Structural and compositional controls on transpiration in 40- and 450-year-old riparian forests in western Oregon, USA

GEORGIANNE W. MOORE,[1–3] BARBARA J. BOND,[1] JULIA A. JONES,[4] NATHAN PHILLIPS[5] and FREDERICK C. MEINZER[6]

[1] *Forest Science Department, Oregon State University, Corvallis, OR 97331, USA*

[2] *Present address: Texas A&M University, Uvalde Research and Extension Center, 1619 Garner Field Road, Uvalde, TX 78801, USA*

[3] *Corresponding author (gwmoore@ag.tamu.edu)*

[4] *Geosciences Department, Oregon State University, Corvallis, OR 97331, USA*

[5] *Geography Department, Boston University, Boston, MA 02215, USA*

[6] *USDA Forest Service, Forestry Sciences Laboratory, Corvallis, OR 97331, USA*

Summary   Large areas of forests in the Pacific Northwest are being transformed to younger forests, yet little is known about the impact this may have on hydrological cycles. Previous work suggests that old trees use less water per unit leaf area or sapwood area than young mature trees of the same species in similar environments. Do old forests, therefore, use less water than young mature forests in similar environments, or are there other structural or compositional components in the forests that compensate for tree-level differences? We investigated the impacts of tree age, species composition and sapwood basal area on stand-level transpiration in adjacent watersheds at the H.J. Andrews Forest in the western Cascades of Oregon, one containing a young, mature (about 40 years since disturbance) conifer forest and the other an old growth (about 450 years since disturbance) forest. Sap flow measurements were used to evaluate the degree to which differences in age and species composition affect water use. Stand sapwood basal area was evaluated based on a vegetation survey for species, basal area and sapwood basal area in the riparian area of two watersheds. A simple scaling exercise derived from estimated differences in water use as a result of differences in age, species composition and stand sapwood area was used to estimate transpiration from late June through October within the entire riparian area of these watersheds. Transpiration was higher in the young stand because of greater sap flux density (sap flow per unit sapwood area) by age class and species, and greater total stand sapwood area. During the measurement period, mean daily sap flux density was 2.30 times higher in young compared with old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees. Sap flux density was 1.41 times higher in young red alder (*Alnus rubra* Bong.) compared with young *P. menziesii* trees, and was 1.45 times higher in old *P. menziesii* compared with old western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees. Overall, sapwood basal area was 21% higher in the young stand than in the old stand. In the old forest, *T. heterophylla* is an important co-dominant, accounting for 58% of total sapwood basal area, whereas *P. menziesii* is the only dominant conifer in the young stand. Angiosperms accounted for 36% of total sapwood basal area in the young stand, but only 7% in the old stand. For all factors combined, we estimated 3.27 times more water use by vegetation in the riparian area of the young stand over the measurement period. Tree age had the greatest effect on stand differences in water use, followed by differences in sapwood basal area, and finally species composition. The large differences in transpiration provide further evidence that forest management alters site water balance via elevated transpiration in vigorous young stands.

Introduction

Forest management in the Pacific Northwest has led to large shifts in stand ages. In western Oregon forests, for example, almost 20% of the total 4.6 million hectares of forest was clear-cut between 1972 and 1995 (Cohen et al. 2002). Fundamental differences in structure and composition that alter ecosystem function occur as a consequence of changes in the age class of forest cover. We examined whether such changes can alter stand-level transpiration. Because evapotranspiration is such a large component of the water budget in forested lands (Hewlett 1982), it is critical to understand how changes in transpiration, combined with other elements of the water cycle, affect site water balance.

There are multiple reasons why young mature trees can potentially transport water more efficiently (i.e., more flow per unit leaf area or cross-sectional sapwood area) than old trees of the same species in similar environments. For example, changes in stem and branch hydraulics with age (Domec and

Gartner 2001, McDowell et al. 2002*b*) may decrease the maximum rate at which old trees can transport water and increase stomatal sensitivity to vapor pressure deficit (Hubbard et al. 1999). Evidence suggests that old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and *Pinus* spp. have lower whole-tree leaf-specific hydraulic conductances than young trees of the same species (Yoder et al. 1994, Hubbard et al. 1999, Phillips et al. 2002), and are more vulnerable to cavitation (Domec and Gartner 2002). However, decreased leaf area:sapwood area ratio with age (a_l:a_s, McDowell et al. 2002*a*) tends to offset the differences in whole-tree leaf-specific hydraulic conductance. Some age- or size-related changes in water use can be attributed to factors directly associated with height, such as the pressure gradient due to gravity and increased hydraulic resistance (Ryan and Yoder 1997, Ryan et al. 2000). Also, as trees progress from juvenile to young mature stages, roots may access increasingly deeper water reserves (Irvine et al. 2002), although this process may only be important during the early developmental stages.

If young mature trees use more water per unit sapwood area than old trees, do young mature forests use more water than old-growth forests on a ground area basis, or do changes in species composition or stand density compensate for the age-related changes? Changes in species composition with stand age may affect stand-level transpiration independently of changes in stand-level sapwood area or leaf area. There is abundant evidence for physiological differences between species at the leaf scale (e.g., Running 1976, Bond and Kavanagh 1999). At the whole-plant scale, sap flow measurements have revealed that co-occurring species respond differently to drought (Cienciala et al. 1998), with varying sensitivities to soil water content and vapor pressure deficit (Pataki et al. 1998, 2000). Different species may also access different soil water reserves (Čermák et al. 1995, Cienciala et al. 1998, Stratton et al. 2000). However, it is not known if differences between species at the leaf and whole-tree levels result in differences at the stand scale.

The magnitude and seasonal timing of water use in Pacific Northwest forests may change as species composition changes through succession (Franklin and Hemstrom 1981, Bredensteiner 1998). In the Pacific Northwest and many temperate ecosystems, young mesic or riparian forests typically have a greater abundance of angiosperms compared with older, late successional forests. Mesic angiosperms typically have the ability to transport more water per unit of sapwood area than conifers because their xylem contains vessels whereas conifer xylem does not (Jarvis 1975). Because deciduous angiosperms are leafless during the winter, potential transpiration varies more widely in deciduous forests than in coniferous forests as a function of seasonal dynamics in leaf area, although large changes in leaf area may also occur from spring through fall in coniferous forests as new needle cohorts are formed and the oldest needle cohorts are lost. In contrast with young forests, late successional forests are increasingly dominated by slow-growing shade-tolerant species. Slow-growing species probably use less water—at least while they are in the understory—although it is not known what happens when they become components of the overstory.

Total basal area is typically much higher in old forests than in young forests, but sapwood basal area may be less (Dunn and Connor 1993). At the stand scale, forest succession leads to differences in tree spacing and crown diameters that can either increase or decrease transpiration. As forests age, self-thinning reduces stem density after canopy closure occurs, which alters stand-level a_l:a_s while tree diameters gradually increase (Callaway et al. 2000). Thinning experiments have demonstrated that trees compensate for reduced stem density by expanding crowns and increasing a_l:a_s (Whitehead et al. 1984, Morikawa et al. 1986).

Other structural differences between young and old forests may also be important to transpiration. For example, the profound changes in both the amount and vertical distribution of leaf area that can occur as stands age can alter canopy conductance. Leaf area index (LAI) typically increases with stand age, but LAI declines in some late successional forests (Ryan et al. 1997). Leaf area index is often considered the most important determinant of differences in transpiration among different forest stands (Hewlett 1982). Generally, young forests (e.g., *P. menziesii* forests of the Pacific Northwest) have most of their leaf area in a single canopy layer, whereas old-growth forests are characterized by more evenly distributed vertical leaf area profiles (Parker et al. 2002). These changes in stem and leaf distribution may have marked effects on transpiration from canopies. In this study, we considered changes in LAI but not distribution of leaf area within canopies.

The objectives of this study were to evaluate the effects of *P. menziesii* age, species composition and sapwood area on transpiration in the riparian areas of two forests, an old-growth coniferous stand (about 450 years since disturbance) and a vigorously growing young coniferous stand (about 40 years since disturbance). We used a simple scaling exercise to estimate potential differences in water use at the stand level, based on the general approach:

$$E = fA \qquad\qquad\qquad (1)$$

where E is transpiration, or sap flow per unit ground area, f is sap flux density and A is sapwood area per unit ground area.

We predicted that younger *P. menziesii* trees would exhibit higher sap flux densities during the growing season than old trees, based on previous evidence in similar forests (Phillips et al. 2002). There is evidence, as cited above, to suggest that angiosperms (more abundant in young forests) may use more water per unit sapwood than conifers. Shade-tolerant species (more abundant in old forests) use less water per unit sapwood while in the understory than shade-intolerant species, but it is unknown whether these differences persist when the shade-tolerant species emerge into the overstory. Total basal area is greater in older stands than in younger stands, but sapwood basal area and LAI could be either greater or less. This case study was designed to examine these structural and compositional alternatives in a 40- and a 450-year-old riparian forest.

Methods

Study area

Our study was conducted at the H.J. Andrews Experimental Forest, located in the western Cascades of central Oregon, USA (44.2° N, 122.2° W). Two main study sites were established in riparian areas (defined here as within a 100-m swath centered on the stream within which the vegetation survey was conducted) of adjacent watersheds (Figure 1). The vegetation of Watershed One (WS01) was harvested in the mid 1960s; the regenerating young forest consists primarily of *P. menziesii*, but also has a significant angiosperm component. Watershed Two (WS02), whose last major disturbance occurred around 450 years ago, has a mix primarily of old-growth *P. menziesii* and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Swanson and James (1975) described the local geology and geomorphology, where the predominant soil type is classified as gravelly clay loam. The western Cascades have a maritime climate, with wet mild winters and dry cool summers (mean annual rainfall is 2300 mm). Mean monthly temperature ranges from about 1 °C in January to 18 °C in July. The growing season extends from late April until late September.

Climate

Climatic conditions were monitored at a nearby weather station (H.J. Andrews Primary Meteorological Station) within 0.75 km of the study area. Meteorological data sets were provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon

Xylem sap flow

During the growing season, sap flow was measured with constant-heat sap flow sensors (Granier 1987) in seven *P. menziesii* and seven red alder (*Alnus rubra* Bong.) trees in the young stand, and in three *P. menziesii* and three *T. heterophylla* trees in the old stand. Power was supplied by solar panels. The need for close access to a canopy gap for maximum solar exposure restricted our sampling design. Trees were selected along a 60-m transect normal to the stream near the base of each watershed (see Figure 1). Sensors were installed at two to five positions around the circumference of each tree at radial depths of 0 to 20 (outer sapwood) or 20 to 40 mm (inner sapwood) at a height of ~0.5 m in the young trees and ~5 m in the old growth trees in order to minimize potential influences of buttressing. More extensive radial and circumferential sampling in individual trees offset the lower sample size of trees in the older stand. Specific information about individual measurement trees is presented in Table 1. Instantaneous measurements taken at 30 s intervals were averaged every 20 min and recorded on a data logger (CR10X, Campbell Scientific, Logan, UT).

We scaled measurements from individual sensors to mean whole-tree flux per unit sapwood per day. First, sapwood depths were measured at the height of the sap flow sensors on each tree by visual examination of a 5 mm-diameter core (Table 1). For *A. rubra*, a 0.2% safranin dye injection was used to facilitate visual assessment of sapwood depth. To account for radial patterns in sap flux, in *T. heterophylla*, a linear decline to zero was used to estimate fluxes in sapwood between 20 mm and the heartwood boundary based on our own observations from these trees plus an additional six trees with radial profiles of flow measured at 20, 50, 100 and 150 mm (F. Meinzer, unpublished data) with variable length constant heat sensors (James et al. 2002). In *P. menziesii*, the relationship between inner ring sap flux (15–35 mm beneath cambium) to outer ring sap flux (0–20 mm beneath cambium) and diameter at breast height (DBH) from Phillips et al. (2002) was used to account for radial patterns in sap flux. Our observations of radial patterns of sap flux in *P. menziesii* fell within the range reported by Phillips et al. (2002). We assumed that there was no change in flux between the depth of the inner sensor and the heartwood boundary. Because sapwood depth is rarely much greater than 40 mm in *P. menziesii* (the range in the trees we measured was 28 to 56 mm), any errors introduced will be small. In *A. rubra*, the average relationship between inner ring sap flux (20–40 and 40–60 mm beneath cambium) and outer ring sap flux (0–20 mm beneath the cambium) in the four trees with inner sensors (Table 1) was used to account for radial patterns in sap flux in the remaining three trees. The flux within each ring of sapwood was calculated as the product of the area of that ring and the measured or predicted flux; then we
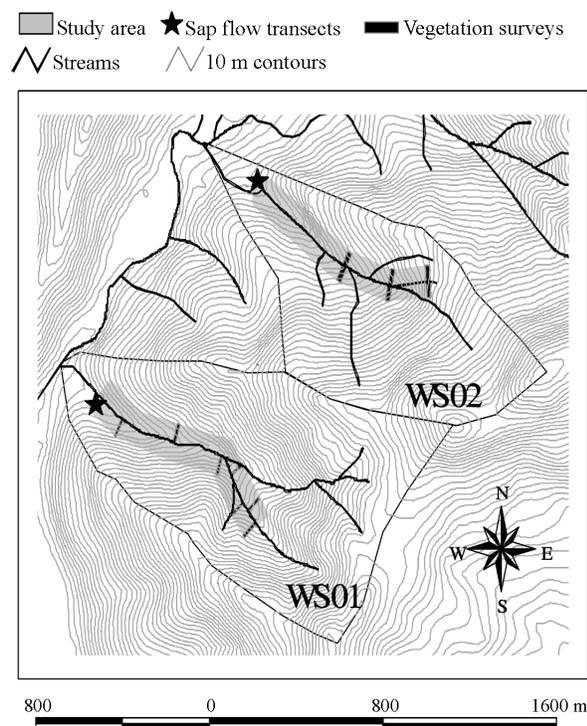

Figure 1. Map of study site locations. Abbreviations: WS01 is the young stand (~40 years since disturbance) and WS02 is the old stand (~450 years since disturbance). Topographic and stream coverages were provided by the Forest Science Data Bank, a partnership between the Department of Forest Science, Oregon State University, and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, Oregon.

Table 1. Specific information about trees in which sap flow measurements were made. Outer sensors were in the outer 0 to 20 mm of xylem; inner sensors were in the inner 20 to 40 mm of xylem, except in four *A. rubra* trees where an additional sensor was placed from 40 to 60 mm (*). Numbers in parentheses are standard errors based on three cores in the old growth trees and two cores in the young *P. menziesii*. Abbreviations: Ht. = height; Diam. = diameter at breast height; SD = sapwood depth; SBA = sapwood basal area; N-Outer = number of outer sensors; and N-Inner = number of inner sensors.

Age class	Species	Ht. (m)	Diam. (m)	SD (mm)	SBA (m^2)	N-Outer	N-Inner
Old growth	*Pseudotsuga menziesii*	59.4	1.41	56 (9)	0.212	3	2
Old growth	*Pseudotsuga menziesii*	79.3	1.56	54 (5)	0.218	3	2
Old growth	*Pseudotsuga menziesii*	63.1	1.27	42 (4)	0.146	3	0
Old growth	*Tsuga heterophylla*	46.8	0.60	97 (16)	0.144	3	2
Old growth	*Tsuga heterophylla*	41.0	0.59	93 (10)	0.134	3	2
Old growth	*Tsuga heterophylla*	44.5	0.75	102 (18)	0.193	3	1
Young	*Pseudotsuga menziesii*	27.9	0.27	35 (14)	0.022	2	1
Young	*Pseudotsuga menziesii*	24.3	0.22	37 (11)	0.018	2	1
Young	*Pseudotsuga menziesii*	24.8	0.30	35 (19)	0.026	2	1
Young	*Pseudotsuga menziesii*	21.7	0.22	36 (0.7)	0.018	2	1
Young	*Pseudotsuga menziesii*	18.0	0.17	28 (13)	0.010	2	1
Young	*Pseudotsuga menziesii*	25.7	0.28	36 (13)	0.025	2	1
Young	*Pseudotsuga menziesii*	27.2	0.27	40 (8)	0.025	2	1
Young	*Alnus rubra*	27.7	0.35	85	0.066	2	0
Young	*Alnus rubra*	27.3	0.32	80	0.056	2	0
Young	*Alnus rubra*	16.9	0.24	66	0.032	2	2 *
Young	*Alnus rubra*	25.5	0.29	135	0.059	2	2 *
Young	*Alnus rubra*	17.8	0.26	111	0.045	2	2 *
Young	*Alnus rubra*	18.6	0.32	140	0.071	2	2 *
Young	*Alnus rubra*	24.0	0.28	142	0.053	2	0

summed the fluxes for each sapwood depth to estimate total flux per tree. Finally, for all species, total flux per tree was divided by total sapwood area to estimate mean flux per unit sapwood area for each tree. These calculations were performed for each 20-min time step. Total daily fluxes are the summation of the 20-min observations. This paper focused on daily totals because of our primary interest in differences in seasonal stand-level water use. Details of water flux dynamics at the sub-daily level will be presented in a future paper.

In some cases, especially late in the season when the number of sensors was restricted by power limitations, individual sensors were not functional over periods of several days. We interpolated to fill the missing data (around 10%) based on relationships among the sensors when all functioned properly.

Estimates of sap flow based on the constant heat measurement approach are sensitive to natural temperature gradients between sensors in the absence of applied heat (Do and Rocheteau 2002). The maximum potential effect on sap flow estimates caused by background temperature gradients was evaluated and found to be detectable yet small. Based on measurements taken of background temperature gradients during six, warm sunny days in July, we found that sap flow may be underestimated by a maximum of 3.7 ± 0.5 and $0.2 \pm 0.5\%$ per day in young and old *P. menziesii*, respectively, and overestimated by a maximum of $6.0 \pm 1.1\%$ in *T. heterophylla* during the month of July. Therefore we did not correct estimated sap flow for errors caused by temperature gradients.

Vegetation survey

To estimate species composition and sapwood basal area in the study areas, we sampled vegetation along transects that ran normal to the stream at the same distance from the stream as the sap flow transects (Figure 1, rectangular bars). In WS01, 50-m transects containing five contiguous 10×10 m plots were established about every 200 m on alternating north and south sides of the stream, beginning at a random location near the mouth of the watershed for a total of seven transects. In WS02, 60-m transects containing three contiguous 20×20 m plots were established about every 200 m on the north and south sides of the stream, beginning at a random location near the mouth of the watershed for a total of six transects. We used a larger plot size in the old growth stand because the trees were much larger than the trees in the young stand. All of the above spatial dimensions are given in horizontal distances (i.e., corrected for slope angle). In each plot, species and DBH (1.37 m) were recorded for each woody plant greater than 0.01 m in diameter. In each plot, for each species larger than about 0.08 m DBH, height and sapwood depth (based on visual inspection of a 5 mm-diameter tree core) were recorded for up to five individuals. For each tree in each plot, sapwood basal area was calculated or estimated based on measured trees. Estimated sapwood basal area was categorized into functional groups representing the classes we used for sap flow measurements: gymnosperms and angiosperms in the young stand, and *P. menzesii*, *T. heterophylla* and angiosperms in the old stand.

Leaf area index

Leaf area index was estimated with an LAI 2000 (Li-Cor, Lincoln, NE) at four random locations within each sap flow transect. Runyon et al. (1994) found that results obtained with this instrument compared well with results of two other common methods for measuring LAI in forests. The same four locations at both sites were visited on May 25, July 30 and August 30, 2001. The May and August measurements were taken at dusk under a uniformly clear sky and the July measurement was taken during the late morning under a uniformly overcast sky. Of the five zenith angles recorded, we removed the lowest to avoid interference with obstructions. A correction factor (1.89 for the young stand, based on clumping in young *P. menziesii*; 1.94 for the old stand, based on average clumping in old *P. menziesii* and *T. heterophylla*) was used to compensate for within-shoot leaf clumping (Frazer et al. 2000). Stem interference was accounted for by subtracting the wood area index (W), which was estimated from the vegetation survey in the young stand ($W = 0.525$) and old stand ($W = 0.746$), based on the methods from Law et al. (2001).

Scaling up to the riparian area

Results of sap flow measurements and the vegetation survey were combined to estimate vegetation water use in the entire riparian area of each study watershed based on species-specific versions of Equation 1:

$$E_y = f_{PSMEy} A_{GYMy} + f_{ALRUy} A_{ANGy} \qquad (2)$$

and

$$E_o = f_{PSMEo} A_{PSMEo} + f_{TSHEo} A_{TSHEo} \\ + f_{PSMEandTSHEo} A_{OTHERGYMo} + f_{ALRUy} A_{ANGo} \qquad (3)$$

The area used for sap flux density (f; kg m^{-2} day^{-1}) measurement is different from the area used for estimating sapwood basal area (A; m^{-2} ha^{-1}) and only represents a small fraction of the sapwood basal area in the stand. This was a consequence of the limited power supply for sap flow measurements, and admittedly may produce errors in extrapolating the sap flow data, but at least the approach was similar for the two watersheds. Sap flow of young ($_y$) *P. menziesii* (PSME) was used to estimate water use by all gymnosperms (GYM) in the young stand (*P. menziesii* constitutes 90% or more of gymnosperm basal area). Sap flow of *A. rubra* (ALRU) in the young stand was used to estimate water use by all angiosperms (ANG) in both the young and old ($_o$) stands. We acknowledge that using *A. rubra* to represent all angiosperms is not ideal, but our experimental capability precluded observations on more species. The only other prevalent angiosperms in the young stand are vine maple (*Acer circinatum* Pursh) and big-leaf maple (*Acer macrophyllum* Pursh), which together comprised less than 20% of total basal area. Sap flux of *A. rubra* was measured only in 1999, so a relationship was established to predict *A. rubra* sap flux in the year 2000 (Days 175 to 301) based on the ratio between *A. rubra* and *P. menziesii* in 1999:

$$f_{yALRU} / f_{yPSME} = -163.3 + 165.1(1 - e^{-0.0293t}) \qquad (4)$$

where t is day of year between Days 182 and 251 ($n = 62$, $r^2 = 0.78$, $P < 0.0001$). It was necessary to include t in this equation to allow for seasonal differences. Mean sap flow of old *P. menziesii* and old *T. heterophylla* (TSHE) was used to estimate water use by the remaining gymnosperms in the old stand (*P. menziesii* and *T. heterophylla* combined constituted 90% or more of gymnosperm basal area).

Statistical analyses

Sapwood areas (A) for individual trees of each species were predicted with least squares regression models from either diameter or total cross-sectional area of wood (basal area, BA). The choice of a linear versus a nonlinear model, and the choice of independent variables, differed for each species in order to obtain the model with the best predictive power for each species. We applied a linear model except where a power function gave a better fit. The small-diameter species, particularly angiosperms such as *A. circinatum*, rhododendron (*Rhododendron macrophyllum* L.) and California hazel (*Corylus cornuta* Marsh. var. *californica* (A. DC.) Sharp) were assumed to be entirely sapwood, minus the estimated bark depth. The same was also assumed for small individuals of other species (*P. menziesii* and *A. macrophyllum* in the young stand) with diameters less than 6 cm. Linear equations ($A = a + b$BA) were used for bitter cherry (*Prunus emarginata* Dougl. ex Hook.) and *A. macrophyllum* in the young stand and *P. menziesii* in the old stand ($r^2 = 0.80$, 0.71 and 0.48, respectively), which were used to predict sapwood areas only in small individuals (sapwood areas in all large trees were measured directly). Power function equations ($A = a + b$BA^c) were used for all other species (for *P. menziesii* and *T. heterophylla* combined for the young stand and *T. heterophylla*, pacific yew (*Taxus brevifolia* Nutt.), *A. macrophyllum* and western redcedar (*Thuja plicata* J. Donn ex D. Don) in the old stand, $r^2 = 0.94$, 0.91, 0.79, 0.68 and 0.91, respectively). The model for *P. menziesii* in the old stand was used only to predict the sapwood area of eight trees out of the 32 total for that species; sapwood area of the rest was measured directly.

The significance of differences in LAI among sites and in mean sap flow among measurement trees of each species or age class on each day was determined by a *t*-test.

Results

Variations in water use per unit sapwood area based on tree age and species

Over the measurement period, we noted a seasonal decline in light (Figure 2a), vapor pressure deficit (Figure 2b) and sap flux density (Figure 3) for all species and both ages of *P. menziesii*. Mean sap flux density was 2.30 times higher in young *P. menziesii* than in old *P. menziesii* on a daily basis (Figure 3a) from late June until late October 2000 (Days 175– 301, SE = 0.017 kg m^{-2} day^{-1}). Significant differences were observed during the majority of the measurement period except for
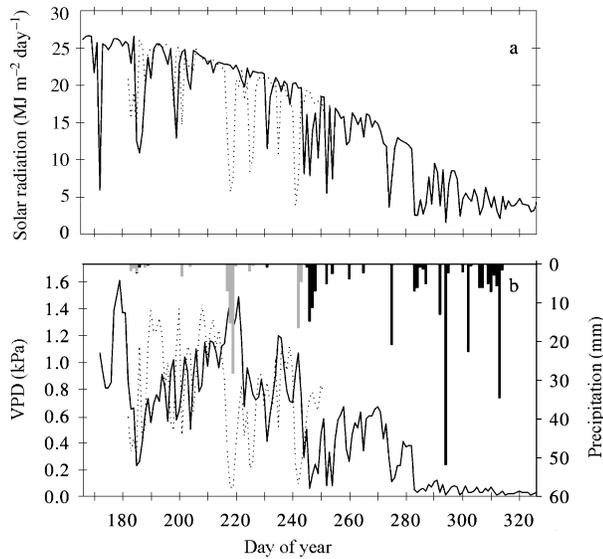
Figure 2. (a) Total solar radiation (MJ m^{-2} day^{-1}), (b) mean daily vapor pressure deficit (VPD; kPa) and daily total precipitation (mm) for 1999 (grey bars, dotted line) and 2000 (black bars, solid line).

rainy or cloudy days when sap flow was low (Figures 2 and 3). The rate of change in sap flow over the measurement period was much greater for young *P. menziesii* than for old *P. menziesii* (Figure 3a); thus, it may be inferred that young trees were more responsive to climatic variability than old trees. Tree-to-tree variation was quite large, especially in old growth trees (coefficient of variation, CV = 0.42 and 0.63 in young and old trees, respectively).

Mean sap flux density was 1.41 times higher in young *A. rubra* than in young *P. menziesii* (Figure 3b) from early July until early September 1999 (Days 182–251, SE = 0.017 kg m^{-2} day^{-1}). Water use by *A. rubra* declined only slightly through the season compared with water use by *P. menziesii*, and thus water use by *A. rubra* (and, we infer, angiosperms in general) comprised an increasing proportion of vegetation water use in the young stand throughout the growing season. The difference was statistically different ($P < 0.05$) starting in late July (Day 207) and continuing thereafter. Sap flux density in *A. rubra* reached a maximum almost a month later than in *P. menziesii*. Tree-to-tree variation was slightly higher in *P. menziesii* than in *A. rubra* throughout the measurement period (CV = 0.37 and 0.36 in *P. menziesii* and *A. rubra*, respectively).

Mean sap flux density was 1.45 times higher in old *P. menziesii* than in old *T. heterophylla* (Figure 3c) from late June until late November 2000 (Days 168–325, SE = 0.010 kg m^{-2} day^{-1}). *Pseudotsuga menziesii* consistently used more water on a daily basis throughout most of the growing season, but water use declined more steeply in *P. menziesii* than in *T. heterophylla* over the season. As a result, *T. heterophylla* used slightly more water than *P. menziesii* at the end of the season (Figure 3d). Because of the small sample size and high tree-to-tree variation, this difference was statistically significant
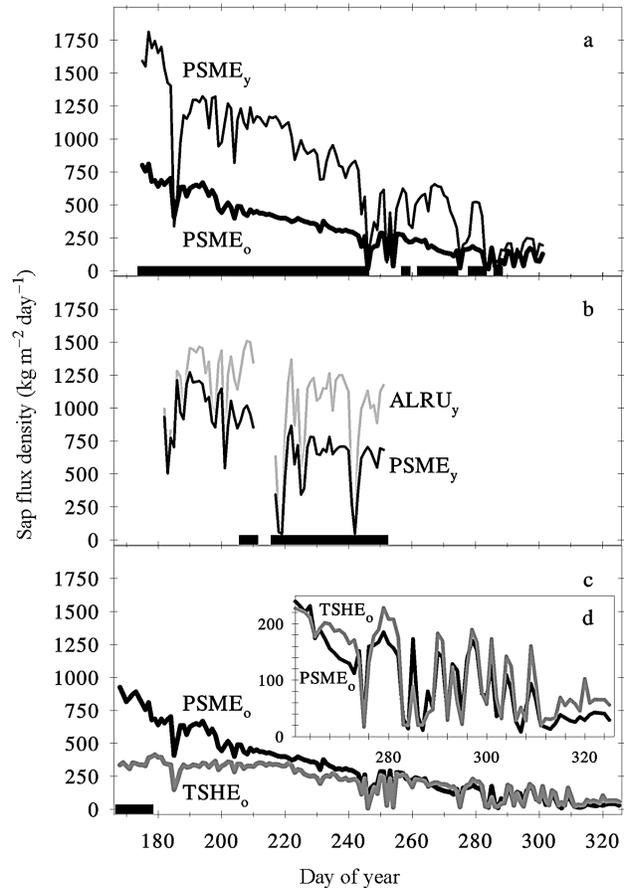

Figure 3. (a) Effects of age on sap flux density (kg m^{-2} day^{-1}) in the young ($_y$) (thin black line, mean of seven trees) and old ($_o$) (thick black line, mean of three trees) *P. menziesii* (PSME) from early June until late October 2000. (b) Effects of species on sap flux density in *A. rubra* (ALRU) (thin gray line, mean of seven trees) and *P. menziesii* (thin black line, mean of seven trees) in the young stand from early July until early September 1999. (c) Effects of species on sap flux density in *P. menziesii* (thick black line, mean of three trees) and *T. heterophylla* (TSHE) (thick gray line, mean of three trees) in the old growth stand from early June until late November 2000. (d) Magnification of late-season fluxes for *P. menziesii* and *T. heterophylla* shown in 2c. The black bars at the bottom of graphs a, b and c represent days when the mean sap flux density among trees in the two groups was significantly different ($P < 0.05$ from a Student's *t*-test).

only during early summer (Days 168–177). Tree-to-tree variation was especially large in *P. menziesii* (CV = 0.62 and 0.34 in *P. menziesii* and *T. heterophylla*, respectively).

We found no trends in the relationship between mean seasonal sap flux density and sapwood basal area of individual trees within species (Figure 4). Rather, values tended to group within age categories (Figure 4).

Overall, differences in sap flux density between tree ages (measured in *P. menziesii* only) were greater than those between trees of different species but similar age. There was a slightly greater difference between the two old growth conifer species than between young *A. rubra* and young *P. menziesii* trees.
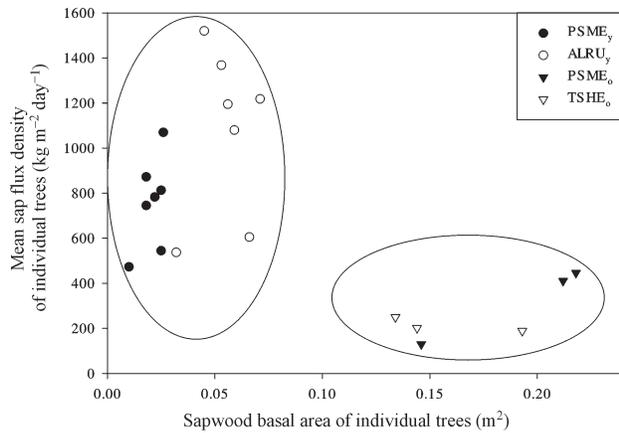
Figure 4. Relationship between mean seasonal sap flux density (kg m^{-2} day^{-1}) for individual trees equipped with sap flow sensors and sapwood basal area (m^2). Note that trees in the young stand (circled at left) seem to group together, as do trees in the old stand (circled at right), but there is no clear trend within species. Abbreviations: $PSME_y$ = young *P. menziesii*; $ALRU_y$ = young *A. rubra*; $PSME_o$ = old *P. menziesii*; and $TSHE_o$ = old *T. heterophylla*.

Variations in basal area and sapwood area

Tree size was distributed normally in the young stand but bimodally in the old stand, indicating a more pronounced understory component; however, more than 40% of the basal area was in the largest 20% of the trees in the old stand (Figure 5).

There was more than twice as much total basal area in the riparian area in the old stand than in the young stand (85.8 versus 33.3 m^2 ha^{-1}; Figure 6a). In contrast, estimated sapwood basal area in the riparian area of the young stand was 21% greater than in the riparian area of the old stand (Figure 6b) as a result of the large amount of heartwood in old growth trees. Old gymnosperms had much less sapwood per unit basal area
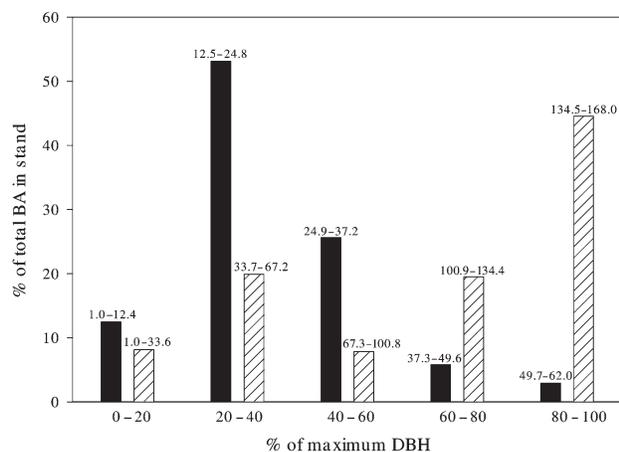

Figure 5. Distribution of basal area (BA; %) in the young stand (solid bars) and old stand (hatched bars) among the five relative diameter at mass height (DBH) size classes. Actual diameter ranges (cm) are noted above each bar.
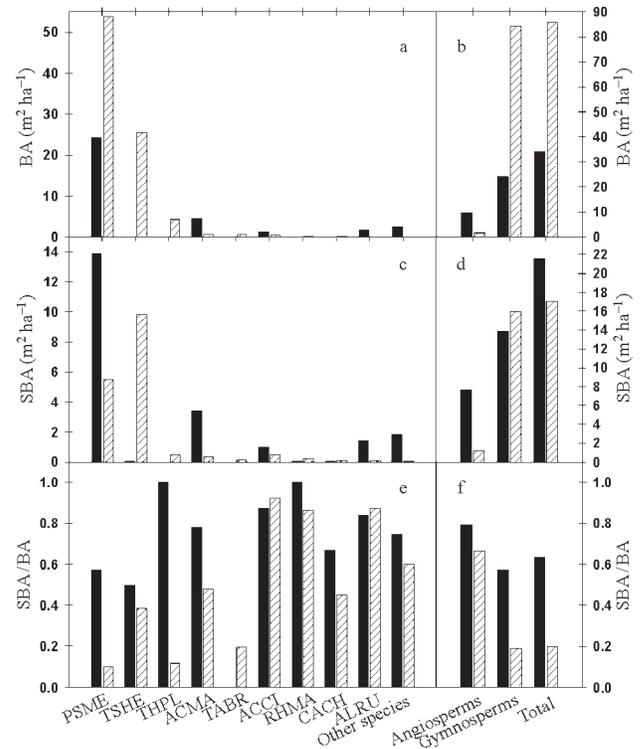

Figure 6. (a) Differences in total basal area (BA; m^2 ha^{-1}) among the young stand (solid bars) and old stand (hatched bars) by species and (b) summarized by grouping. (c) Differences in total sapwood basal area (SBA; m^2 ha^{-1}) among the young stand (solid bars) and old stand (hatched bars) by species and (d) summarized by grouping. (e) Ratio of total SBA to BA among the young stand (solid bars) and old stand (hatched bars) by species and (f) summarized by grouping. Abbreviations: PSME = *Pseudotsuga menziesii*; TSHE = *Tsuga heterophylla*; THPL = *Thuja plicata*; ACMA = *Acer macrophyllum*; TABR = *Taxus brevifolia*; ACCI = *Acer circinatum*; RHMA = *Rhododendron macrophyllum*; CACH = *Castanopsis chrysophylla* (Dougl.) A. DC.; and ALRU = *Alnus rubra*. Other species includes: *Cornus nuttallii* Audub., *Vaccinium parvifolium* Sm., *Prunus emarginata* (Dougl. ex Hook.) Walp, *Amelanchier alnifolia* Nutt., *Populus tremuloides* Michx., *Holodiscus discolor* (Pursh) Maxim., *Rhamnus purshiana* DC. and *Corylus cornuta* var. *californica*.

than young gymnosperms or angiosperms (Figures 6e and 6f).

In the riparian area of the young stand, angiosperms had over six times more sapwood basal area than in the old stand (Figure 6d). In the young stand, *P. menziesii* comprised almost 100% of the coniferous sapwood basal area and 64% of the total sapwood basal area, whereas in the old growth stand, *T. heterophylla* comprised 62% of the coniferous sapwood basal area and 58% of the total sapwood basal area. This is in contrast to the total basal area (sapwood plus heartwood) of *T. heterophylla* and *P. menziesii* in the old stand, where *P. menziesii* made up 64% of the coniferous basal area. This is because sapwood depth of *P. menziesii* was small (average of 7% of bole radius), whereas *T. heterophylla* had thick sapwood (average of 50% of bole radius) (Figure 6e). Because *T. heterophylla* dominance is associated with late successional forests in the Pacific Northwest (Franklin and Hemstrom 1981), the

large *T. heterophylla* component in the old stand indicates that this stand is in the stages of late succession. *Alnus rubra*, *Acer macrophyllum* and *Acer circinatum* make up the majority of angiosperms in both stands, but are a much smaller component of the old stand. Additionally, *Rhododendron*, almost nonexistent in the young stand, is a significant component of the old stand angiosperms, albeit a small component of sapwood basal area.

Leaf area index

Leaf area index was about 14% higher ($P = 0.04$) in the old stand (12.1 ± 0.3) than in the young stand (10.6 ± 0.5) on July 30. Similar values were obtained on May 25 and August 30, although on these dates, the measurements were not statistically different between the stands ($P > 0.05$; 9.5 ± 0.4 and 10.5 ± 0.5 for the young and 11.0 ± 0.5 and 11.5 ± 0.4 for the old stand, respectively). No phenological trend in LAI was detected over the measurement period. Our LAI estimates in both stands average about 1 to 3 larger than those determined by others for similar stands (M. Lefksky and O. Sun, Oregon State University, unpublished data, Thomas and Winner 2000, Turner et al. 2002). This may be a measurement error rather than a real difference associated with stem interference and branch clumping. Measurements with the LAI 2000 instrument are known to have errors of 15 to 20% under typical forest conditions (J. Welles, Li-Cor, personal communication).

Scaling-up tree water use to the riparian area

Estimated tree water use was 3.27 times greater in the young stand than in the old stand during the period from late June until late October 2000 (Days 175–301, Figure 7). All three factors considered in this study, *P. menziesii* age, species composition and sapwood area, contributed to this large difference. The seasonal trends for the two stands were similar, declining steadily through the measurement period. At low vapor pressure deficit, the difference in transpiration between the two stands was much smaller than at high vapor pressure deficit (Figure 8).
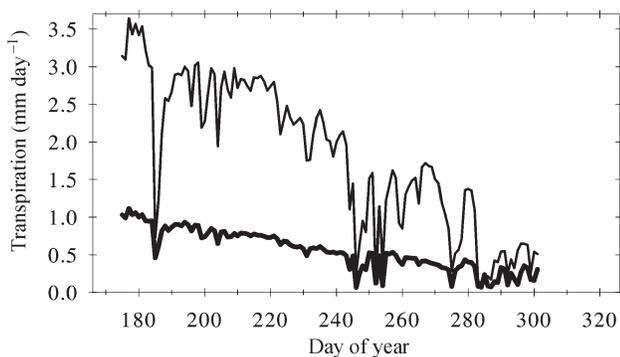
Discussion

As shown previously (Phillips et al. 2002), sap flux density was greater in young mature *P. menziesii* than in old growth *P. menziesii* trees. The age and size-related differences were much greater in our study than those reported previously (Phillips et al. 2002). We speculated that other structural and compositional characteristics of the stands would compensate for the change in tree-level water use. However, on the contrary, we found that greater sapwood basal area and a larger component of angiosperms in the young stand only increased the total water use of that ecosystem compared with the old-growth ecosystem. *Alnus rubra* had greater sap flux density than *P. menziesii* in the young stand, consistent with previous comparisons of mesic angiosperms versus gymnosperms (Jarvis 1975). Shade-tolerant species (overstory *T. heterophylla*), in addition to growing more slowly, had less sap flux density than *P. menziesii* in the old stand, but *T. heterophylla* had much greater sapwood area per unit basal area. Also, total sapwood basal area was significantly greater in the young stand than in the old stand.

The lower sap flux density early in the season in *T. heterophylla* than in *P. menziesii* (Figure 3c), could be partially attributed to its slightly smaller mean height and thus partial shading by adjacent trees. However, if this were entirely the case, we would expect the differences to intensify in the late summer as the solar zenith increases. Instead, sap flux density in *T. heterophylla* became more similar to that of *P. menziesii* as the season progressed, eventually surpassing it (Figure 3d). A possible explanation for these seasonal differences is that *T. heterophylla* is less sensitive to vapor pressure deficit than *P. menziesii*, but at high vapor pressure deficits, stomatal conductance is higher in *T. heterophylla* than in *P. menziesii* (Waring and Franklin 1979). However, it is also possible that rooting or hydraulic differences account for these seasonal differences. We predicted that *T. heterophylla*, which is shade tolerant, uses less water when it is in the understory compared
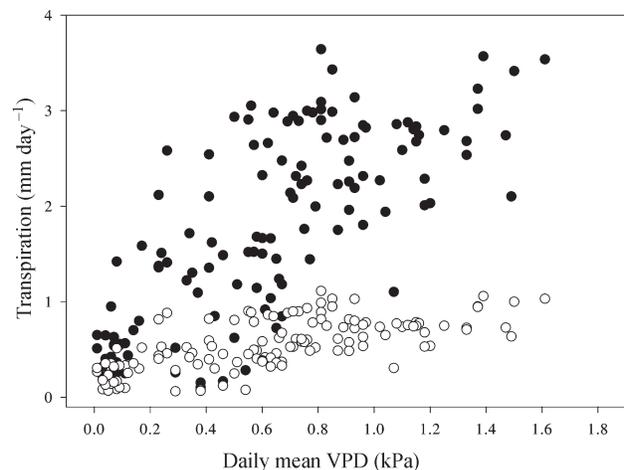

Figure 7. Estimated water use per unit ground area (transpiration; mm day^{-1}) in the young stand (thin line) and the old growth stand (thick line) from late June until late October 2000.

Figure 8. Relationship between daily transpiration (mm day^{-1}) in the young stand (●) and old stand (○) and mean daily vapor pressure deficit (VPD; kPa), as measured at a nearby weather station.

with overstory *P. menziesii*. However, our results indicate that the differences between species may persist when *T. heterophylla* emerges into the overstory and receives full sunlight, suggesting that the physiological adaptations associated with shade tolerance are maintained when an individual reaches overstory status.

Our estimates of basal area in the investigated stands (34 and 86 m^2 ha^{-1} in the young and old stand, respectively) compare well with those made in similar aged stands in other studies carried out in the Pacific Northwest. Within the old growth plot, slightly higher estimates of *P. menziesii* basal area (66 and 67 m^2 ha^{-1}) and slightly lower estimates of *T. heterophylla* basal area were found (21 and 8 m^2 ha^{-1}; Dyrness and Acker 1999 (http://www.fsl.orst.edu/lter/)) compared with our study. These survey plots contained proportionately less riparian area, consistent with a lower density of *T. heterophylla*. Franklin and Hemstrom (1981) reported a basal area of 27 m^2 ha^{-1} for *P. menziesii* and a total basal area of 98 m^2 ha^{-1} for forests of ages 350 to 600 years throughout the Oregon and Washington Cascades. In other studies, estimated basal areas of *P. menziesii*–*T. heterophylla* forests ranged from 25 to 44 m^2 ha^{-1} for young stands (age 30–50) and from 69 to 92 m^2 ha^{-1} for old growth stands (Spies and Franklin 1991, Cohen et al. 1995, Means et al. 1999).

Alnus rubra constituted 18% of the angiosperm sapwood basal area in the young stand and 6% of the angiosperm sapwood basal area in the old stand. Use of *A. rubra* from the young stand to represent angiosperms in the old stand introduced little error, because hardwoods are a small component (7%) of the sapwood basal area in the old stand—especially for overstory trees, where it is essentially zero. Power limitations also inhibited adequate sampling of the magnitude and variation in sap flow among understory species in the old stand. Because these trees receive low or patchy light, we predict that they use significantly less water than their overstory counterparts.

It is often assumed that LAI is the most important determinant of differences in transpiration among forest stands (Hewlett 1982). In models of forest transpiration, LAI often plays a theoretical role in determining differences among forest stands (Running and Coughlan 1988, Williams et al. 1996). This was not the case in our study. Although we noted a small increase in LAI in the older stand, estimated transpiration was actually lower in the old than in the young stand. Several chronosequence studies have found a decline in leaf area in older forests (Ryan et al. 1997). In forests of similar type and age, others have found LAI to be about 2 less in old compared with young *P. menziesii*–*T. heterophylla* forests (M. Lefksky and O. Sun, unpublished data). However, despite the small changes in LAI with forest age, there appears to be a general trend toward reduced transpiration in old growth stands. Maximum transpiration rates reported in the literature for 20- to 60-year-old conifer stands ranged between 1.8 and 3.9 mm day^{-1} (mean = 3.0 mm day^{-1}; Morikawa et al. 1986, Martin et al. 1997, Alsheimer et al. 1998, Irvine et al. 1998, Granier et al. 1990, Roberts et al. 2001). In contrast, in conifer forests over 240 years of age, maximum transpiration ranged between 0.4 and 1.5 mm day^{-1} (mean = 0.9 mm day^{-1}; Zimmermann et al. 2000, Irvine et al. 2002, Unsworth et al. 2004). There must be some explanation other than LAI for transpiration differences between young and old stands.

In a meta-analysis of 13 whole-tree studies, McDowell et al. (2002*a*) found that the ratio between leaf area and sapwood area (a_l:a_s) is typically reduced as trees grow taller and older. They proposed that the change in a_l:a_s could at least partially compensate for the impact of increased height on leaf-specific hydraulic conductance. McDowell et al. (2002*a*) noted two exceptions to the general trend of decreasing a_l:a_s with increasing tree height. In both of these studies, a_l:a_s was calculated from stand-level surveys in stands that included an abundance of shade-tolerant species, such as Norway spruce (*Picea abies* (L.)) or balsam fir (*Abies balsamea* (L.) Mill.). Our study appears consistent with these exceptions. Given that we found that sapwood basal area was substantially lower in the old growth stand than in the young stand, the slightly higher LAI in the older stand means that a_l:a_s was greater in the old stand than in the young stand (0.67 and 0.47 m^2 cm^{-2}, respectively). It is possible that, during late succession, the emergence of shade-tolerant species with a high a_l:a_s caused stand-level a_l:a_s to change in the opposite direction from the tree-level trends that occur as early successional species reach maturity (McDowell et al. 2002*a*).

Implications for land use

Evapotranspiration by forest canopies influences seasonal hydrologic trends in the Pacific Northwest (Jones 2000, Post and Jones 2001). Our study indicates that the many changes in the structure and composition of forests as they age may significantly decrease evapotranspiration. Our previous findings and those of others suggest that stream flow in watersheds covered by young stands is dynamically influenced by rapidly transpiring young vegetation (Bren 1997, Bond et al. 2002). However, water use by dominant tree species alone presents an incomplete picture of how stream flow volumes during low stream flow in summer are impacted by forest management practices (Hicks et al. 1991).

We found that the largest differences in water use between young and old stands occurred during late spring, but that differences persisted throughout the measurement period (Figure 7), corresponding with the period of low stream flow. Trends in stream flow after harvest in managed forests have demonstrated that stream flow can be reduced to below preharvest values in young regenerating stands during periods of low stream flow (Hicks et al. 1991, Lane and Mackay 2001, Perry et al. 2001). Few studies have directly evaluated the role of transpiration by forests, independent of evaporation, on water yield (but see Vertessy et al. 2001). We intend to explore relationships between transpiration and water yield in further analyses using existing stream flow data from these sites.

Conclusions

We posed two questions. If young mature trees use more water per unit sapwood area than old trees, do young mature forests use more water than old growth forests on a ground area basis, or, do changes in species composition or stand density compensate for the age-related changes? We found evidence that all three factors investigated (age-related changes in whole-tree hydraulic conductance, species-related differences in water use, and structurally related changes in sapwood area distribution within stands) contribute to decreased stand-level water use with stand age. Each factor alone led to increases in transpiration in the young stand compared with the old growth forest, but when combined, they accrued large differences between old and young stands. Holding all else constant and substituting into Equations 2 and 3, we were able to rank these three factors according to their relative impact on stand transpiration. For example, if sap flux density of *P. menziesii* in the young stand was the same as that of *P. menziesii* in the old stand ($f_{PSMEy} = f_{PSMEo}$), young stand transpiration would be reduced by 32%. We found that *P. menziesii* age had the greatest effect on stand-level differences in water use, followed by differences in sapwood basal area, and finally species composition.

References

Alsheimer, M., B. Köstner, E. Falge and J.D. Tenhunen. 1998. Temporal and spatial variation in transpiration of Norway spruce stands within a forested catchment of the Fichtelgebirge, Germany. Ann. Sci. For. 55:103–123.

Bond, B.J. and K.L. Kavanagh. 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. Tree Physiol. 19:503–510.

Bond, B.J., J.A. Jones, G. Moore, N. Phillips, D.A. Post and J.J. McDonnell. 2002. The zone of vegetation influence on baseflow revealed by diel patterns of streamflow and vegetation water use in a headwater basin. Hydrol. Process. 16:1671–1677.

Bredensteiner, K. 1998. An investigation of vegetation: hydrology interactions in watershed 1 at the H.J. Andrews Experimental Forest. M.Sc. Thesis, Oregon State Univ., Corvallis, 168 p.

Bren, L.J. 1997. Effects of slope vegetation removal on the diurnal variations of a small mountain stream. Water Resour. Res. 33:321–331.

Callaway, R.M., A. Sala and R.E. Keane. 2000. Succession may maintain high leaf area:sapwood ratios and productivity in old sub-alpine forests. Ecosystems 3:254–268.

Čermák, J., E. Cienciala, J. Kučera, A. Lindroth and E. Bednarova. 1995. Individual variation of sap-flow rate in large pine and spruce trees and stand transpiration: a pilot study at the central NOPEX site. J. Hydrol. 168:17–27.

Cienciala, E., J. Kučera, M.G. Ryan and A. Lindroth. 1998. Water flux in boreal forest during two hydrologically contrasting years; species specific regulation of canopy conductance and transpiration. Ann. Sci. For. 55:47–61.

Cohen, W.B., T.A. Spies and M. Fiorella. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, U.S.A. Int. J. Remote Sens. 16:721–746.

Cohen, W.B., T.A. Spies, R.J. Alig, D.R. Oetter, T.K. Maiersperger and M. Fiorella. 2002. Characterizing 23 years (1972–95) of stand replacement disturbance in western Oregon forests with Landsat imagery. Ecosystems 5:122–137.

Do, F. and A. Rocheteau. 2002. Influence of natural temperature gradients on measurements of xylem sap flow with thermal dissipation probes. 1. Field observations and possible remedies. Tree Physiol. 22:641–648.

Domec, J.C. and B.L. Gartner. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. Trees 15:204–214.

Domec, J.C. and B.L. Gartner. 2002. Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. Tree Physiol. 22:91–104.

Dunn, G.M. and D.J. Connor. 1993. An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. Tree Physiol. 13:321–336.

Franklin, J.F. and M.A. Hemstrom. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. *In* Forest Succession: Concepts and Application. Eds. D.C. West, H.H. Shugart and D.B. Botkin. Springer-Verlag, New York, pp 212–229.

Frazer, G.W., J.A. Trofymow and K.P. Lertzman. 2000. Canopy openness and leaf area in chronosequences of coastal temperate rainforests. Can. J. For. Res. 30:239–256.

Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3:309–320.

Granier, A., V. Bobay, J.H.C. Gash, J. Gelpe, B. Saugier and W.J. Shuttleworth. 1990. Vapor flux density and transpiration rate comparisons in a stand of Maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. Agric. For. Meteorol. 51:309–319.

Hewlett, J.D. 1982. Principles of forest hydrology. University of Georgia Press, Athens, GA, 183 p.

Hicks, B.J., R.L. Beschta and R.D. Harr. 1991. Long-term changes in streamflow following logging in Western Oregon and associated fisheries implications. Water Resour. Bull. 27:217–226.

Hubbard, R.M., B.J. Bond and M.G. Ryan. 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol. 19:165–172.

Irvine, J., M.P. Perks, F. Magnani and J. Grace. 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. Tree Physiol. 18:393–402.

Irvine, J., B.E. Law, P.M. Anthoni and F.C. Meinzer. 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. Tree Physiol. 22:189–196.

James, S.A., M.J. Clearwater, F.C. Meinzer and G. Goldstein. 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. Tree Physiol. 22:277–283.

Jarvis, P.G. 1975. Water transfer in plants. *In* Heat and Mass Transfer in the Biosphere: Part 1. Transfer Processes in the Plant Environment. Eds. D.A. deVries and N.H. Afgan, Scripta Book, Washington, DC, pp 369–394.

Jones, J.A. 2000. Hydrologic processes and peak discharge response to forest removal, regrowth, and roads in 10 small experimental basins, western Cascades, Oregon. Water Resour. Res. 36: 2621–2642.

Lane, P.N.J. and S.M. Mackay. 2001. Streamflow response of mixed-species eucalypt forests to patch cutting and thinning treatments. For. Ecol. Manage. 143:131–142.

Law, B.E., S. Van Tuyl, A. Cescatti and D.D. Baldocchi. 2001. Estimation of leaf area index in open-canopy ponderosa pine forests at different successional stages and management regimes in Oregon. Agric. For. Meteorol. 108:1–14.

Martin, T.A., K.J. Brown, J. Čermák, R. Ceulemans, J. Kučera, F.C. Meinzer, J.S. Rombold, D.G. Sprugel and T.M. Hinckley. 1997. Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. Can. J. For. Res. 27:797–808.

McDowell, N., H. Barnard, B.J. Bond, T. Hinckley, R.M. Hubbard, F.C. Meinzer, N. Phillips, M.G. Ryan and D. Whitehead. 2002*a*. The relationship between tree height and leaf area:sapwood area ratio. Oecologia 132:12–20.

McDowell, N.G., N. Phillips, C. Lunch, B.J. Bond and M.G. Ryan. 2002*b*. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. Tree Physiol. 22:763–774.

Means, J.E., S.A. Acker, D.J. Harding, J.B. Blair, M.A. Lefsky, W.B. Cohen, M.E. Harmon and W.A. McKee. 1999. Use of large-footprint scanning airborne Lidar to estimate forest stand characteristics in the western Cascades of Oregon. Remote Sens. Environ. 67:298–308.

Morikawa, Y., S. Hattori and Y. Kiyono. 1986. Transpiration of a 31-year-old *Chamaecyparis obtusa* Endl. stand before and after thinning. Tree Physiol. 2:105–114.

Parker, G.G., M.M. Davis and S.M. Chapotin. 2002. Canopy light transmittance in Douglas-fir–western hemlock stands. Tree Physiol. 22:147–157.

Pataki, D.E., R. Oren, G. Katul and J. Sigmon. 1998. Canopy conductance of *Pinus taeda*, *Liquidambar styraciflua* and *Quercus phellos* under varying atmospheric and soil water conditions. Tree Physiol. 18:307–315.

Pataki, D.E., R. Oren and W.K. Smith. 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. Ecology 81:2557–2566.

Perry, C.H., R.C. Miller and K.N. Brooks. 2001. Impacts of short-rotation hybrid poplar plantations on regional water yields. For. Ecol. Manage. 143:143–151.

Phillips, N., B. Bond, N. McDowell and M.G. Ryan. 2002. Canopy and hydraulic conductance in young, mature, and old Douglas-fir trees. Tree Physiol. 22:205–211.

Post, D.A. and J.A. Jones. 2001. Hydrologic regimes of forested, mountainous, headwater basins in New Hampshire, North Carolina, Oregon, and Puerto Rico. Adv. Water Resour. 24:1195–1210.

Roberts, S., R.A. Vertessy and R. Grayson. 2001. Transpiration from *Eucalyptus sieberi* (L. Johnson) forests of different age. For. Ecol. Manage. 143:153–161.

Running, S.W. 1976. Environmental control of leaf water conductance in conifers. J. For. Resour. 6:104–112.

Running, S.W. and J.C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model. 42:125–154.

Runyon, J., R.H. Waring, S.N. Goward and J.M. Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon transect. Ecol. Appl. 42:226–237.

Ryan, M.G. and B.J. Yoder. 1997. Hydraulic limits to tree height and tree growth. BioScience 47:235–242.

Ryan, M.G., D. Binkley and J.H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27: 213–262.

Ryan, M.G., B. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Cienciala and J. Kučera. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. Oecologia 124:553–560.

Spies, T.A. and J.F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. *In* Wildlife and Vegetation of Unmanaged Douglas-fir Forests. Eds. K.B. Aubry and M.H. Brookes. USDA Forest Service PNW Research Station, Portland, OR, pp 91–110.

Stratton, L.C., G. Goldstein and F.C. Meinzer. 2000. Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. Oecologia 124:309–317.

Swanson, F.J. and M.E. James. 1975. Geology and geomorphology of the H. J. Andrews Experimental Forest, western Cascades, Oregon. PNW Forest Range Experiment Station, Portland, OR, 14 p.

Thomas, S.C. and W.E. Winner. 2000. Leaf area index of an old-growth Douglas-fir forest estimated from direct structural measurements in the canopy. Can. J. For. Res. 30:1922–1930.

Turner, D.P., M. Guzy, M.A. Lefsky, S. Van Tuyl, O. Sun, C. Daly and B.E. Law. 2002. Effects of land use and fine scale environmental heterogeneity on net ecosystem production over a temperate coniferous forest landscape. Tellus 55:657–668.

Unsworth, M.H., N. Phillips, T. Link, B. Bond, M. Falk, M. Harmon, T. Hinckley, D. Marks and K.-T. Paw U. 2004. Components and controls of water flux in an old-growth Douglas-fir/western hemlock ecosystem. Ecosystems. In press.

Vertessy, R.A., F.G.R. Watson and S.K. O'Sullivan. 2001. Factors determining relations between stand age and catchment water balance in mountain ash forests. For. Ecol. Manage. 143:13–26.

Waring, R.H. and J.F. Franklin. 1979. Evergreen coniferous forests of the Pacific Northwest. Science 204:1380–1386.

Whitehead, D., P.G. Jarvis and R.H. Waring. 1984. Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment. Can. J. For. Res. 14:692–700.

Williams, M., E.B. Rastetter, D.N. Fernandes, M.L. Goulden, S.C. Wofsy, G.R. Shaver, J.M. Melillo, J.W. Munger, S.-M. Fan and K.J. Nadelhoffer. 1996. Modelling the soil–plant–atmosphere continuum in a *Quercus–Acer* stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen, and soil/plant hydraulic properties. Plant Cell Environ. 19:911–927.

Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40:513–527.

Zimmermann, R., E.-D. Schulze, C. Wirth, E.-E. Schulze, K.C. McDonald, N.N. Vygodskaya and W. Ziegler. 2000. Canopy transpiration in a chronosequence of Central Siberian pine forests. Global Change Biol. 6:25–37.