⁻¹; thereafter, trees at the *Y* site showed increasing drought stress with canopy stomatal resistance increasing 6-fold by mid-August relative to values for trees at the *O* site. Over the same period, predawn water potential (Ψ_{pd}) of trees at the *Y* site declined from -0.54 to -1.24 MPa, whereas Ψ_{pd} of trees at the *O* site remained greater than -0.8 MPa throughout the season. Soil respiration at the *O* site showed a strong seasonal correlation with soil temperature with no discernible constraints imposed by declining soil water. In contrast, soil respiration at the *Y* site peaked before seasonal maximal soil temperatures and declined thereafter with declining soil water. No pronounced seasonal pattern in daytime NEE was observed at either site between April and September. At the *Y* site this behavior was driven by concurrent soil water limitations on soil respiration and assimilation, whereas there was no evidence of seasonal soil water limitations on either process at the *O* site.

Keywords: chronosequence, eddy covariance, net ecosystem exchange, *Pinus ponderosa*, soil CO₂ fluxes, soil water deficit, stomatal conductance, transpiration.

Introduction

In an effort to understand the role of terrestrial ecosystems in global climate change, much research is currently focused on measuring net ecosystem exchange of carbon (NEE) between forested landscapes and the atmosphere (Baldocchi et al. 2001). Net ecosystem exchange of carbon is the balance between two large and opposing fluxes, photosynthesis and ecosystem respiration. The NEE can be measured directly using eddy-covariance techniques, and although these measurements are essential to determine the carbon sink or source strengths of forest ecosystems, they do not provide sufficient information to understand and predict the underlying processes. These underlying processes are strongly influenced by environmental factors, such as soil water content. In response to soil water deficit, photosynthesis is usually limited first by reduced rates of CO₂ supply as a consequence of declining stomatal conductance. Continued soil water deficit may lead to reduced cell expansion and growth (Hsiao 1973). Ecosystem respiration, on the other hand, is often dominated by CO₂ efflux from the soil (Raich and Schlesinger 1992, Lavigne et al. 1997, Law et al. 1999a) and reduced soil water may constrain both root and microbial respiration (O'Connell 1990, Davidson et al. 1998, Law et al. 1999b). The degree and timing of such water constraints on these processes may strongly affect the observed seasonal patterns of NEE.

To our knowledge, the interaction of seasonal water availability and forest age on the underlying processes of NEE has not been investigated. To model and predict NEE at the landscape level, assumptions about the nature of these processes in stands at different developmental stages must be made. Therefore, we investigated how soil water deficit influences the processes driving NEE in two seasonally water-limited ponderosa pine (*Pinus ponderosa* Doug. ex Laws.) stands of contrasting ages. The stands were selected from opposite ends of a ponderosa pine chronosequence in an effort to improve our understanding of the current and future potential of forests to sequester carbon. We hypothesized that a recently regenerating ponderosa pine stand places a smaller demand on limited soil water than an old-growth stand because of its lower leaf

area index (LAI). This will result in the recently regenerating stand showing less seasonally constrained net ecosystem carbon uptake compared with the mature stand. This hypothesis assumes that ecosystem respiration will show similar seasonal patterns in both stands. However, it is conceivable that the lower LAI of the recently regenerating stand will result in higher soil temperatures, perhaps resulting in higher soil respiratory CO₂ fluxes than in the old stand. The interaction of such factors is likely to result in contrasting seasonal patterns of carbon and water exchange in stands of differing ages.

To examine this hypothesis we measured three processes: (i) sap flow; (ii) soil respiration; and (iii) NEE. Sap flow techniques were used to determine soil water deficit limitations on canopy conductance and the associated restraint on carbon uptake. This methodology was chosen over chamber-based gas-exchange techniques because it allows continuous canopy-scale integration of stomatal conductance by employing sensors installed in the boles of trees. In the ponderosa pine stands studied, it has been shown that soil respiration contributes over 70% of ecosystem respiration (Law et al. 1999a) and the diurnal and seasonal patterns of soil CO₂ fluxes will most likely determine the overall trends exhibited by ecosystem respiration. The other major components of ecosystem respiration are foliage and stem respiration. Because the physiological control of water status by vegetation is likely to prevent substantial drought-related seasonal variability of these respiratory fluxes, they were excluded from the current analysis. The data presented in this paper were collected during the 1999 and 2000 field seasons. Eddy covariance and periodic chamber-based flux measurements of the components of NEE have been made at the old-growth site since 1996 (Anthoni et al. 1999, Law et al. 1999b).

Methods

Study sites

Both sites are situated in the eastern Cascades, near Sisters, Oregon, USA (Table 1), and are part of the AmeriFlux network. The young ponderosa pine site (Y) was previously an

Table 1. Characteristics of the old (O) and young (Y) ponderosa pine sites. Height data for the O site are given for the two size classes (0–30 cm, > 30 cm diameter breast height). Standard deviations where available are in parenthesis.

	O site	Y site
Latitude	44°30' N	44°26' N
Longitude	121°37' W	121°34' W
Elevation (m)	915	1188
Mean annual temperature (°C)	8.1	7.5
Annual precipitation (mm)	524	552
Age (years)	50, 250	14
Mean height (m)	10 (0.2), 34 (0.8)	2.7 (1.3)
Leaf area index	2.1	1.0
Soil sand:clay fractions (%)	62:8	65:10

old-growth forest that had been clear-cut in 1978, and allowed to regenerate naturally. The understory includes manzanita (*Arctostaphylos patula* Greene) and bitterbrush (*Purshia tridentata* (Pursh) D.C.) and accounts for approximately 40% of the site LAI. The soils are ultic haploxeralfs, and are 62% sand, 30% silt and 8% clay when averaged over a 1-m depth (a detailed description is given by Law et al. 2001). The old-growth site (O) is located in the Metolius Research Natural Area and includes old (250 years), young (50 years) and mixed patches of ponderosa pine. Each age class accounts for approximately half the site LAI. The site has never been logged. The understory is sparse with patches of bitterbrush, bracken fern (*Pteridium aquilinum* (L.) Kuhn) and strawberry (*Fragaria vesca* L.). The soils are alfic vitrixerands, and texture (65% sand, 25% silt and 10% clay) is similar to that of the Y site. Total soil carbon content to 1 m depth was 4.31 and 5.87 kg m⁻² and total soil nitrogen was 0.50 and 0.33 kg m⁻² at the Y and O sites, respectively (Law et al. 2001b). Both sites are freely draining and experience warm dry summers and cool wet winters.

Sap flow and transpiration

Sap flux density was measured continuously by the heat dissipation technique (Granier 1987). On all age classes of tree, sap flux was detected across the outer 20 mm of xylem with a generic probe design. In addition, sensors capable of detecting sap flux rates at greater sapwood depths (James et al. 2002) were used in the old-growth trees. The sap flux sensors employed over the outer 20 mm of xylem consisted of two probes, each 1.5 mm in diameter and 20 mm in length. The downstream heater probe was tightly wrapped with a coil of insulated constantan wire and supplied with a constant voltage to provide a power dissipation of 0.2 W. The probe was coated with a thermally conductive paste and placed in an aluminum tube that had previously been inserted into a radially orientated drill hole in the xylem. The reference probe was inserted into a similarly orientated drill hole situated 100 mm upstream from the heated probe. The temperature difference between the probes was measured with a pair of type-T thermocouples at 60-s intervals, averaged and stored on a CR10X data logger every 10 min (Campbell Scientific, Logan, UT). Sap velocities were calculated from probe temperature differentials based on a published empirical relationship (Granier 1987).

At the O site, sap flux density was measured continuously on five old-growth trees and ten 50-year-old trees. In the old-growth trees, sap flux was measured at the base of the live crowns (7.5 to 15 m above ground) to overcome suspected circumferential variability in flux density at ground level. Probes 20 mm in length were installed at three azimuths per tree (approximately north, south and west) and shielded with aluminized bubble film (Reflectix, Markleville, IN). On average, the sap flux probes measured across a sapwood annulus encompassing 21% of the sapwood area of the tree. To determine the radial gradients in sap flux beyond this sapwood depth and allow extrapolation of sap flux density measurements from the outer 20 mm of sapwood to the entire sapwood area, we mea-

sured sap flux density at four sapwood depths at the base of the live crown on two trees during the summer of 2001. Probes with a heater length of 10 mm were installed on the north side of each tree with the sensor tip placed at 20, 50, 100 and 150 mm sapwood depths, the deepest probe placed close to the sapwood–heartwood boundary. Data collected from these radially placed sap flux sensors during June and July showed similar patterns of decline of sap flux density with sapwood depth in both trees when expressed relative to sap flux density measured at 10–20 mm sapwood depth. On average, the relative values of sap flux density at 40–50, 90–100 and 140–150 mm sapwood depth were 74, 30 and 3%, respectively, of the values measured at 10–20 mm sapwood depth. Standard deviations of these values based on the daily calculation of relative sap flux densities over the 2-month period were less than 3% in all cases. The decline in sap flux density with sapwood depth could most simply be described as a linear function of sapwood depth ($r^2 = 0.99$, $P < 0.01$). This relationship was used to extrapolate sap flux density determined at 0–20 mm sapwood depth to the remainder of the xylem. Naturally occurring temperature gradients between the heater and reference probe, detectable when power to the heater probe was disconnected, were an appreciable source of error. Such gradients, which were caused by large diel temperature fluctuations at the sites, were assessed at 0–20 mm sapwood depth in all age classes of trees at both sites. Errors associated with these temperature gradients were assumed to be significant only for sap flux measurements made across the outer 20 mm of sapwood because of its proximity to the tree surface and the fast changing ambient environment. Sap flux measurements made across this sapwood zone were corrected accordingly. On average, mean daily sap flux density for the old-growth trees would have been overestimated by 6% if such temperature gradients were ignored.

In the 50-year-old trees at the *O* site, sensors were installed 2 m above ground on the north side. Because initial sampling suggested greater between-tree variability in flux density than between sides of individual trees, only one sensor was employed per tree. On average, the sap flux probes used on the 50-year-old trees sampled across a sapwood annulus encompassing 57% of the xylem area of the tree. Wood cores indicated that, on average, 9% of the xylem cross-sectional area was heartwood. No sap flux probes crossed between hydro-active xylem and the heartwood. To estimate sap flux densities in the sapwood annulus beyond 20 mm depth, it was assumed that a linear rate of decline of sap flux density occurred with sapwood depth based on the pattern observed in the old-growth trees. Phillips et al. (1996) determined that sap flux densities at 20–40 mm sapwood depth were about 40% of the values measured at 0–20 mm sapwood depth in the closely related species loblolly pine (*Pinus taeda* L.). Assuming a linear rate of decline of sap flux density with sapwood depth for the 50-year-old trees in our study would result in a relative sap flux density at 30 mm sapwood depth of about 50% of that measured in the outer 20 mm of sapwood (cf. Phillips et al. 1996). If we assume that no radial gradients in sap flux density

occurred in the 50-year-old trees, total site tree transpiration at the *O* site would be about 17% greater than the estimates presented in this paper. Errors associated with naturally occurring temperature gradients were significant and additional sensors were employed on all 10 trees to detect such gradients continuously. On average, mean daily sap flux density in the 50-year-old trees would be overestimated by 12% if such temperature gradients were ignored.

To determine total sapwood area at the *O* site and enable scaling of sap flux density measurements to total site tree transpiration, the diameters of all trees at 1.4 m height were measured across three plots centered on patches of old, young and mixed trees (total area of all plots was 1.9 ha). All trees measured for sap flux, plus a subset of trees in both age classes across the three plots, were cored to determine sapwood and heartwood area and bark thickness. An empirical relationship between sapwood area at the base of the live crown and sapwood area at 1.4 m height was determined for the old-growth trees used to measure sap flux ($r^2 = 0.85$, $P = 0.02$, $n = 5$) to enable estimates of transpiration to be calculated from the sapwood area measured at 1.4 m height.

At the *Y* site, sap flux density was measured simultaneously on 25 trees covering a range of tree heights (1.5 to 6.4 m) and sapwood areas at the base of the live crown (5 to 238 cm²). One sensor was installed in each tree stem at the highest point below the first living branch. Wood cores indicated no heartwood area development in trees at the *Y* site and all xylem was considered to transport water. Because of the relatively wide range of tree sapwood areas at this site, trees were divided into two size classes and different methods for computing tree transpiration were used for each size class. For trees < 3 m tall with a sapwood area < 46 cm², the sap flux probes measured across a sapwood annulus that, on average, encompassed 91% of the sapwood area. To estimate sap flux densities for the remaining 9% of the sapwood area, it was assumed that sap flux densities were 40% of the values measured by probes installed at 0–20 mm sapwood depth (cf. Phillips et al. 1996). Errors associated with naturally occurring temperature gradients resulted on average in a 13% overestimation of mean daily sap flux density and were corrected accordingly. For trees > 3 m tall with a sapwood area > 46 cm², the sap flux probes measured across a sapwood annulus that, on average, encompassed 55% of the sapwood area. To estimate sap flux densities for the inner sapwood annulus, we assumed that a linear rate of decline of sap flux density occurred with sapwood depth, as was observed in the old-growth trees, with zero flow occurring at the central axis of the tree. If we had assumed that no radial gradients in sap flux density occurred in this taller class of trees, total site tree transpiration at the *Y* site would be about 21% greater than the estimates presented in this paper. Errors associated with naturally occurring temperature gradients on average resulted in a 7% overestimation of mean daily sap flux density and were corrected accordingly. To minimize errors associated with differential heating of the tree stems by direct solar radiation, all stems with installed sensors at the *Y* site were insulated to ground level with aluminized bubble film.

Total *Y*-site tree transpiration was estimated from sap flux density and total sapwood area across the site as determined by survey data. Sapwood area at the base of the live crown of all trees was determined across four randomly located plots covering a total area of 1250 m² and encompassing 206 trees. Total sapwood area per unit ground area was divided into the two tree size classes previously outlined and tree transpiration was scaled to ground area based on mean daily sap flux density for each size class.

Canopy stomatal conductance

Mean midday canopy stomatal conductance was computed from sap flux estimates by a simplified form of the Penman-Monteith equation (Jarvis and McNaughton 1986):

$$g_c = E_T \left(\frac{\gamma \lambda}{c_p \rho_a} \right) \left(\frac{1}{D} \right) \quad (1)$$

where g_c is canopy stomatal conductance (m s⁻¹), E_T is canopy transpiration expressed on a ground area basis (kg m⁻² s⁻¹), γ is the psychrometric constant (Pa K⁻¹), λ is latent heat of vaporization of water (J kg⁻¹), c_p is specific heat of air (J kg⁻¹ K⁻¹), ρ_a is density of dry air (kg m⁻³) and D is saturated vapor pressure deficit of air (Pa). Mean values of E_T and D between 1100 and 1300 h were used in this analysis, because lags between sap flow at the base of the live crown in the old-growth trees and through shoots were considered to be minimal during this period. Analysis of branch-level sap flow collected in mid-May suggested that, during the morning, a proportion of transpired water came from storage between shoots and the base of the live crown, and later in the afternoon and during the night this storage was refilled. Consequently, the use of variables averaged between 1100 and 1300 h in the calculation of mean midday canopy stomatal conductance was considered appropriate. A study on similarly aged ponderosa pine trees made 2 km away from the present study (Ryan et al. 2000) provided evidence that the influence of capacitance was negligible when measurements of sap flux made 2–3 m above ground were used to compute canopy conductance.

Use of the simplified form of the Penman-Monteith equation assumes that the imposed evaporation rate prevails because of a high degree of coupling of the canopy to the atmosphere. This was verified with data from the *Y* site by implementation of the complete Penman-Monteith equation, where canopy aerodynamic conductance was estimated from the equation for resistance to momentum transfer (Monteith and Unsworth 1990). The degree of coupling (Ω , where values approaching one indicate significant decoupling) during this midday period was large, averaging 0.05 (Jarvis and McNaughton 1986). Therefore, we assumed it was appropriate to use the simplified form of the Penman-Monteith equation in this study. Mid-season LAI, determined with optical techniques (Law et al. 2001a), was used to compute canopy stomatal conductance expressed on a foliage area basis (hemi-surface area):

$$g_{cl} = \frac{g_c}{\text{LAI}}, \quad (2)$$

where g_{cl} is mean canopy stomatal conductance per unit hemi-surface leaf area (m s⁻¹).

Soil respiration

Measurements of soil CO₂ efflux were made with an automated, multiplexing closed-chamber system based on the design of Goulden and Crill (1997). Six chambers each with a 0.21 m² sampling area were permanently installed at each site. Chambers were connected to a central control and measurement box containing an infrared gas analyzer, pump, solenoids, logging and control equipment. A single control box was moved between sites at approximately 2-week intervals. Measurements were made on each chamber sequentially, all six chambers being measured during a 1.5-h period, the process being repeated 16 times per day. To minimize alteration of temperature and water conditions the chamber lids remained open except during a measurement. At the time of a measurement, soil temperature was recorded at 2, 8 and 15 cm depths and soil volumetric water content (θ_v) was recorded at 10 and 30 cm depths below each chamber (CS615, Campbell Scientific).

Soil water content and water potential

In addition to soil water measurements below each soil respiration chamber, θ_v was measured periodically at six locations per site over 0–30 and 0–80 cm depths by time domain reflectometry (TDR, Tektronics 1502B, Tektronics, Redmond, OR). Site-specific calibrations were used to compute soil water values. Soil water availability was also determined monthly from predawn needle water potential (Ψ_{pd}) measurements. Previous-year needles were sampled from 10 trees per site and soil water potential inferred from foliage Ψ_{pd} after accounting for gravitational potential.

Net ecosystem exchange of carbon

Half-hourly carbon and energy flux measurements were made with the eddy covariance technique (Baldocchi et al. 1988) at the *O* site at a height of 47 m (~14 m above the dominant trees), and at the *Y* site at a height of 12 m (~9 m above the mean tree height). Carbon dioxide and water vapor exchange rates were estimated as described by Baldocchi and Vogel (1996). Wind speed and virtual temperature were measured with three-dimensional sonic anemometers (Model 1012 R2, Gill Instruments, Lyngington, England; CSAT-3, Campbell Scientific). Carbon dioxide and water vapor fluctuations were measured with open-path, infrared gas analyzers (IRGA) from NOAA/ATDD (Oakridge, TN) and Li-Cor (LI-7500, Li-Cor, Lincoln, NE). Half-hourly eddy covariances and statistics were computed from ~10 Hz raw data. Above-canopy fluxes were rotated to allow interpretation of the exchange rates normal to the streamlines following the local terrain. The CO₂ fluxes were corrected for density fluctuations arising from variations in temperature and humidity (Webb et al. 1980).

For calculation of daily aggregated NEE, data gaps were filled using an empirical relationship that combined the response of NEE to light and air vapor pressure deficit (Anthoni et al. 1999). We limited the current analysis to daytime NEE to avoid systematic uncertainties associated with calm conditions at night (Aubinet et al. 2000, Baldocchi et al. 2000).

Results

The seasonal patterns of soil water depletion and soil temperatures (Figure 1) are typical of conditions on the eastern side of the Cascades. During the winter, soil water attained field capacity at both the *O* and *Y* sites with θ_v values of 0.25 and 0.32, respectively, when integrated over the top 80 cm of soil. Between April and October, gradual soil drying occurred at both sites resulting in minimum seasonal θ_v values of 0.06 at the 10-cm horizon, 0.07 when integrated over the upper 30 cm of the soil profile, and 0.10 and 0.14 when integrated over the top 80 cm at the *O* and *Y* sites, respectively (Figures 1 and 2). Daily mean soil temperatures peaked in early August at both sites (Figure 1), however values at 15 cm depth at the *Y* site averaged 1.8 °C higher than values at the *O* site during the summer months. Mean daily soil fluxes showed similar seasonal

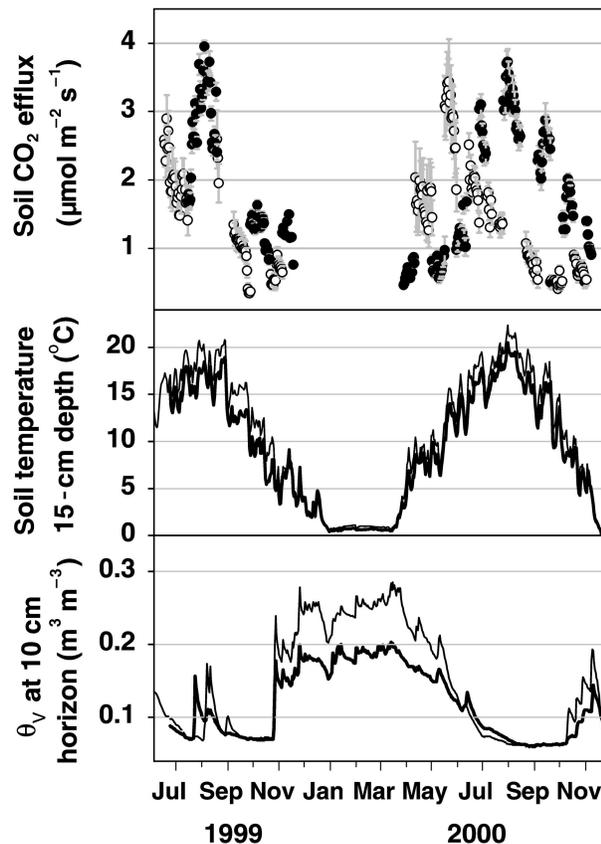


Figure 1. Seasonal variations in mean daily soil CO₂ efflux, mean daily soil temperature measured at 15 cm depth and mean daily soil volumetric water content at 10 cm depth for *Y* (○, thin line) and *O* (●, thick line) sites. Error bars indicate ± 1 SE.

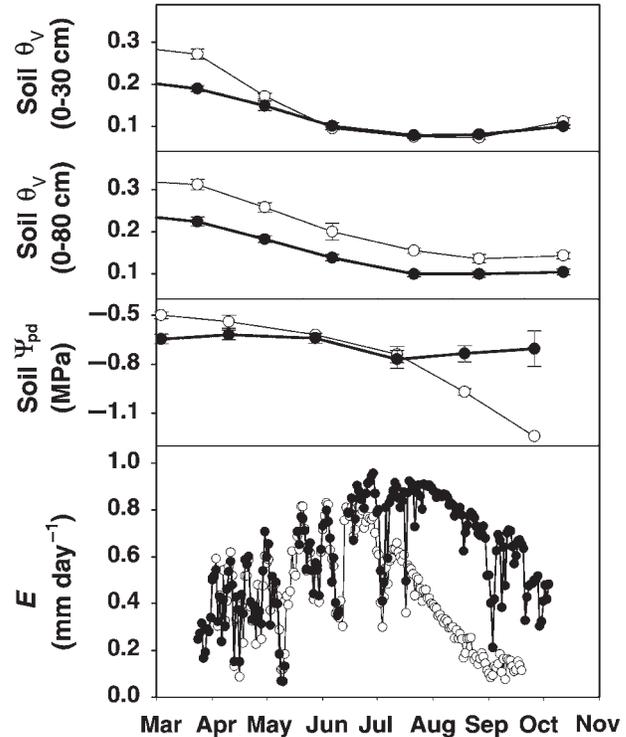


Figure 2. Seasonal changes in soil water content (θ_v) integrated over the top 30 and 80 cm of soil, rooting zone soil water potential inferred from predawn foliage water potentials (soil Ψ_{pd}), and daily tree transpiration rates (E) for *Y* (○, thin line) and *O* sites (●, thick line) during the 2000 field season. Error bars indicate ± 1 SE.

ranges (0.4–4.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at both sites, but markedly different seasonal trends (Figure 1, upper panel). At the *O* site, soil fluxes showed a strong positive seasonal correlation with soil temperature, whereas at the *Y* site soil fluxes peaked in late May, about 2 months before maximal soil temperatures occurred, and thereafter declined with increasing soil water deficit.

Soil water availability (as inferred from foliage Ψ_{pd}) at the *Y* site showed a continuous seasonal decline reaching a minimum of -1.24 MPa in early October (Figure 2). At the *O* site, no strong seasonal pattern in soil water availability was evident and values remained greater than -0.8 MPa throughout the year. Values in September and October differed significantly between sites ($P < 0.001$).

Tree transpiration at both sites showed similar seasonal patterns until mid-June (Figure 2), peaking at 0.96 mm day^{-1} in trees at the *O* site. Greater day-to-day variability was evident at the beginning of the season than later in the season. After mid-June, transpiration at the *Y* site declined significantly reaching 0.1 mm day^{-1} in early September. Transpiration at the *O* site showed no substantial late-season decline and followed a pattern most likely attributable to changes in day length.

We removed the day-to-day variability in canopy stomatal resistance associated with variable weather conditions by calculating the ratio of mean midday canopy resistance per unit

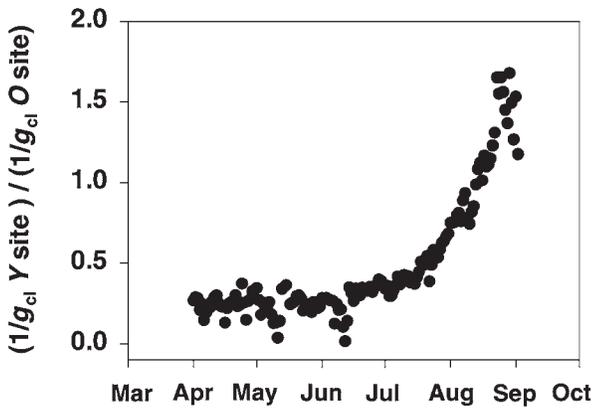


Figure 3. Ratio of midday canopy stomatal resistance on a leaf area basis at the *Y* site (s m^{-1}) to that at the *O* site (s m^{-1}) during the 2000 field season. The ratio illustrates the soil drought limitations on canopy stomatal resistance at the *Y* site.

leaf area at the *Y* site (the reciprocal of canopy conductance) to that at the *O* site (Figure 3). Between April and mid-June, canopy resistance at the *Y* site was about one quarter of that at the *O* site, thereafter canopy resistance at the *Y* site increased to 1.7 times that at the *O* site by late August.

No distinct seasonal pattern in daytime NEE was evident at either site between April and September (Figure 4). Day-to-day variability was large, as indicated by the standard deviations for 10-day averaged NEE. Daytime NEE showed similar day-to-day variability across the season at each site. Between April and September, mean daytime NEE was 2.7 and 1.7 $\text{g C m}^{-2} \text{day}^{-1}$ at the *O* and *Y* sites, respectively.

Discussion

Based on soil water measurements in various zones of the top 80 cm of soil, seasonal patterns of soil water depletion were

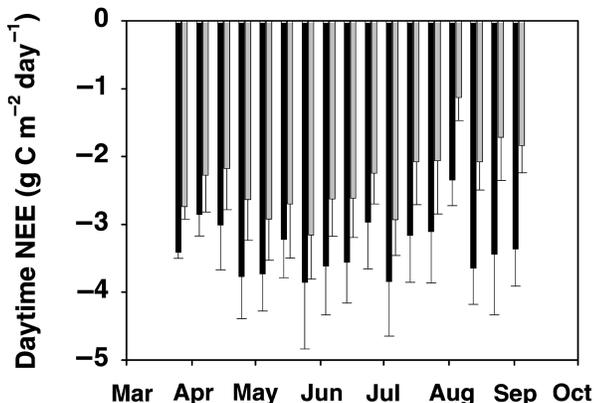


Figure 4. Seasonal variation of 10-day bin averaged daily NEE for the *Y* (shaded) and *O* (solid) sites during the 2000 field season. Negative values indicate net gain of carbon by the ecosystem. Error bars indicate 1 SD. Net C uptake was consistently less at the *Y* site than at the *O* site.

similar at both sites (Figures 1 and 2). This finding is substantiated by the almost identical rates of tree transpiration at both sites before July (Figure 2). Consequently, we reject our hypothesis that a recently regenerating ponderosa pine stand places a smaller demand on limited soil water than an old-growth stand. Our expectation of lower transpiration rates per unit ground area at the *Y* site because its LAI was about half that at the *O* site was unfounded. Transpiration on a ground area basis at the *Y* site likely exceeded that at the *O* site during the first half of the year if water use by understory shrubs is taken into account. At the *Y* site, understory shrubs account for about 40% of site LAI, whereas at the *O* site understory shrubs are sparse and do not contribute significantly to site LAI. Studies conducted in a comparable central Oregon site indicated that, at a tree LAI similar to that of the *Y* site, water use by understory vegetation accounted for about 20% of transpiration (Figure 5, Oren et al. 1987) and that, at a tree LAI of > 1.5 , understory transpiration became insignificant. Eddy covariance estimates of water vapor exchange, which includes evaporation from all surfaces, was similar at the two sites through May and June (109 mm at *O* site, 116 mm at *Y* site), but lower at the *Y* site than at the *O* site during July and August (110 mm at *O* site, 92 mm at *Y* site). Rates of water use at the *Y* site were unsustainable, as demonstrated by the large decrease in canopy conductance from July onward (Figure 3), which also resulted in reduced carbon assimilation.

Measurements of net assimilation rate (A) versus leaf intercellular carbon dioxide concentration (C_i) curves in June 1999 indicated no significant differences in maximum rate of carboxylation by Rubisco (V_{cmax}) between the two sites, with values of 28.6, 22.3 and 26.2 $\mu\text{mol m}^{-2}$ (half-total surface area) s^{-1} for previous-year needles of old-growth trees, 50-year-old trees and young site trees, respectively. The significantly lower foliage Ψ_{pd} at the *Y* site compared with the *O* site in September and October (Figure 2) suggests that trees at the *Y* site had a shallower rooting depth than trees at the *O* site. Shallow-rooting species or trees growing under conditions where deep rooting is prevented show rapid declines in canopy stomatal conductance (Bréda et al. 1993, Oren et al. 1998), as illustrated in Figure 3. We suspect that, at the *Y* site, the relatively small trees have yet to establish deep rooting patterns, and that limited root development rather than limited soil depth has resulted in the seasonally constrained patterns of transpiration at this site. The similar texture of soils at both sites, together with the lack of a seasonal decline in foliage Ψ_{pd} at the *O* site suggest substantial water extraction from below the first 80 cm of soil at this site. Williams et al. (2001) reached similar conclusions when modeling carbon exchange at the *O* site and predicted that over 80% of water extraction occurred from below 80 cm by early September. This conclusion was further supported by measurements of ^{18}O in foliage water at the *O* site, which was found to have a signature resembling that of deeper soil water (D. Bowling, University of Utah, personal communication).

Because LAI was higher at the *O* site than at the *Y* site, the similarity in tree transpiration per unit ground area at the two

sites before July indicates that, compared with the *Y* site, transpiration per unit leaf area was significantly lower at the *O* site before the young trees became water stressed. This finding supports the growing body of evidence for the existence of hydraulic constraints on transpiration in older trees (Yoder et al. 1994, Kolb and Stone 2000, Ryan et al. 2000).

When using sap flux techniques to calculate whole-site tree transpiration and canopy conductance, measurements from sensors that detect sap fluxes from a relatively small sapwood area are scaled on the basis of simplified relationships. The limitations and assumptions associated with this process have been widely discussed (e.g., Köstner et al. 1998, Ewers and Oren 2000). In our study, we made assumptions about radial patterns of sap flux within the xylem in both the 50-year-old trees at the *O* site and the larger size class of trees at the *Y* site (see Methods). We consider our assumptions to be reasonable and in broad agreement with radial sap flux profile data collected by Phillips et al. (1996) on loblolly pine. If no such radial sap flux profiles occurred in these two size classes of trees, tree transpiration would be increased by 17 and 21% at the *O* and *Y* sites, respectively. Thus, although our scaling assumptions may affect whole-site tree transpiration estimates, they have no influence on the seasonal patterns of tree water use and little influence on the ratio of canopy conductances between sites.

The strikingly different seasonal patterns of soil respiration flux between the *O* and *Y* sites, despite almost identical seasonal patterns of soil temperature and soil water availability within the upper soil profile, was contrary to expectations. At the *O* site, seasonal soil CO₂ efflux appeared to be unconstrained by declining soil water within the upper soil profile, whereas at the *Y* site, declines in CO₂ efflux were highly correlated with declining soil water within the upper soil profile. Currently, little is known about which zones within the soil profile make the major contribution to respiratory flux; however, on a diel basis, correlation of soil CO₂ efflux with soil temperature at various depths suggest that the region is within the top 15 cm of the soil. The majority of fine root biomass is found within the top 20 cm of soil, and these roots account for about 50% of total soil CO₂ efflux in summer (Law et al. 2001b). It therefore remains an enigma why reduced soil water in the soil zone that contains the majority of the roots did not lead to constrained soil CO₂ efflux rates at the *O* site. One hypothesis is that hydraulic redistribution of deep soil water to fine roots in the surface layer maintains a constant rate of rhizosphere respiration (mycorrhizae, fine roots and tightly associated microbes) during the drought period. However for this to occur, redistributed water would have to remain in close contact with the roots and not leak into the bulk soil where it would have likely been detected by the TDR measurements. Ongoing studies using a capacitance type soil water sensor, which is less influenced by large diurnal fluctuations in soil temperature than the CS615 TDR probes that we used, appear to indicate at least some degree of hydraulic redistribution is occurring at the *O* site.

The lack of a strong seasonal pattern in daytime NEE at both sites between April and September (Figure 4) is a result of soil water constraints on carbon exchange processes at the *Y* site, and the lack of soil water constraints on these processes at the *O* site. At the *Y* site, declines in soil CO₂ efflux between June and October were matched by concurrent declines in assimilation caused by large reductions in canopy conductance, resulting in daytime NEE remaining stable between 2 and 3 g C m⁻² day⁻¹. Between April and July, soil CO₂ efflux rates at the *O* site increased in response to soil warming. During the same period, there were no seasonal soil water deficit constraints on carbon uptake, and assimilation rates increased in response to rising air temperatures and increasing light availability, with the net result being a stable daytime NEE. Between July and October this pattern was reversed; soil CO₂ efflux rates decreased in parallel with reductions in assimilation as temperatures fell and day length decreased.

Conclusions

There were highly contrasting responses of the underlying processes of NEE to soil water within the upper soil profile in ponderosa pine ecosystems at different developmental stages. We suggest that both the transpiration and soil CO₂ efflux responses exhibited at the *O* site are a consequence of deep rooting and that until trees at the *Y* site develop deep rooting patterns these contrasting responses will prevail. This suggestion is supported by the predawn foliage water potential data and the sap flux data showing that, at the *Y* site, smaller trees (~2 m tall) developed drought stress earlier in the season than larger trees (~6 m tall) in both 1999 and 2000.

Drought limitations to carbon assimilation have been extensively studied, and the inclusion of water limitations in models of forest productivity is now widespread. In comparison, soil respiratory processes have received far less attention. Although models of soil efflux typically use soil temperature and soil water to predict autotrophic and heterotrophic respiration, we observed an insensitivity of soil CO₂ efflux to soil water within the upper soil profile at the *O* site, a zone containing the majority of fine roots. Soil water availability as determined by predawn foliage water potential is perhaps a better predictor of soil efflux than direct measurement of soil water (Davidson et al. 1998, Law et al. 1999b). However, further studies are required to differentiate between the direct effect of soil water deficit on soil respiratory processes, and the indirect effect of soil water deficit on the supply of photosynthates to roots, resulting from the decrease in carbon assimilation. Current efforts to model carbon fluxes in forest ecosystems of different ages growing under variable climatic conditions need to consider these underlying processes. We conclude that the use of relationships developed in one stand type and age to predict the behavior of carbon exchange across a range of developmental stages will require a better mechanistic interpretation of the underlying processes.

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