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Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine

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Summary As forests age, their structure and productivity change, yet in some cases, annual rates of water loss remain unchanged. To identify mechanisms that might explain such observations, and to determine if widely different age classes of forests differ functionally, we examined young (Y, ~25 years), mature (M, ~90 years) and old (O, ~250 years) ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws.) stands growing in a drought-prone region of central Oregon. Although the stands differed in tree leaf area index ($\mathrm{LAI_T}$) ($Y = 0.9$, $M = 2.8$, $O = 2.1$), cumulative tree transpiration measured by sap flow did not differ substantially during the growing season (100–112 mm). Yet when water was readily available, transpiration per unit leaf area of the youngest trees was about three times that of M trees and five times that of O trees. These patterns resulted from a nearly sixfold difference in leaf specific conductance (K_L) between the youngest and oldest trees. At the time of maximum transpiration in the Y stand in May–June, gross carbon uptake (gross ecosystem production, GEP) was similar for Y and O stands despite an almost twofold difference in stand leaf area index ($\mathrm{LAI_S}$). However, the higher rate of water use by Y trees was not sustainable in the drought-prone environment, and between spring and late summer, K_L of Y trees declined fivefold compared with a nearly twofold decline for M trees and a < 30% reduction in O trees. Because the Y stand contained a significant shrub understory and more exposed soil, there was no appreciable difference in mean daily latent energy fluxes between the Y stand and the older stands as measured by the eddy-covariance technique. These patterns resulted in 60 to 85% higher seasonal GEP and 55 to 65% higher water-use efficiency at the M and O stands compared with the Y stand.

Keywords: eddy-covariance, evapotranspiration, gross ecosystem production, hydraulic conductance, sap flux, stomatal conductance.

Introduction

Understanding how changes in forest structure influence the exchange of carbon and water with the atmosphere is critical for assessing the variability of such fluxes across the landscape, and for developing models that can accurately predict such fluxes at regional scales. At the ecosystem level, gross photosynthesis is strongly coupled with water vapor loss (Law et al. 2002). If processes controlling water vapor loss change with stand structure as forests age, it is likely to result in dissimilar rates of carbon exchange in stands of different ages growing in the same climatic conditions.

Our knowledge of water flux through vegetation is mainly based on the responses of individual organisms. Controls over the flux of water from forested ecosystems are, however, more complicated. As forests age, individual trees grow in diameter and height as the total number of stems present in the stand is reduced exponentially. As trees age, the hydraulic properties of individual trees change, and at the same time, the amount of radiation intercepted by tree crowns varies substantially, compared with that of other vegetation and soil surfaces. In a young forest, a pioneering community of herbs, grasses and shrubs share space with establishing trees and contribute to total transpiration. Hydraulic redistribution of water by vegetation may increase soil water availability to shallow-rooted vegetation, allowing greater transpiration rates. Studies at the individual tree level cannot, therefore, predict fluxes at the forest scale at which numerous interacting processes control water and carbon exchange.

Studies on individual trees suggest that, as trees grow taller, the sustainable flux of water (Ryan et al. 2000, McDowell et al. 2002), as well as the uptake of carbon (Yoder et al. 1994, Mencuccini and Grace 1996*a*, Niinemets 2002), may be restricted because of hydraulic limitations of the stem, roots and branches. In some studies, compensatory mechanisms such as changes in sapwood-to-leaf area relationships (Schäfer et al. 2000, Barnard and Ryan 2003) and xylem permeability (Domec and Gartner 2003) have been documented, which minimize changes in hydraulic resistance with increasing tree age. At the tree level, transpiration is controlled by stomatal conductance in a manner considered to minimize loss of hydraulic system function, while minimizing restriction to carbon uptake (Meinzer 2002). Increases in soil water deficits can lead to reductions in stomatal conductance and photosynthesis, but the magnitude of the response may partly depend on age-related tree physiology (e.g., buffering capacity of stem and canopy water storage, hydraulic resistance) and partly on stand dynamics (e.g., resource competition with understory, root development relative to water source). Younger trees with lower hydraulic resistance may have higher photosynthetic rates when soil water availability is high, but under extreme drought conditions, may suffer hydraulic system failure through xylem cavitation, resulting in the shut-down of photosynthesis (Goldstein et al. 2000, Law et al. 2001*a*).

Although studies at the tree level suggest age-related patterns in tree water use, little is known about how age-related hydraulic limitations in trees influence carbon and water exchange at the stand or ecosystem level. It is conceivable that, as forests age, changes in tree transpiration result in differences in total latent energy (LE) losses. If true, variation of forest age across a landscape would influence evaporative water losses, affecting the local surface energy balance, mesoscale climate and runoff (Vertessy et al. 2001).

With the advent of techniques to measure whole-ecosystem LE and carbon fluxes in conjunction with sap flow and other ecophysiological processes, we are now in a position to explore some of the interactions outlined above. In this study, we assessed the extent to which structural and functional differences affect the exchange of water and carbon in ponderosa pine forests ranging in age between 25 and 250 years.

Materials and methods

Study sites

The three study sites are within 2 to 8 km of each other on the east side of the Cascade Mountains, near Sisters, Oregon, USA (Table 1), and are part of the AmeriFlux network of flux sites. The young pine stand (*Y*, mean age of the oldest 10% of trees = 23 years) regenerated naturally following logging in 1978. The understory includes manzanita (*Arctostaphylos patula* Greene) and bitterbrush (*Purshia tridentata* (Pursh) D.C.) and accounts for about 40% of the $\mathrm{LAI_S}$. The mature stand (*M*, 90 years) comprises almost exclusively ponderosa pine with a few scattered incense cedar (*Calocedrus decurrens* (Torr.) Florin) and a sparse understory of similar composition to the *Y* stand. The old-growth stand (*O*) is located in the Metolius Research Natural Area and includes old (250 years), young (90 years) and mixed patches of ponderosa pine. Each age class accounts for about half the $\mathrm{LAI_S}$. The stand has never been logged. The understory is sparse with patches of bitterbrush, bracken fern (*Pteridium aquilinum* (L.) Kuhn) and strawberry (*Fragaria vesca* L.).

All three sites have sandy soils, are freely draining and have warm dry summers and cool wet winters. Precipitation is usually between about 300–600 mm year^{-1}, the majority falling between November and April as a combination of rain and snow. Further site details and meteorological conditions are reported in Anthoni et al. (2002) and Law et al. (2001*c*).

Sap flux and tree transpiration

Sap flux was measured continuously by the heat dissipation technique (Granier 1987) between April and November over a 4-year period at the *Y* and *O* stands (1999–2002) and over late summer 2001 and the complete 2002 season at the *M* stand. Details of the methodology used at the *Y* and *O* stands are given in Irvine et al. (2002). Here we provide an overview and additional details of measures taken to improve our tree transpiration estimates at the *Y* stand, together with details of measurements at the *M* stand.

To calculate rates of tree transpiration, sap flux was measured across the outer 20 mm of sapwood at each stand. Based on stand surveys, we installed sap flux sensors across a range of tree sizes to investigate variation in sap flux associated with tree size and to scale tree transpiration to the stand level (Table 2). Tree transpiration was quantified based on mean sap flux for each age class, the proportion of sapwood area at different sapwood depths and the decline in sap flux with sapwood depth.

Table 1. Characteristics of the young (*Y*), mature (*M*) and old (*O*) ponderosa pine sites, based on data collected during 2001–2002 from plot surveys of four 10-m radius subplots in each age class. Data for the *O* stand are given for the two distinct cohorts at the site. Ages are given as both plot mean and the mean of the oldest 10% of trees. Stand leaf area index ($\mathrm{LAI_S}$) includes both tree and understory canopies. Soil textures are averaged over the 0–50-cm soil depth. Values in parentheses are standard errors.

	Y	*M*	*O*
Latitude	44°26′ N	44°27′ N	44°30′ N
Longitude	121°34′ W	121°33′ W	121°37′ W
Elevation (m)	1165	1232	895
Mean plot age (years)	15	56	156, 61
Oldest 10% mean age (years)	23	89	250, 90
Mean height (m)	4.3 (0.16)	14.0 (0.59)	32.6 (1.5), 11.5 (1.2)
Mean diameter at breast height (cm)	11.3 (0.49)	29.0 (1.3)	55.0 (3.3), 14.6 (1.6)
$\mathrm{LAI_S}$	1.1	2.8	2.1
Soil sand/clay fractions (%)	66/6	67/7	66/10

Table 2. Sap flux tree characteristics for ponderosa pine sites (Y = young stand; M = mature stand; and O = old-growth stand). Measurement depth refers to the probe location, where zero is the cambium. The range reflects the length of the sap flux probe installed. Profile refers to probes installed at all four depths: 0–20, 25–35, 45–55 and 65–75 mm. Mean daily sap fluxes between Days 120 and 160 represent conditions of non-limiting soil water.

Site	Measurement depth (mm)	Range of tree diameter (cm) (n)	Range of sapwood depth (cm)	Mean daily sap flux DOY 120–160 (kg m^{-2} h^{-1}) (SE)	Correlation of sap flux to sapwood depth r (P)
Y	0–20	5.3–21.6 (15)	2.2–9.1	60.0 (5.7)	0.46 (0.49)
	20–40	11.5–19.4 (4)	4.3–7.8		
	Profile	15.0–21.6 (4)	6.0–9.1		
M	0–20	21.0–38.4 (12)	6.7–13.4	37.2 (2.7)	0.15 (0.66)
	20–40	21.0–38.4 (8)	6.7–13.4		
	Profile	29.3–37.6 (4)	9.9–13.1		
O (250 years)	0–20	55.2–84.3 (15)	8.5–15.5	25.89 (1.8)	0.44 (0.76)
	Profile	71.0–73.0 (2)	12.9–15.0		
O (90 years)	0–20	12.0–27.1 (10)	3.3–8.1	17.6 (2.1)	0.81 (< 0.01)

The decline in sap flux with sapwood depth was measured for four trees in both the Y and M stands and, as previously reported in Irvine et al. (2002), for two trees at the O stand. Three sensors, each with a 10-mm probe (James et al. 2002), were installed at 25–35, 45–55 and 65–75 mm sapwood depths for the profiles in addition to the sap flux probes installed over 0–20 mm sapwood depth. The decline in sap flux with sapwood depth was estimated from mean daily sap fluxes from the profiles expressed relative to the sap flux over the 0–20 mm sapwood depth.

To determine sapwood areas at different sapwood depths, we measured tree diameters and collected increment cores in each stand for stand-specific relationships between tree diameter and sapwood depth. Five 10-m radius plots were surveyed at the Y and M stands, and additional plots were surveyed at the more variable O stand (Law et al. 2001*c*). For each tree surveyed at Y and M, sapwood areas in 2-cm wide annuli were determined through to the heartwood boundary, and values were summed by annulus to the plot level.

Between 15 and 30 dendrometer bands were used at each stand to record increases in tree basal area across the years. At the Y stand, increment cores showed no heartwood formation and large increases in basal area were observed each year (~20% per year). These increases in sapwood area were factored into the transpiration calculations on an annual basis. In addition, because trees at this site were growing rapidly and sap flux probes were not replaced annually, probes that remained in place sensed sap flux across sapwood in which sap flux was gradually declining as its depth increased. Measurements of the decline of sap flux with sapwood depth indicated that, on average, sap fluxes would be underestimated by about 8% for every season a probe was left installed. This was factored into the transpiration calculations for Y. At O, both tree age classes showed much smaller increases in basal area, less than 0.5% $year^{-1}$ and ~3% $year^{-1}$ for the 250-year-old trees and 90-year-old trees, respectively. However, such increases in basal area could not be viewed as increases in sapwood area because new heartwood was simultaneously being formed at a comparable rate.

Variation among trees in sap flux over the outer 20 mm of sapwood together with variation in sap flux with sapwood depth were used to estimate our degree of confidence around the scaled estimates of transpiration. We note that these estimates refer to trees sampled within a relatively small area of the footprint sampled by the above canopy eddy-covariance system, whereas, optimally, sap flux and sapwood-to-ground area ratios should be measured at multiple random points within the footprint to enable rigorous statistical comparison of transpiration and ET at the stand level (Oren et al. 1998). In practice, limits imposed by wiring (power attenuation) and capacity of data loggers prevented such an approach. However, the locations of the measured trees were generally within the mean wind direction and eddy-covariance footprint.

Canopy conductance

We determined canopy stomatal conductance (G_c) based on sap flux data collected during the midday period and a simplified form of the Penman-Monteith equation (Jarvis and McNaughton 1986). Details and justification of the approach are given in Irvine et al. (2002). Briefly, we used only data collected between 1100 and 1300 h to minimize errors associated with lags between sap flux measured in the bole of the tree and transpiration from the foliage caused by hydraulic capacitance of the system. The use of the simplified form of the Penman-Monteith equation was appropriate because needle–leaf forests with low LAI show high degrees of canopy coupling to the atmosphere, and the energy term in the Penman-Monteith equation becomes insignificant compared with vapor pressure deficit (D) and the boundary layer conductance.

Leaf specific conductance

Leaf specific conductance (K_L; mol m^{-2} s^{-1} MPa^{-1}) was estimated as:

$$K_L = Q_L/(\Psi_{soil} - \Psi_{leaf})$$

where Q_L (mol m^{-2} s^{-1}) is xylem water flux per unit leaf area averaged over the midday period (1100 to 1300 h), Ψ_{soil} is the soil water potential determined from predawn leaf water potential (Ψ_{pd}) measurements and Ψ_{leaf} is leaf water potential measured during the midday period (both with gravitational potential deducted).

Ecosystem evapotranspiration and gross ecosystem production

Total ecosystem latent energy (LE) and carbon exchange were measured by the eddy-covariance technique (Baldocchi et al. 1988). Three-dimensional sonic anemometers (CSAT-3; Campbell Scientific, Logan, UT) and open-path infrared gas analyzers (Li-Cor 7500 IRGA, Li-Cor, Lincoln, NE) were installed above the canopy and half-hourly eddy covariances and statistics were computed from 10 Hz of raw data. Details of the methodology and the computation of gross ecosystem production (GEP) based on nighttime respiration–temperature response curves have been reported for *Y* and *O* for the year 2000 (Anthoni et al. 2002) and were applied at the *M* stand. In this study, GEP estimates at *Y* and *O* were updated to include the 2001 growing season. Because sonic anemometers and open-path gas analyzers do not function reliably when it is raining, data collected on days when it rained were discarded. Annual total LE was computed by averaging daily fluxes across multiple years (*Y* and *O*) and then multiplying the mean daily flux by the number of days per year.

Soil water potential and water content

Soil water availability was determined between spring and late fall by monthly measurements of Ψ_{pd}. Previous-year needles were sampled from between 5 and 10 trees per stand and soil water potential inferred from Ψ_{pd} after accounting for gravitational potential. To better determine the rates of soil water depletion across different soil horizons, we installed pairs of 30-cm long steel pins in the side walls of three soil pits at each stand in early spring 2002 at depths of 10, 30 and 50 cm (all stands), 70 cm (*Y*) and 90 cm (*M* and *O*) to act as wave guides for periodic time domain reflectometry (TDR) measurements. The pins were connected to a coaxial cable brought to the soil surface before the soil pits were backfilled. We determined probe specific TDR calibrations for each depth and soil pit. Measurements were made periodically during 2002 with a Tektronix cable testing oscilloscope (1502B, Tektronix, Beaverton, OR) connected to a CR10X data logger and SMD1502 interface (Campbell Scientific).

Leaf area index

To calculate transpiration rates per unit leaf area, leaf area index (half-total surface area) was determined by optical techniques. Following methods in Law et al. (2001*d*), 39 measurements per 1-ha plot were made with a Li-Cor LAI-2000, above and below any shrub understory, to determine LAI_T and LAI_S, respectively, and corrected for wood interception and clumping at the shoot scale based on shoot silhouette measurements or, at scales larger than the shoot, based on TRAC measurements of diffuse and direct radiation transmittance along transects.

Results

Age-related changes in tree-level physiology

Scaling sap flux to tree transpiration Under conditions of non-limiting soil water, sap flux across the outer 20 mm of the sapwood varied widely across age classes, with a trend of increasing flux per unit sapwood area with decreasing tree age (Table 2). Sap flux was significantly higher in the youngest trees compared with the remaining three age classes ($P < 0.05$, ANOVA, Tukey's HSD). There was no significant correlation between sap flux measured across the outer 20 mm of the sapwood and sapwood depth within *Y*, *M* and *O* (250-year-old trees), supporting stand-specific tree-size-independent scaling of transpiration from sap flux measurements (Table 2). For the 90-year-old age class at *O*, there was a strong correlation between sap flux and sapwood depth (Table 2), likely because the suppressed nature of these trees resulted in highly variable sapwood conductive properties within this age class. However, because this age class accounted for about one third of total stand transpiration, we assumed size independence to scale sap flux to tree transpiration. We note that, when comparing age-specific hydraulic parameters, this age class was excluded from the analysis and focus was given to the old trees at the site.

Sapwood depth varied from about 2 to15 cm across the age classes studied (Table 2), highlighting the need to measure radial patterns of sap flux across the xylem to scale sap flux to tree transpiration in ponderosa pine. For the 250-year-old trees at *O*, an almost linear reduction in sap flux was observed with sapwood depth (Irvine et al. 2002). At both *Y* and *M*, radial profiles in sap flux showed strong declines with sapwood depth (Figure 1); however, variability within a given depth was large. This pattern was approximated by a linear decline with depth at *Y*, and an exponential decline at *M*.

Tree age or size related hydraulic properties with non-limiting soil water To compare rates of transpiration across stands under non-limiting soil water conditions, we calculated mean daily total tree transpiration between Days 120 and 160 (Table 3). Values for all 4 years are given for the rapidly growing *Y* stand, but only the 2002 values are presented for the *M* and *O* stands. To compare age-specific hydraulic relationships, we computed transpiration rates for old-growth trees based on the stand density of a 1-ha pure old-growth stand at *O*. The LAI for the old-growth stand was also determined. Because of the difficulty in determining LAI for different components of mixed stands by optical techniques, we did not attempt to determine hydraulic relationships for the 90-year-old trees at *O*.

Between 1999 and 2002, mean daily tree transpiration at *Y* under conditions of non-limiting soil water increased from 0.60 to 0.98 mm day^{-1} (Table 3). During the same period, tree LAI increased from 0.61 to 0.96 and sapwood area increased

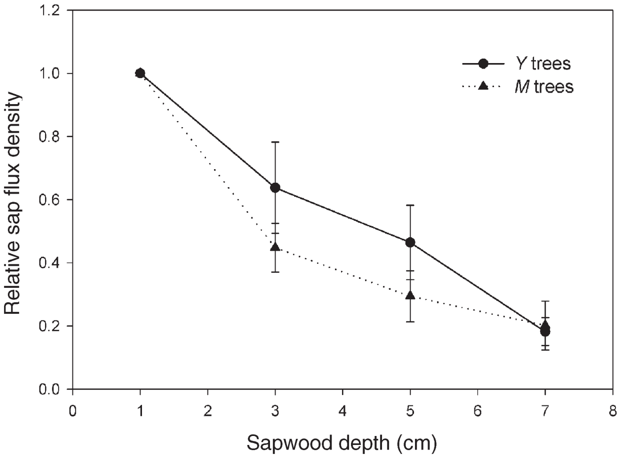

Figure 1. Radial trends in sap flux with sapwood depth for young (*Y*) and mature (*M*) ponderosa pine stands. Measured values for each tree are expressed relative to the sap flux across the outer 20 mm of sapwood. Ratios of the daily mean sap fluxes were averaged between Days 120 and 160. Probes were installed at four sapwood depths: 0–20, 25–35, 45–55 and 65–75 mm (bars indicate ± 1 SE).

from 5.5 to 9.4 m^2 ha^{-1}. These concurrent changes in leaf and sapwood areas resulted in a relatively constant ratio of leaf area to sapwood area across the 4 years and, consequently, relatively constant rates of transpiration per unit sapwood or leaf area across the 4 years (Table 3). Transpiration rates per unit ground area for the pure old-growth stand under conditions of non-limiting soil water were about 40% that of *Y* (average across all years) or about 19% that of *Y* on a leaf area basis. Transpiration rates for *M* and *Y* (average across all years) under conditions of non-limiting soil water were similar on a ground area basis; however, transpiration rates per unit leaf area at *M* were about one third those at *Y* because leaf area at *M* was almost three times that at *Y*. Transpiration per unit sapwood area at 1.3 m height decreased with tree age with the greatest difference between *Y* and *M* trees. Contrary to expectations, leaf area per unit sapwood increased with tree age; *Y* trees had about two thirds the leaf area per unit sapwood compared with old-growth trees.

With non-limiting soil water in early June, K_L decreased with stand age (Figure 2); it was lowest in the *O* trees (0.43 and 0.69 mmol m^{-2} s^{-1} MPa^{-1} in 2001 and 2002, respectively), moderate in the *M* trees (0.85 mmol m^{-2} s^{-1} MPa^{-1}) and highest in the *Y* trees, even when considering the large interannual variability (2.29 and 4.19 mmol m^{-2} s^{-1} MPa^{-1} in 2001 and 2002, respectively). No significant differences ($P > 0.05$) in soil water potentials were observed across stands, but minimum midday leaf water potentials (after correction for the gravitational component) were slightly more negative in the 250-year-old trees than in the *Y* trees (–1.49 and –1.27 MPa respectively, $P < 0.05$) such that the water potential gradient was ~14% greater in the 250-year-old trees, suggesting a minor degree of hydraulic compensation (McDowell et al 2002). The approach we adopted to determine K_L based on stand-level estimates of sap flux and LAI_T gave estimates comparable with those determined on an individual tree basis (Hubbard et al. 1999) for old-growth ponderosa 10 km from the *O* stand (~0.75 mmol m^{-2} s^{-1} MPa^{-1}).

To determine the response of G_c to *D* across trees of different ages, we removed the confounding effects of low light (all sites) and low soil water availability (*Y* and *M* stands only) on G_c values during the midday period by excluding data with mean midday above-canopy PAR < 1600 μmol m^{-2} s^{-1} and data collected after Day 190 (*Y* and *M* stands only) from the analysis. In addition, to exclude a small number of values that fell noticeably below the remaining boundary line relationship, we eliminated data with a midday period *D* of < 0.4 kPa. These latter values likely resulted from days with rainfall preceding the midday period such that estimates of G_c from sap flux measurements did not represent steady-state conditions and the response of G_c to *D*. Data were analyzed from year 2000 (*Y* and *O*) and 2002 (*M*). Absolute G_c showed a trend of increasing sensitivity to *D* with decreasing tree age (Figure 3); data were plotted with logarithmic transformed *D* to enhance the linearity of the relationship and enable sensitivity analysis. The linear relationship of the absolute response of G_c to ln*D* was significant at each stand ($P < 0.01$) and the slopes of the responses from all stands were significantly different from each other ($P < 0.01$). Absolute sensitivity of G_c to ln*D* at *Y*

Table 3. Transpiration at the young (*Y*), mature (*M*) and old (*O*, pure old-growth component only) ponderosa pine stands under conditions of non-limiting soil water (May through mid-June). Abbreviations: Age = mean age of the oldest 10% of trees in the stand; *E* = tree transpiration on a unit ground area basis; A_s = sapwood area at 1.3 m height; LAI_T = tree leaf area index (half-total surface area); and Relative sensitvity G_c = sensitivity of midday period canopy conductance to vapor pressure deficit (*D*) relative to canopy conductance at *D* of 1 kPa, $(-dG_c/d\ln D):G_{c\ ref}$.

	Y				*M*	*O*-old growth
	1999	2000	2001	2002	2002	2002
Age	20	21	22	23	89	250
E (mm day^{-1})	0.6	0.71	0.8	0.98	0.77	0.31
A_s (m^2 ha^{-1})	5.5	6.6	8	9.4	20.4	11.2
LAI_T	0.61	–	0.9	0.96	2.76	1.68
LAI_T/A_s	0.11	–	0.11	0.1	0.14	0.15
E/LAI_T	0.99	–	0.89	1.02	0.28	0.18
Relative sensitivity G_c	–	–	–	0.63	0.7	0.46

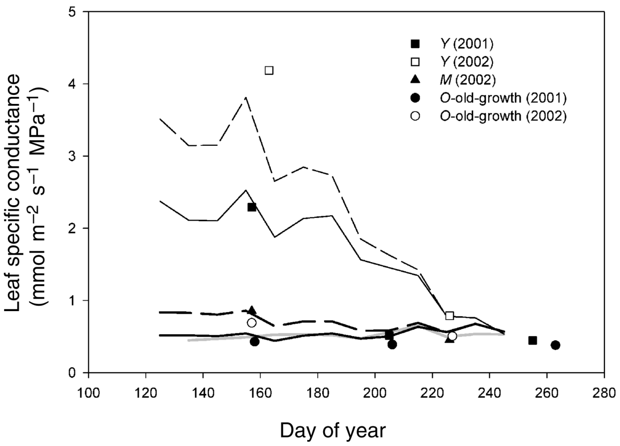

Figure 2. Seasonal dynamics of leaf specific conductance including modeled estimates assuming a constant gravitationally corrected daily minimum leaf water potential of –1.7 MPa for ponderosa pine stands (young (*Y*) = fine solid line; mature (*M*) = heavy solid line; and *O*-old-growth = grey solid line), and a seasonally decreasing daily minimum leaf water potential (–1.3 to –1.7 MPa between June and mid-August, *Y* = fine dashed line and *M* = heavy dashed line).

was ~8-fold that of the 250-year-old trees at *O* and ~3.5-fold that at *M* (Figure 3). The sensitivity of G_c to $\ln D$ expressed relative to the magnitude of G_c at low *D* ($-dG_c/d\ln D$ to G_c at *D* of 1 kPa) was not constant across the different age stands (Table 3). The relative sensitivity of G_c was lowest for old-growth trees (0.46), lower than the previously reported generic value of 0.6 based on a hydraulic model that assumes tight stomatal regulation of leaf water potential (Oren et al. 1999). The relative sensitivity of G_c to *D* at *M* was the highest at 0.70, whereas the value at *Y* was 0.63, suggesting age-specific hydraulic behavior.

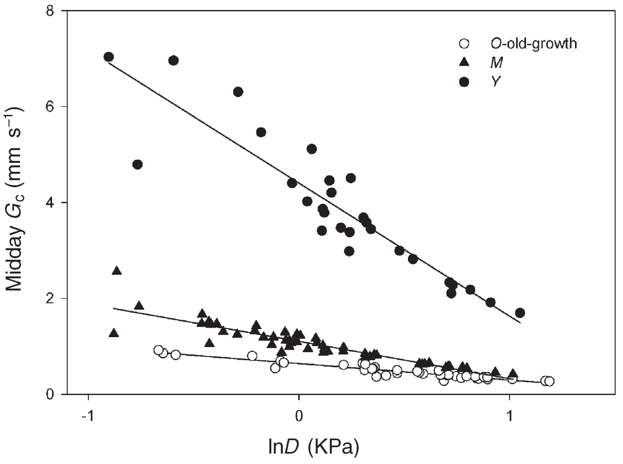

Figure 3. Response of midday canopy stomatal conductance (G_c) to the natural logarithm of midday air vapor pressure deficit (*D*). Data are presented only from the days with non-limiting light (PAR > 1600 μmol m^{-2} s^{-1}) and non-limiting soil water (data after Day 190 excluded at young (*Y*) and mature (*M*) ponderosa pine stands). Overlaid lines are linear regressions by tree age class.

Feedbacks between tree-level controls and site water balance

Tree transpiration Maximum seasonal rates of transpiration were comparable across stands at about 1 mm day^{-1} except at *Y* during 2002, where rates peaked at 1.4 mm day^{-1} (Figures 4a–c). Transpiration at each stand showed distinct seasonal patterns and inter-annual variability that was reflected in the measurements of soil water potential. The *O* stand showed the least inter-annual variability, with maximum transpiration rates occurring during mid- to late July; rates during the unusually dry summer of 2001 were less than those of other years, reflecting a decrease in soil water potential to less than –0.9 MPa (Figure 4f). At *Y*, inter-annual variability was large; maximum seasonal transpiration rates occurred in late May during 1999 and 2001, and during late June in both 2000 and 2002. In all years, soil water potential declined to less than –0.9 MPa, the apparent threshold for soil water limitations on transpiration at *O*. Among stands, the seasonal rate of decline of soil water potential was greatest at *M* (Figure 4e). When averaged over multiple years, it is evident that, between April and mid-July, tree transpiration at *Y* exceeded that at *O* (Figure 5). For the remainder of the season, tree transpiration at *O* surpassed that at *Y*, and by late August, tree transpiration was barely detectable at *Y* and *M*, whereas transpiration at *O* continued into November. Therefore, if young trees transpire water faster than older trees and there is a seasonal drought, the young trees run out of water sooner than the older trees.

Although the three stands showed a threefold range in $\mathrm{LAI_T}$ (Table 3), cumulative tree transpiration between Days 110 and 270 (the period during which ~70% of annual LE exchange occurs), when averaged across all years, showed only small differences among the *Y*, *M* and *O* stands with values of 100, 112 and 107 mm, respectively.

To indicate the degree of confidence in the estimates of plot transpiration, we used the upper 95% confidence intervals (CI) of both the measured sap flux over the outer 20 mm of sapwood and the sap fluxes at the various sapwood depths in the scaling calculations. Statistically robust error propagation requires combining the variability of such measurements with estimates of covariance between such measurements (Oren et al. 1998); however, this information was unavailable across all the measured trees. We consider that simply using the 95% CI values of these two significant sources of variation provides an indication of the confidence of the transpiration estimates. At *Y*, using the 95% CI for sap flux in the outer sapwood in the scaling calculations would increase transpiration estimates by 18% and using the 95% CI values of sap flux at each sapwood depth would result in a 14% greater estimate of tree transpiration. At *M*, transpiration estimates would increase by 14 and 16%, respectively, because of these sources of variability. At *O*, insufficient data on the variability of sap flux at different sapwood depths prevented the evaluation of the 95% CI for transpiration estimates; however, a qualitative assessment of the variability between radial sap flux profiles in two old-growth trees over four depths showed closer agreement than those presented in Figure 1 (Irvine et al. 2002). Employing the 95% CI for sap flux in the outer sapwood would result in a 14

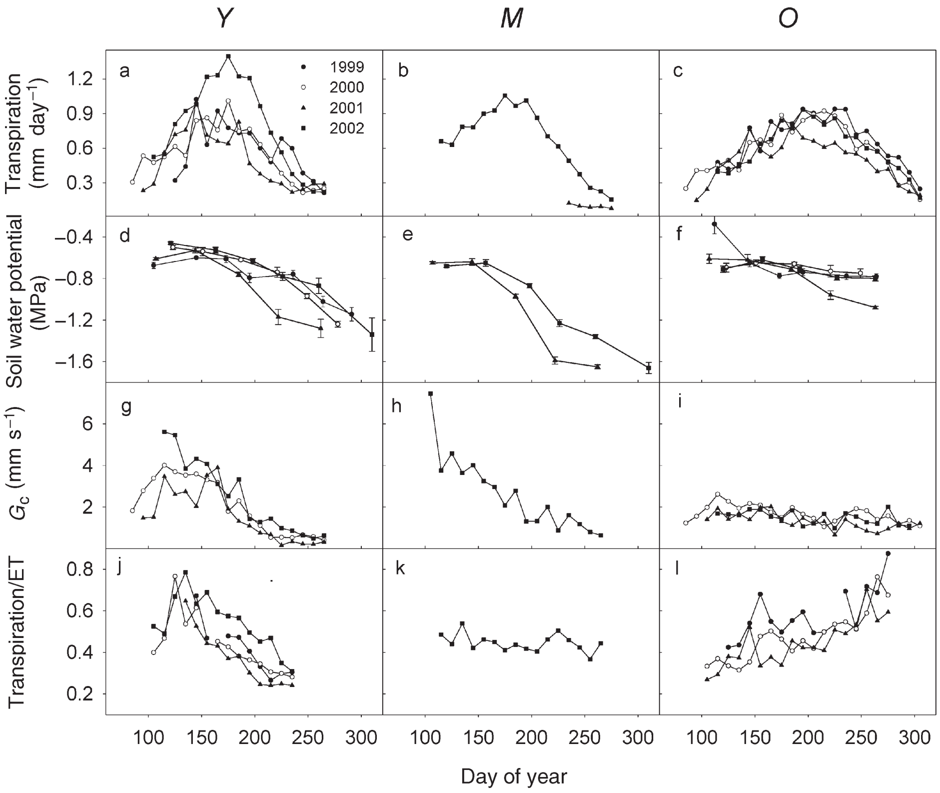

Figure 4. Seasonal variations in tree transpiration, soil water potential inferred from predawn foliage water potential, midday canopy stomatal conductance expressed on a ground area basis (G_c) and the fraction of site evapotranspiration (ET) from tree transpiration over a 4-year period across young (*Y*), mature (*M*) and old (*O*) ponderosa pine stands. Variables were 10-day block-averaged (bars indicate ± 1 SE).

and 23% increase in transpiration estimates for the 250-year-old and the 90-year-old trees at *O*, respectively.

Leaf specific conductance The differences between stands in seasonal patterns of tree transpiration were driven by seasonally decreasing K_L (Figure 2). Between spring and late summer, only a small decline in K_L was observed in the old-growth trees (11 and 28% reduction in 2001 and 2002, respectively), a larger decline at *M* (46% in 2002) and a substantial reduction at *Y* (80 and 81% reduction in 2001 and 2002, respectively). The modeled estimates of K_L (overlaid lines Figure 2) were generated based on 10-day means of midday transpiration (1100 to 1300 h) and soil water potential estimated by linear interpolation between periodic measurements. We assumed that midday foliage water potential (less the gravitation component) was either constant throughout the season at –1.7 MPa (all stands, Figure 2 solid lines) or underwent a seasonal decline, falling from –1.3 to –1.7 MPa between early June and mid-August (only *Y* and *M*, Figure 2 broken lines). A constant leaf water potential would be expected to maximize gas exchange across the season, whereas a falling trend is more representative of what was observed at *Y* and *M* where midday water potential fell significantly ($P < 0.01$) between June and August. The modeled estimates of K_L accounted for the seasonal dynamics of leaf area. In addition, the influence of seasonal changes in temperature on K_L (due to temperature driven changes in the viscosity of water) were removed by expressing K_L to a constant temperature (20 °C).

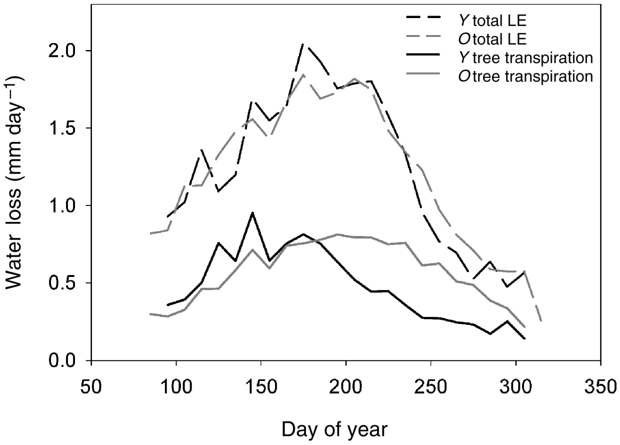

Figure 5. Seasonal trends in total latent energy exchange (broken lines) and the contribution from tree transpiration (solid lines) at the *Y* (black lines) and *O* (gray lines) stands averaged between 1999 and 2001. Variables were 10-day block means.

Interactions between vegetation-level control of transpiration and evaporation

Latent energy measurements were unavailable across all years at all the stands. We therefore restricted seasonal comparison of LE fluxes to a comparison of the mean of 3 years of data (1999–2001) at *Y* and *O* stands (Figure 5). The patterns of LE were similar at *Y* and *O* stands, largely masking the substantial differences in tree transpiration. The distinct seasonal patterns of transpiration across the three stands resulted in widely varying season patterns of the contribution of tree transpiration to LE (Figures 4j–l, Figure 5). Between May and September (averaged across years), the fraction of LE from tree transpiration decreased from 70 to 29% at *Y*, increased from 33 to 64% at *O*, and remained almost constant at *M* (46 to 41%, 2002 data). Measurements made with below-canopy eddy-covariance equipment at *Y* during July 2001 indicated that 74% of LE fluxes originated from below 1.75 m height (D.D. Baldocchi, University of California, Berkeley, personal communication), 66% of the leaf area below this height was shrub foliage (Law et al. 2001*b*) and soil evaporation accounted for only 9% of LE (F.M. Kelliher, personal communication), suggesting that, during late summer at this stand, shrub transpiration accounts for the majority of the LE fluxes.

Measurements of soil water content during the period of soil drying between April and September indicated that a significant fraction of water was extracted from below 80 cm depth at all stands. Water budget calculations suggest that 21, 45 and 47% of water used was extracted from below this depth at *Y*, *M* and *O*, respectively.

Mean precipitation between 1999 and 2002 was 440 and 419 mm at *Y* and *O*, respectively. The *M* stand is about 1 km from the *Y* stand and likely receives similar annual precipitation. Mean annual LE fluxes over 3 years were 363 and 377 mm at *Y* and *O*, respectively, and 376 mm for 2002 at *M*; consequently, LE fluxes from these three stands account for something like 83 to 90% of annual precipitation. The total LE values were remarkably similar across sites despite differential contributions from shrubs and soil evaporation.

Relationships between tree water use and ecosystem carbon dioxide and water vapor exchange

Because GEP data were collected simultaneously only at the *Y* and *O* stands, we restricted our seasonal analysis of GEP to these sites. The seasonal pattern of GEP at the *Y* stand was strongly correlated with tree transpiration and declined between June and November (Figure 6). Although transpiration from understory shrubs at this stand accounted for the majority of transpiration later in the summer, this was not obviously reflected in the seasonal pattern of GEP. The correlation of GEP and tree transpiration at *O* exhibited a seasonal hysteresis. Such a pattern would be consistent with the saturating response of transpiration to VPD in conjunction with lower VPD during spring that would be associated with higher stomatal conductance, resulting in higher water-use efficiency during these months. This pattern was masked at *Y* by the large seasonal decline in canopy conductance.

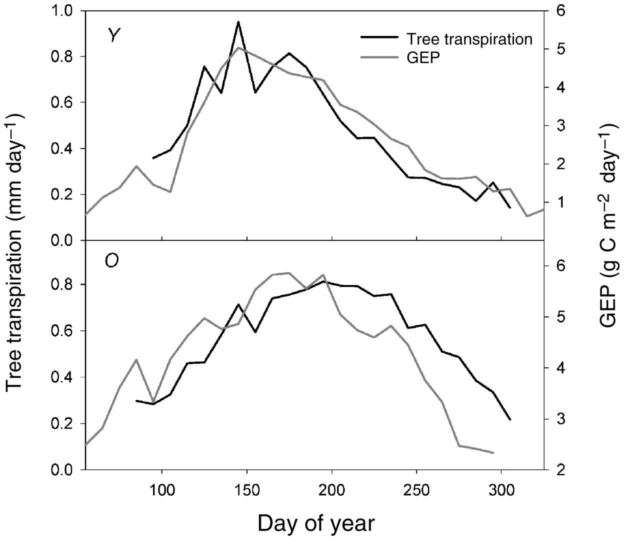

Figure 6. Seasonal dynamics of tree transpiration (black lines) and gross ecosystem productivity (GEP) (grey lines) averaged between 2000 and 2001 at the young (*Y*) and old-growth (*O*) ponderosa pine stands. Variables were 10-day block averaged.

During late May, when trees at *Y* were transpiring at their maximum, GEP was comparable among stands; at all other times, GEP was considerably greater at *O* (Figures 6 and 7). At *Y*, the seasonal pattern of GEP between stands was tightly correlated with the decline in tree transpiration. The ratio of LAI_S at *Y* to LAI_S at *O* was about 0.50, indicating that, on a leaf area basis, *Y* was fixing about twice as much carbon as *O* during late May when soil water was not limiting. By September, *Y* was fixing about the same amount of carbon per unit leaf area as *O*.

Integrated over the growing season, GEP was highest at the *M* stand, 15% lower at the *O* stand and 46% lower at the *Y* stand (Table 4). Accumulated tree transpiration and LE fluxes were similar across sites. Site-level water-use efficiency computed from GEP and LE was similar for the *O* and *M* stands but was substantially lower for the *Y* stand, which has not yet reached maximum potential leaf area and productivity for the area, and appears to be more vulnerable to drought.

Table 4. Summary of growing season (Days 110–270) cumulative gross ecosystem production (GEP), tree transpiration, total water vapor exchange (LE) and ecosystem water-use efficiency (WUE) in young (*Y*), mature (*M*) and old-growth (*O*) ponderosa pine stands.

Site	GEP[1] (g C m^{-2})	Transpiration[2] (mm)	LE[1] (mm)	WUE (g C m^{-2} mm^{-1})
Y	549	100	229	2.4
M	1016	113	254	4.0
O	865	108	231	3.7

[1] For the *Y* and *O* stands, data were averaged over 2000–2001 seasons, for *M* stand 2002 only.
[2] For the *Y* and *O* stands, data were averaged between 1999 and 2002, for *M* stand 2002 only.

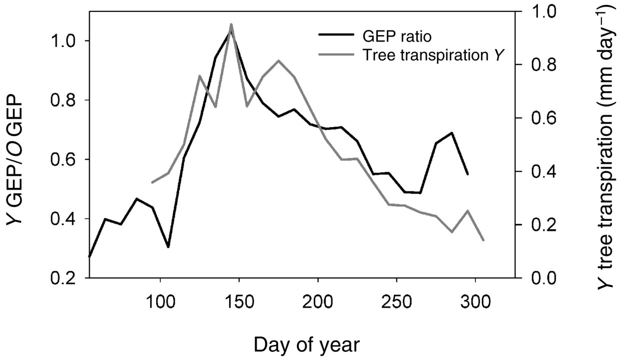

Figure 7. Seasonal trends in the ratio of young (*Y*) to old-growth (*O*) ponderosa pine gross ecosystem productivity (GEP) averaged across 2000–2001, shown in relation to the decline in tree transpiration at *Y* averaged across 1999–2001. Variables were 10-day block averaged.

Discussion

We investigated the extent to which structural and functional differences affect the exchange of water and carbon in ponderosa pine forests ranging in age between 25 and 250 years. We found that, although LAI_T varied by a factor of three across the three stands of different ages, there were no substantial differences in the cumulative tree transpiration between mid-April and the end of September (the period during which ~70% of annual LE exchange occurs). The seasonal pattern of tree water use, however, varied across the stands in a manner consistent with age-specific hydraulic properties. The tree-age-related patterns of transpiration were reflected in the seasonal patterns of carbon uptake.

Under conditions of non-limiting water supply, trees at *Y* transpired five times as much water per unit leaf area as trees at *O*, such that before July, tree transpiration was greater at *Y* than at *O*. These high rates of water use by the young trees were made possible by an almost sixfold difference in K_L between the 250-year-old and 25-year-old trees. Such differences in K_L with tree age have been observed in both conifers and broadleaf species (Ryan et al. 2000, Schafer et al. 2000, McDowell et al. 2002), with the greatest changes occurring among the younger age classes (Mencuccini and Grace 1996*b*). High rates of tree transpiration during spring at *Y* resulted in comparable GEP at *O* during this period even though LAI_S at *Y* was about half that at *O*.

The greater inter-annual variability in the patterns of transpiration that we observed at *Y* than at *O* indicates that young trees are able to respond to inter-annual variability in water availability to maximize growth. However, rapid use of available water risks potential hydraulic dysfunction through cavitation and embolism formation in the xylem (Tyree and Sperry 1988), as may have been observed by Goldstein et al. (2000) in a young plantation of ponderosa pine in California.

The study of the sensitivity of G_c to $\ln D$ expressed relative to the magnitude of G_c at low VPD ($-dG_c/d\ln D$ to G_c at VPD of 1 kPa) suggested tree age-related variability of the relative sensitivity of stomatal conductance to VPD (Table 3). The *M* stand showed a more sensitive (relative) response of G_c to VPD than would be predicted from a simple hydraulic model (Oren et al 1999). At this stand, hydraulic conductance may increase during the day, such that a greater stomatal response to VPD would be required to maintain a constant soil-to-leaf water potential gradient. The stand showed the most rapid seasonal depletion of soil water, and considering the highly sandy nature of the soil, it is possible that diel increases in resistance across the rhizosphere soil interface could occur as a result of diel patterns of soil water extraction through tree transpiration. Examination of stomatal sensitivity to VPD may be a useful tool for exploring possible effects of soil type on carbon uptake through dynamic changes in the hydraulic resistance of the soil–plant system. The lower relative stomatal sensitivity to VPD observed in the old-growth trees than would be predicted from a simple hydraulic model suggests less rigid stomatal response to VPD in this age class of tree, allowing for greater declines in leaf water potential with increases in VPD. This behavior would allow more extended periods of carbon fixation with increasing VPD, a mechanism that could partially offset the effects of the age-related decline in hydraulic conductance on carbon uptake.

The transpiration rates that occurred during spring at *Y* were not sustainable in the drought-prone environment, and we observed an age-related seasonal reduction in K_L across the sites, with the largest reduction of ~80% at *Y* between June and August. Although the differences in the seasonal nature of K_L and tree transpiration among the sites were striking, the seasonal patterns of LE fluxes across the stands were more comparable. These patterns were driven by both a combination of age-related differences in ecosystem structure and hydraulic pathway resistance. At *Y*, the seasonal decline in tree transpiration was offset by shrub transpiration later in the summer. By July, soil water evaporation accounted for only 9% of total LE fluxes at *Y*, with three quarters of the LE fluxes originating from below 1.75 m height, a height below which shrub foliage accounted for two thirds of the LAI_S. At *M*, the seasonally conservative nature of the ratio of tree transpiration to LE was driven by an approximately equivalent seasonal reduction in tree transpiration and below-canopy evapotranspiration. There is a minimal shrub layer at this site and at *O*. At *O*, tree transpiration accounted for an increasing fraction of LE across the season. Previous below-canopy eddy-covariance measurements made at this site would support such a pattern, although estimates of the contribution of LE from below the tree canopy were greater in that study (Anthoni et al. 1999). It is possible that, at this site, the patchy bracken fern understory that is not seen at the other sites may play a role in characterizing this seasonal pattern. The LAI of this patchy seasonal component of the understory is minimal, but the stomatal response of bracken to air VPD is weak (Roberts et al. 1984), such that, under conditions of high VPD that are typically observed at the *O*, bracken fern may account for a disproportionate contribution to LE fluxes as the soil surface dries early in the summer before the bracken senesces. Whether the similarity of the LE fluxes among stands encompassing the extremes in forest age and stand structure can be considered a more general phenomenon remains to be established. Further studies are needed to examine such relationships across a wider range of seasonally water-limited stands.

Although it is evident that changes in stand structure and the inherent age-related hydraulic properties of the individual trees played an important role in determining the nature of the carbon exchange across the stands of different ages, they appeared to play a less significant role in shaping the total LE fluxes from the different stands. Total water use across sites was similar and constrained by low annual precipitation. Much of the influence of tree size or age-related hydraulic properties was manifested through the differing seasonal use of this water as driven by the differing seasonal nature of K_L across the stands of different ages. It remains to be resolved exactly where in the soil-plant-atmosphere continuum these changes in resistance occur, and whether the apparent age-related variability in these patterns occur more universally or are in part related to site conditions. Limited measurements at *Y* suggest that much of the seasonal increase in hydraulic resistance may reside in the soil or root component of the system. Consequently studies that focus on understanding tree-age-related hydraulic behavior should include efforts at understanding the belowground aspects of these systems as this may be the weak hydraulic link in seasonally water-limited ecosystems.

The ecosystem-level data that we collected for these sites allowed us to examine how the different tree-level responses translate to whole-ecosystem responses across the growing season. Although canopy stomatal conductance was more constrained across the entire season at the *O* stand, the greater leaf area at this stand resulted in higher GEP when averaged across the entire season compared with the *Y* stand. The importance of leaf area on GEP was also evident at the *M* stand. This stand showed a similar seasonal decline in canopy stomatal conductance to the *Y* stand, but had the highest LAI and growing season GEP of all three stands.

It has been shown that monthly GEP is linearly related to total water vapor exchange across a wide range of forest sites (Law et al. 2002), but our data suggest that the water-use efficiency of the youngest stand was ~60% that of the older stands. Such observations in conjunction with the seasonally contrasting patterns of GEP would suggest that to model and predict carbon exchange accurately at the regional scale will require approaches that recognize stand-age-specific behavior.

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