Oecologia (2001) 129:481–491
DOI 10.1007/s004420100758

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Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine

Received: 21 November 2000 / Accepted: 1 June 2001 / Published online: 17 July 2001

Abstract Conifers decrease the amount of biomass apportioned to leaves relative to sapwood in response to increasing atmospheric evaporative demand. We determined how these climate-driven shifts in allocation affect the aboveground water relations of ponderosa pine growing in contrasting arid (desert) and humid (montane) climates. To support higher transpiration rates, a low leaf:sapwood area ratio (A_L/A_S) in desert versus montane trees could increase leaf-specific hydraulic conductance (K_L). Alternatively, a high sapwood volume:leaf area ratio in the desert environment may increase the contribution of stored water to transpiration. Transpiration and hydraulic conductance were determined by measuring sap flow (J_S) and shoot water potential during the summer (June–July) and fall (August–September). The daily contribution of stored water to transpiration was determined using the lag between the beginning of transpiration from the crown at sunrise and J_S. In the summer, mean maximum J_S was 31.80±5.74 and 24.34±3.05 g m^{-2} s^{-1} for desert and montane trees (a 30.6% difference), respectively. In the fall, J_S was 25.33±8.52 and 16.36±4.64 g m^{-2} s^{-1} in desert and montane trees (a 54.8% difference), respectively. J_S was significantly higher in desert relative to montane trees during summer and fall ($P<0.05$). Predawn and midday shoot water potential and sapwood relative water content did not differ between environments. Desert trees had a 129% higher K_L than montane trees in the summer (2.41×10^{-5} versus 1.05×10^{-5} kg m^{-2} s^{-1} MPa^{-1}, $P<0.001$) and a 162% higher K_L in the fall (1.97×10^{-5} versus 0.75×10^{-5} kg m^{-2} s^{-1} MPa^{-1}, $P<0.001$). Canopy conductance decreased with D in all trees at all measurement periods ($P<0.05$). Maximum g_C was 3.91 times higher in desert relative to montane trees averaged over the summer and fall. Water storage capacity accounted for 11 kg (11%) and 10.6 kg (17%) of daily transpiration in the summer and fall, respectively, and did not differ between desert and montane trees. By preventing xylem tensions from reaching levels that cause xylem cavitation, high K_L in desert ponderosa pine may facilitate its avoidance. Thus, the primary benefit of low leaf:sapwood allocation in progressively arid environments is to increase K_L and not to increase the contribution of stored water to transpiration.

Keywords Biomass allocation · Leaf-specific hydraulic conductance · Transpiration · Water storage · Xylem cavitation

Introduction

Rapid changes in biomass allocation often occur in plants in response to variation in resource availability. Because there is an intimate relationship between allocation and resource acquisition, these shifts often facilitate the tolerance of stress (Farrar 1999). In woody plants, structural responses to the environment can take place over many years and are important for growth, survival, and reproduction (Waring and Schlesinger 1985; Grace 1997). One of the most significant ways that trees respond to increasing soil moisture deficits and rising atmospheric evaporative demand is to reduce biomass allocation to leaves relative to sapwood (Whitehead and Jarvis 1981; Whitehead et al. 1984; Mencuccini and Grace 1995).

Declines in leaf versus sapwood allocation in response to increasingly arid climates have been documented for several species (Waring and Schlesinger 1985; Margolis et al. 1995). Recent evidence, however, suggests that the response appears to be particularly strong in the genus *Pinus* (Mencuccini and Grace 1995;

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Table 1 Mean (±1 SE) biomass allocation and xylem hydraulic parameters for desert and montane ponderosa pine trees used in this study. Biomass allocation parameters were calculated from the diameter at the base of the live crown based on relationships described in Callaway et al. (1994). Hydraulic parameters are from Maherali and DeLucia (2000b) (*n.s.* not significant)

Parameter	Desert	Montane	*P*
Diameter at base of live crown (cm)	38.0±5.3	41.2±4.9	n.s.
Sapwood volume (dm^3)	762±317	667±169	n.s.
Height (m)	8.9±1.4	14.3±1.9	<0.001
Sapwood mass (kg)	315±131	280±71	n.s.
Leaf mass (kg)	30.4±7.5	51.4±9.4	<0.001
Leaf:sapwood area ratio (m^2 cm^{-2})	0.116±0.004	0.207±0.002	<0.001
Sapwood:leaf mass ratio (kg kg^{-1})	8.21±1.29	5.93±0.63	<0.001
Sapwood volume:leaf area ratio (dm^3 m^{-2})	6.07±0.95	3.56±0.49	<0.001
Specific conductivity (K_S; kg m^{-1} MPa^{-1} s^{-1})	0.64±0.04	0.54±0.03	<0.05
Xylem tension at 50% cavitation (MPa)	–2.65±0.20	–2.61±0.19	n.s.

DeLucia et al. 2000). Hydraulically important changes in xylem anatomy and function can also occur in contrasting environments (Ewers et al. 2000; Maherali and DeLucia 2000a). For example, in ponderosa pine (*Pinus ponderosa* Laws.), populations growing in warm and dry desert environment had almost half the leaf:sapwood area ratio (A_L/A_S) of trees growing in cooler and more moist montane climates (Table 1; Callaway et al. 1994). Desert populations also had 19% higher sapwood permeability (K_S, kg m^{-1} MPa^{-1} s^{-1}; Maherali and DeLucia 2000b) than montane trees (Table 1). Despite its functional significance for tree water balance, few studies have explored the impact of climate-driven variation in biomass allocation and xylem properties on whole-tree hydraulic conductance and water storage dynamics.

Both a decrease in A_L/A_S and an increase in K_S suggest that pines acclimate to high temperature and atmospheric evaporative demands by increasing leaf-specific hydraulic conductance (K_L), or the physical capacity of the stem and roots to transport water to leaves (Whitehead et al. 1984; Tyree and Ewers 1991; Mencuccini and Grace 1995). Because these populations do not differ in their resistance to xylem cavitation (Table 1; Maherali and DeLucia 2000b), the shift to high K_L may permit desert trees to have high transpiration rates without reaching xylem tensions that cause cavitation. An alternate possibility is that the high volume of sapwood relative to leaf area in desert trees (Table 1) may contribute to tolerance of high evaporative demand by increasing water storage capacity relative to transpiring surface area. In conifers, the amount of water stored in the bole may be large, contributing up to 50% of daily transpiration, depending on the species and soil water availability (Waring et al. 1979; Tyree 1988; Wullschleger et al. 1998). When soil water availability is low, stored water reserves can provide a diurnal buffer that supports transpiration and photosynthesis when evaporative demand is high (Goldstein et al. 1984). Furthermore, increased storage capacity may reduce water potential gradients in the stem (Holbrook and Sinclair 1992b) and permit foliage and meristem hydration for extended periods following stomatal closure (Holbrook and Sinclair 1992a, 1992b; Holbrook 1995). These properties also reduce the potential for drought-induced xylem cavitation.

The objective of this study was to determine how the proportion of biomass allocated to sapwood relative to leaf area and xylem physiology affect the aboveground water relations of trees, using ponderosa pine growing in contrasting desert and montane environments as a model system. We predicted that high K_S and low A_L/A_S increase the leaf-specific hydraulic conductance of desert trees, supporting higher transpiration than montane trees without a concomitant rise in the water potential gradient. We also predicted that increased allocation to sapwood volume provides desert trees with a larger pool of stored water from which to withdraw water for transpiration than montane trees.

Materials and methods

Study sites and plant material

Our experiments were conducted in the eastern Sierra Nevada and adjacent Great Basin, where stands of ponderosa pine occur on islands of soil derived from hydrothermally altered andesite (Billings 1950; DeLucia et al. 1988; Callaway et al. 1994). In the arid Great Basin (desert sites), these tree islands occur in a matrix of sagebrush steppe vegetation and pinyon-juniper woodland. In the cool and humid Sierra Nevada and adjacent ranges (montane sites), the islands occur within a matrix of other conifers. The altered andesitic soils are similar across climates with respect to nitrogen, phosphorus, pH, and other edaphic properties (Schlesinger et al. 1989). Moreover, stand density at these open forest sites is low (70–100 individuals ha^{-1}; DeLucia et al. 1988) and the crowns of individual trees do not overlap (Carey et al. 1998). Desert stands experience 3°C higher average annual temperatures, 60% higher summer vapor pressure deficits (*D*), and 50% less precipitation than the montane stands (Callaway et al. 1994; Carey et al. 1998). Therefore, these stands provide a unique opportunity to determine the effects of variation in soil and atmospheric moisture availability on mature trees without the confounding effects of stand density and nutrient availability.

Technical limitations, the remote locations of some sites, and cost associated with in situ transpiration measurements (e.g., Oren et al. 1996; Ewers et al. 1999) precluded the ability to sample a large number of desert and montane stands. However, sites within each climate group exhibit identical patterns of biomass allocation and physiology (Callaway et al. 1994; Carey et al. 1998). Based on this evidence and our logistical constraints, we selected one representative site in each climate group for all measurements. Measurements on desert trees were made at the Desert Research Institute (DRI) site (39°35′ N, 119°47′ W) which receives 247 mm of precipitation annually and has a mean summer *D* of 4.02 kPa. During the 1997 growing season (April to September), maximum air temperatures varied between 24–39°C during the summer and 28–30°C during the fall, and the area received 58 mm of precipitation. Maximum *D* was 5.7 kPa. Measurements on montane trees were made at the Virginia Range site (39°22′ N, 119°41′ W) which receives 479 mm of precipitation annually and has a mean summer D of 2.55 kPa. During the 1997 growing season, maximum daily air temperatures varied between 15–34°C during the summer and between 20–27°C during the fall, and the area received 86 mm of precipitation. Maximum D was 3.8 kPa.

Sap flow

We measured sap flow using the constant-heating method of Granier (1985, 1987) on six trees at each site. To determine if sap flow varied with size, we sampled trees that were representative of the size distribution at each site, as measured by the diameter at the base of the live crown (BLC). Because trees were open grown, the height of the BLC was often below that of breast height (1.4 m). Our objective was to quantify the relative differences in water balance between desert and montane trees that are attributable to variation in biomass allocation and K_S. To minimize the influence of environmental variation on our ability to detect differences between desert and montane trees during a given season, we made measurements on clear, sunny days when soil moisture availability, temperature, and relative humidity were comparable across sites. The desert population was sampled from 21 to 27 June and from 22 to 28 August. The montane population was sampled from 1 to 7 July and from 2 to 8 September. The June/July measurements will be referred to as 'summer' and the August/September measurements will be referred to as 'fall.'

Sap flow sensors consisted of a pair of probes, each 2 cm long and 0.2 cm in diameter, inserted radially to a depth of 2.5 cm just below the BLC. A single sensor was installed in each tree. The probes were placed into freshly bored holes separated vertically by 10 cm. The upper probe was heated by means of a thermally insulated constantan wire coiled around its length. The constantan heating coil had a resistance of 66 Ω and was heated with a 50-mW power supply. To correct for temperature gradients in the sapwood between the heated and reference sap flow probes, we made temperature measurements of sapwood with a separate pair of unheated probes following procedures described in Goulden and Field (1994). Stems were insulated with reflective insulation (Reflectix Inc., Markleville, Ind.). Following Granier (1985, 1987), sap flow density (J_S, g m^{-2} s^{-1}) was calculated according to the temperature difference between the heated and reference probe by means of an empirically derived relationship. Sap flow was recorded every minute, and 10-min averages were stored using a CR-10 or 21X data logger (Campbell Scientific, Logan, Utah). Simultaneously with sap flow, D and air temperature at each site were measured with a shielded temperature and relative-humidity probe (Model 207; Campbell Scientific). Photosynthetically active incident irradiance (PAR) was measured with an LI-190SB Quantum sensor (LI-COR, Lincoln, Neb.).

Transpiration

To determine whole-tree transpiration (E, g s^{-1}) we multiplied J_S by the area of hydroactive xylem in the stem (A_S; sapwood area). In September, each tree was cored at 90° intervals around the bole circumference at the same height as sap flow measurement. Hydroactive xylem was determined by staining cores with a 4% solution of bromocresol green to delineate sapwood from heartwood (e.g., Callaway et al. 1994). Sapwood area was calculated as the difference between total surface area and heartwood surface area of a stem with a radius equal to 1/2 of underbark diameter.

To determine the degree that J_S varied radially in the sapwood, we placed probes at depths of 2.5 and 7 cm (the greatest depth possible with our probes) into the sapwood of a single large [40 cm diameter(D) BLC] tree at the DRI site. During the 4-day (11–14 July) measurement period, average J_S between probes varied by <3% (H. Maherali, unpublished data) at light saturation (PAR>900 µmol m^{-2} s^{-1}). We could not determine variation in J_S along the entire radius because sapwood extended to a depth of 16 cm in some large trees. We therefore assumed that J_S was uniform through the sapwood for calculations of maximum transpiration. Because we did not sample J_S around the stem, our measurements of absolute transpiration may be overestimates and should be interpreted with caution. Despite these limitations, our measurements of absolute water flux through the stem were very consistent with those reported in the literature for similar-sized pines (Wullschleger et al. 1998). To minimize the potential impact of variation in sap flow velocity in the sapwood among trees, probes were inserted into the north aspect of sampled trees (e.g., Schulze et al. 1985). Tree-to-tree variation in transpiration per unit leaf area (E_L) within populations was lower than the differences between sites (Figs. 1, 2), indicating that our measurements captured the relative differences in E_L between desert and montane trees. The relationship between sapwood area and DBLC also did not differ between desert and montane trees (R.M. Callaway, E.V. Carey, E.H. DeLucia, unpublished data), ensuring that differences in E between desert and montane trees were not driven simply by variation in hydroactive xylem area.

Because of water storage, sap flow through the bole lagged behind transpiration from the crown. Thus, E was calculated by lagging sap flow by 1–3 h, relative to PAR and D, based on the water storage of each tree at each time period (see Water storage, below) as in Granier and Loustau (1994). Mean maximum transpiration rate per tree per measurement period (E_{MAX}, g s^{-1}) was recorded as the mean of transpiration between 1100 and 1300 hours PST, when the effect of water storage was minimal. Total transpiration per day was calculated as the integral of the diel course of E.

Crown conductance

Canopy conductance, an estimate of canopy-averaged stomatal conductance (g_C, mmol m^{-2} s^{-1}) on a projected leaf area basis, was calculated using a modified Penman-Montieth equation (Martin et al. 1997; Ewers et al. 2000) with the assumptions that conifer canopies have strong aerodynamic coupling to the atmosphere and that D has no vertical gradient through the canopy. Therefore, boundary layer conductance is large relative to stomatal conductance, and temperature differences between leaves and the air are negligible (Tan et al. 1978; Whitehead and Jarvis 1981):

$$g_C = \frac{E}{\Delta W \times A_L} \times \frac{\gamma\lambda}{\rho c_p} \tag{1}$$

where A_L is projected leaf area, ΔW is the leaf-to-air vapor pressure gradient, expressed as a mole fraction to correct for differences in altitude between sites (e.g., Pearcy et al. 1991), γ is the psychrometric constant (kPa K^{-1}), λ is the latent heat of vaporization of water (J kg^{-1}), ρ is the density of moist air (kg m^{-3}) and c_p is the specific heat of moist air (J kg^{-1} K^{-1}). Projected leaf area was calculated from sapwood area using separate regressions for desert and montane trees reported in Callaway et al. (1994). Regressions of leaf area versus sapwood area were highly significant and r^2 was 0.96 and 0.94 for desert and montane trees, respectively (Callaway et al. 1994).

Whole-tree hydraulic conductance

In situ hydraulic conductance (K_H) from the soil through the leaf was calculated for all measurement periods after Wullschleger et al. (1998):

$$K_H = \frac{E_{MAX}}{[\Psi_P - \Psi_M]} \tag{2}$$

where Ψ_P is predawn water potential and Ψ_M is midday water potential. Although stored water can uncouple the close relationship between transpiration and leaf water potential, our calculations of K_H were made during peak transpiration at midday (E_{MAX}) when the effects of capacitance on transpiration were minimal (e.g., Ryan et al. 2000). Water potential measurements were made on exposed shoots around the lower third of the crown of each tree. A single shoot was sampled at each of three points (in 60° intervals around the tree) at each measurement period and the value for each tree calculated as the mean of these three samples. Site water potential was calculated as the average of all trees. Predawn water potential measurements were made between 0400–0500 hours PST and midday measurements were made between 1230–1330 hours PST at each site with a pressure chamber (Plant Moisture Status Instrument Company, Corvallis, Ore.). Based on diurnal measurements of water potential at these sites (DeLucia et al. 1988), these times corresponded with maximum and minimum water potential. Pine canopies at each site were open grown, ensuring that all shoots were fully and equally exposed to the atmosphere. We assumed that trees had reached equilibrium with the soil overnight, and that Ψ_P represents an estimate of soil water potential.

In situ leaf-specific hydraulic conductance (K_L) was calculated as K_H/A_L. Calculation of K_L was therefore dependent on direct measurements of sap flow, [$\Psi_P - \Psi_M$], and A_L/A_S as a scalar (Ewers et al. 1999). Because A_L/A_S does not vary with tree size in desert and montane trees (Callaway et al. 1994; R.M. Callaway, personal communication), there are no a priori expectations of size-dependent variation in K_L. To estimate the variance around K_L, we calculated K_L based on the predicted upper and lower 95% confidence limit values of leaf area from the regression equations in Callaway et al. (1994). Thus, error bars around mean K_L represent the 95% confidence limits associated with estimated leaf area per tree. Temperature, by influencing water viscosity, can affect water flux (Cochard et al. 2000). To compare water transport capacity (e.g., hydraulic conductance) between desert and montane trees, we corrected J_S for differences in water viscosity associated with temperature differences in the sapwood of trees between climates. All conductance measurements were standardized to a sapwood temperature of 20°C.

Sapwood relative water content

Sapwood relative water content (RWC, %) was sampled with an increment borer four times during the summer on each desert (n=6) and montane (n=6) tree at a height of 1.3 m above the soil surface and to a depth of 6 cm. To estimate RWC at maximum water content, samples were collected between 0600–0800 hours PST, before sap flow started. RWC was calculated as in Waring and Running (1978) assuming a density of 1.53 g cm^{-3} for lignin and cellulose in wood (Siau 1971).

Water storage

We used the time lag between the time of day that transpiration began (accompanying sunrise and a rise in D) and the beginning of sap flow (J_S) to estimate stored water use by each tree (Holbrook 1995). We verified that transpiration began with the rise in D at sunrise by measuring stomatal conductance during a subset of the measurement period (H. Maherali, personal observations). Stomatal conductance was measured with a steady-state null balance porometer (LI-COR). With the assumption that sap flow through the stem was equal to transpired water over a 24-h period (Schulze et al. 1985; Pallardy et al. 1995; Martin et al. 1997; Phillips et al. 1997), we offset the beginning of the sap flow trace to match the time of day that D began to increase at sunrise (refer to the Transpiration calculations, above). Stored water for each tree was calculated as the difference between the amount of water transpired starting at sunrise and the amount of water taken up by the stem until the point that sap flow intersected with transpiration (i.e., the sum of the difference between E and J_S for all periods that $E \geq J_S$; following Schulze et al. 1985; Holbrook 1995; Goldstein et al. 1998).

Because water storage was quantified based on the lag time between E and J_S and not directly through diurnal leaf-level measurements of E, our estimates of storage may not necessarily be accurate in absolute terms, although they are in agreement with the literature (as reviewed in Wullschleger et al. 1998). Storage was determined in the same way for all trees, ensuring that relative differences among trees are valid.

Because J_S was measured at the BLC, only water stored in the aboveground portions of the tree (sapwood and needles) could be considered. Water storage in heartwood was ignored for two reasons. First, the amount of heartwood in ponderosa pine trees used for our study was small, constituting only 3 and 4.7% of total wood biomass in large (50 cm diameter at breast height) desert and montane trees, respectively (Callaway et al. 1994). Second, occluded xylem conduits and low water content (ca 10%) in pine heartwood prevent water transport (Whitehead and Jarvis 1981; Holbrook 1995; Kravka et al. 1999). Other work also indicates that heartwood is not likely to contribute a biologically significant amount of water to the transpiration stream in conifers (Whitehead and Jarvis 1981; Holbrook 1995). We have no information on allocation to roots in this experimental system, and could not measure root capacitance.

Statistical analysis

We used a one-way repeated-measures analysis of variance (ANOVAR) to test for overall differences between climates and to determine if response variables differed between summer and fall. The analysis was done on mean values calculated over 5 days for each time period. Time was a within-subjects factor, whereas climate was a between-subjects factor in the model. DBLC was used as a covariate when size-dependent variables such as transpiration and hydraulic conductance were analyzed. If the effects of climate were significant in the ANOVAR, statistical comparisons between climate groups and within a given time period were made using analysis of covariance (ANCOVA; Sokal and Rohlf 1995). We tested differences among slope coefficients by including the climate×DBLC interaction term in each model. If the interaction term was non-significant (i.e., the slopes were homogeneous), we removed it from the model and tested for differences between climate groups (intercepts). Relationships between K_H, K_L, E_{MAX}, E_{LMAX}, reliance on water storage, and tree size were fit with linear least-squares regression. Statistical analyses were done with Systat 7.0 (SPSS Inc., Evanston, Ill.)

Results

In the summer, mean maximum J_S was 31.80±5.74 and 24.34±3.05 g m^{-2} s^{-1} for desert and montane trees (a 30.6% difference), respectively. In the fall, J_S was 25.33±8.52 and 16.36±4.64 g m^{-2} s^{-1} in desert and montane trees (a 54.8% difference), respectively. When corrected for sapwood temperature differences between sites, J_S in desert trees was 26.7% higher than in montane trees in the summer and 43.8% higher in the fall. Mean J_S did not vary with tree size in the summer or fall (P>0.10). Regardless of temperature correction, J_S was significantly higher in desert versus montane trees during the summer and fall (P<0.05). Mean J_S declined by 20% in desert trees and 35% in montane trees from summer to fall (P<0.05).

The mean (±1 SE) diurnal patterns of water flux per unit leaf area (E_L) for desert and montane trees measured during summer and fall are shown in Figs. 1 and 2. For the daylight period between 1000 and 1800 hours, when PAR>900 µmol m^{-2} s^{-1}, E_L was always greater in desert than in montane trees. Maximum transpiration rate per tree (E_{MAX}, g/s), measured at midday, increased with tree size (P<0.001) and was significantly higher in desert than in montane trees in the summer (Fig. 3A; P<0.05) and fall (Fig. 3B; P<0.05). Over-

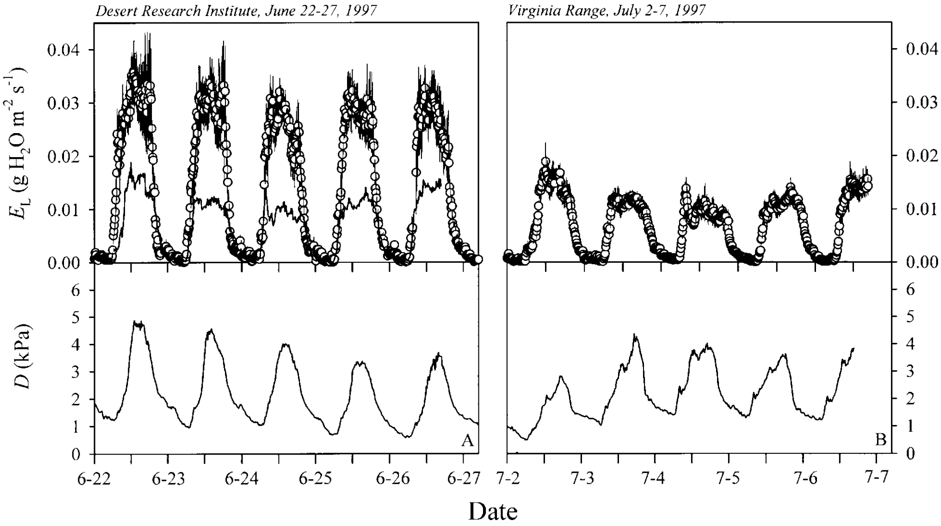

Fig. 1 Mean (±1 SE) diurnal leaf level transpiration (E_L) and vapor pressure deficit (D) during June and July for desert trees (*Desert Research Institute*) (**A**) and montane trees (*Virginia Range*) (**B**), expressed at 10-min intervals. **A** For comparison, mean E_L for montane trees is also shown as a *solid line*

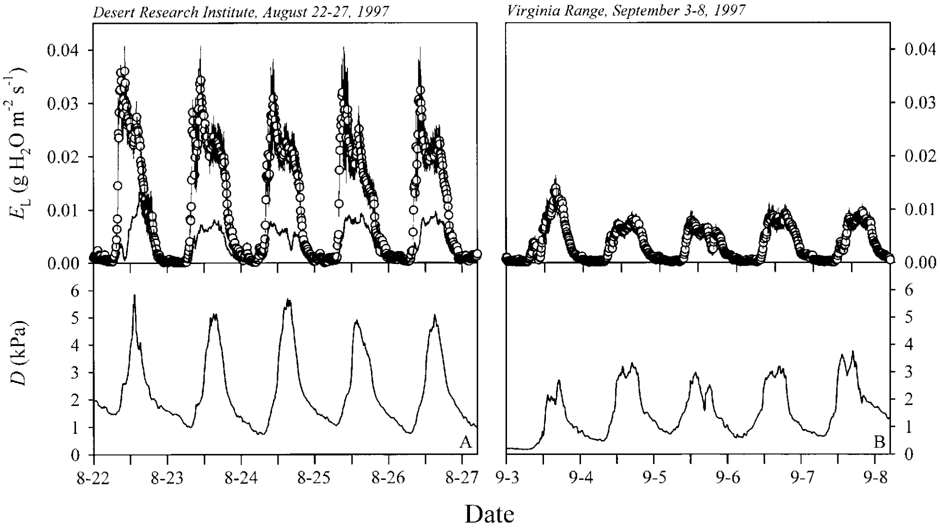

Fig. 2 Mean (±1 SE) diurnal leaf level transpiration (E_L) and vapor pressure deficit (D) during August and September for desert trees (*Desert Research Institute*) (**A**) and montane trees (*Virginia Range*) (**B**), expressed at 10-min intervals. **A** For comparison, mean E_L for montane trees is also shown as a *solid line*

Table 2 Mean (±1 SE) daily transpiration and reliance on water storage by desert (n=6) and montane (n=6) ponderosa pine trees measured during summer and fall. Differences were tested with analysis of variance with repeated measures (ANOVAR). Diameter at the base of the live crown was used as a covariate in the statistical analyses for all size-dependent variables (*n.s.* not significant)

	June		September		ANOVAR (P)	
	Desert	Montane	Desert	Montane	Climate	Time
Daily transpiration (kg)	111.0±28.4	104.1±24.4	82.5±23.1	52.7±10.1	0.005	0.01
Water storage (kg)	10.9±2.6	11.1±3.1	11.7±2.9	9.4±1.8	n.s.	n.s.
Percent of total transpired	10.7±1.3	11.0±1.5	15.2±1.1	18.0±1.9	n.s.	0.03
Lag time (h)	1.1±0.1	1.2±0.1	1.7±0.1	1.9±0.1	n.s.	0.006

all, the mean maximum transpiration rate fell from summer to fall as soil water availability declined (P<0.01). The mean maximum leaf transpiration rate (E_{LMAX}, g m^{-2} s^{-1}) increased with tree size for desert trees in the summer (r^2=0.67, P=0.05; Fig. 3C) but not in the fall (P>0.05; Fig. 3D). E_{LMAX} was relatively constant with size (P>0.05) in montane trees. During the summer, E_{LMAX} was 0.0278 and 0.0125 g m^{-2} s^{-1} in desert versus montane trees, a difference of 123%. In the fall, E_{LMAX} was 0.0211 and 0.0082 g m^{-2} s^{-1} in desert versus montane trees, a difference of 158%. Total water transpired per day (kg day^{-1}) by desert and montane trees was strongly size dependent (Table 2). Desert trees transpired more water than montane trees at both measurement periods (P<0.05). Total transpiration also declined from summer to fall (P<0.05; Table 2).

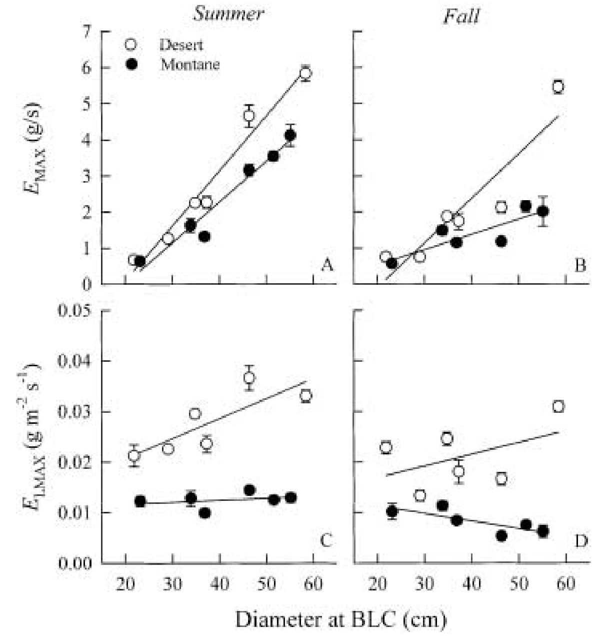

Fig. 3 Mean (±1 SE) maximum whole-tree transpiration rate (E_{MAX}) measured over the course of 5 days as a function of tree diameter at the base of the live crown for desert and montane sites during the summer (**A**) and fall (**B**). Mean (±1 SE) maximum transpiration rate per unit projected leaf area (E_{LMAX}) measured over the course of 5 days as a function of diameter at the base of the live crown for desert and montane trees during the summer (**C**) and fall (**D**). E_{LMAX} is the maximum leaf-level transpiration rate recorded between 1100–1300 hours during each sampling period (Figs. 1, 2). Desert trees had higher E_{MAX} and E_{LMAX} than montane trees in both summer and fall ($P<0.05$)

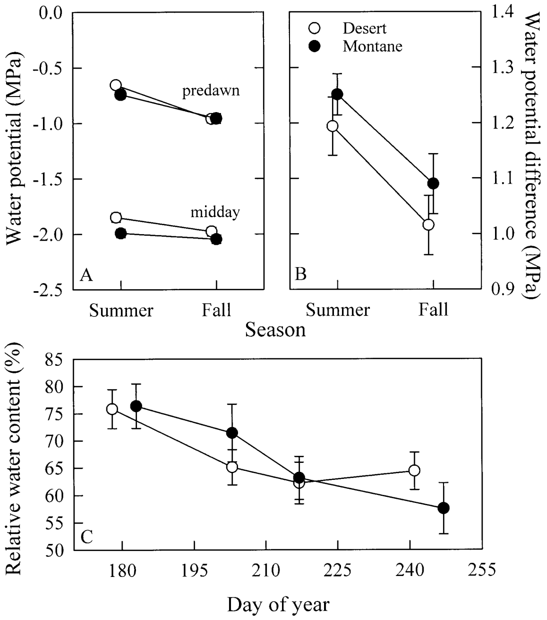

Fig. 4 Mean (±1 SE) predawn and midday shoot water potential measured on desert and montane trees during the summer and fall (**A**). Mean (±1 SE) soil to leaf water potential difference for desert and montane trees during the summer and fall (**B**). The seasonal pattern of mean (±1 SE) sapwood relative water content (RWC) measured on desert and montane trees (**C**). Predawn and midday water potential, water potential difference, and sapwood RWC did not differ between montane and desert trees. All response variables declined from summer to fall. Water potential data were collected for six trees at each site. Each replicate represents a mean water potential calculated from three subsamples on each tree

Predawn and midday needle water potential and the soil-to-needle water potential difference (Fig. 4A, B) did not differ between montane and desert sites in either summer or fall ($P>0.05$), suggesting that trees in both climates were likely deeply rooted and had stable access to soil water (DeLucia et al. 1988). Water potential and the soil-to-needle water potential difference for montane and desert trees declined from summer to fall ($P<0.01$). Water potential variables did not vary with tree size ($P>0.05$). Sapwood RWC declined from a high of circa 76% in late June to 58–64% by early September ($P<0.001$), but did not differ between montane and desert trees ($P>0.05$; Fig. 4C).

Temperature-corrected whole-tree hydraulic conductance (K_H) was 26.2% higher in summer and 47.8% higher in fall in desert versus montane trees (Fig. 5A, B; $P<0.05$). K_H also increased with stem diameter at BLC in all cases and did not change statistically from summer to fall. We calculated leaf-specific hydraulic conductance (K_L) to determine if desert and montane trees differed in their capacity to supply leaves with water. Desert trees had 129% higher K_L than montane trees in the summer (2.41×10^{-5} versus 1.05×10^{-5} kg m^{-2} s^{-1} MPa^{-1}, $P<0.001$; Fig. 5C) and 162% higher K_L in the fall (1.97×10^{-5} versus 0.75×10^{-5} kg m^{-2} s^{-1} MPa^{-1}, $P<0.001$; Fig. 5D). There was a non-significant trend towards increased whole-tree K_L with increasing tree size in desert trees in the summer ($P=0.08$) and the fall ($P=0.23$). In montane trees, K_L remained relatively constant with tree size. Overall, K_L did not change for montane and desert trees from summer to fall ($P>0.05$).

To determine if desert and montane trees also differed in their degree of stomatal opening, we calculated canopy-average stomatal conductance on a leaf area basis using a simplified Penman-Montieth model. Canopy conductance decreased with D in all trees at all measurement periods ($P<0.05$). Maximum g_C, (which occurred at 1.5–2 kPa; Fig. 6) was 3.91 times higher in desert trees relative to montane trees averaged over the summer and fall.

The amount of daily transpiration contributed by water storage did not differ between desert and montane trees and did not vary between summer and fall (Table 2). Absolute water storage (kg day^{-1}) increased with tree size (Fig. 7; $P<0.05$), but was constant with tree size when expressed as a percentage of daily transpiration (Table 2). As total transpiration and soil water availability declined in the fall, the percentage of transpiration coming from stored water increased from 11 to 17% (Table 2). Reflecting greater reliance on stored water, the lag time between

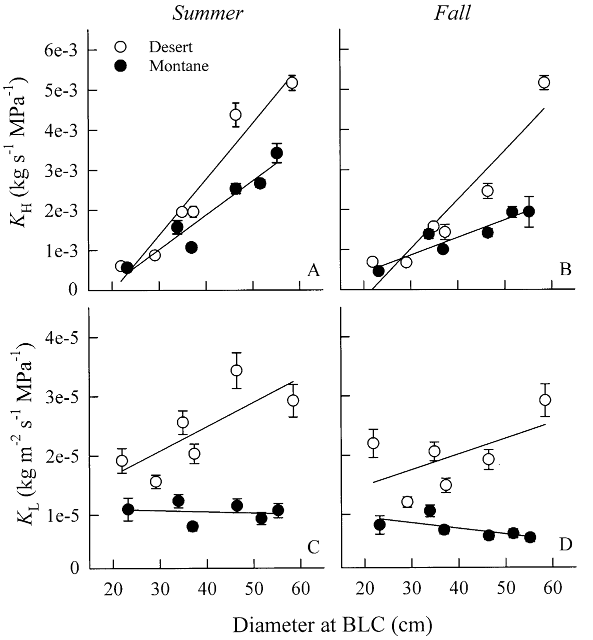

Fig. 5 Mean (±1 SE) maximum in situ hydraulic conductance (K_H) as a function of tree diameter at BLC for desert and montane during the summer (**A**) and fall (**B**). Mean in situ leaf-specific hydraulic conductance (K_L) as a function of diameter at the base of the live crown for desert and montane trees during the summer (**C**) and fall (**D**). Error bars around mean K_L represent the 95% confidence limits associated with the prediction of leaf area per tree from regression equations (Callaway et al. 1994; see text for details). Desert trees had higher K_H and K_L than montane trees at both measurement periods ($P<0.05$). K_H and K_L did not differ significantly from summer to fall. All conductance values were corrected for sapwood temperature differences between desert and montane sites

the beginning of transpiration and the beginning of J_S was longer in the fall than in the summer but did not vary with tree size or between desert and montane trees (Table 2).

Discussion

Differences in leaf versus sapwood biomass allocation and K_S between desert and montane trees corresponded strongly to differences in water transport. Diurnal E_L was always greater in desert than montane trees during high light (1000–1800 hours) in both the summer and fall (Figs. 1, 2). Maximum leaf-level transpiration, measured at midday, was 123% higher and 159% higher in desert versus montane trees in the summer and fall, respectively (Fig. 3C, D). The average 35% increase in sap flow (J_S) and a 48% lower leaf:sapwood area ratio (A_L/A_S) both contributed to the 145% (averaged over summer and fall) increase in K_L in desert relative to montane trees (Fig. 5). In contrast, there was no net difference in diurnal water storage between desert and montane trees (Fig. 7, Table 2). Thus, our results suggest that the primary effect of high allocation to sapwood relative to leaf area in ponderosa pine is to increase K_L.

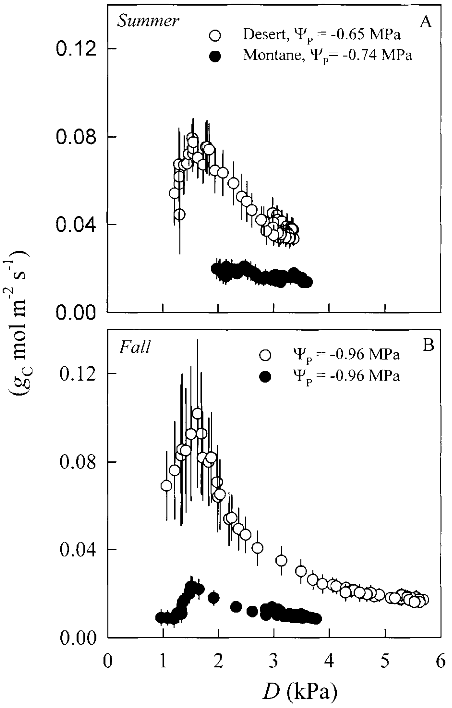

Fig. 6 The response of mean (±1 SE) canopy conductance per unit projected leaf area (g_C) to vapor pressure deficit (D) of six desert and six montane trees during the summer (**A**) and fall (**B**) measurement periods. Data are from measurements made on a single clear day at each sampling period. Only data points above an incident irradiance of 900 µmol m^{-2} s^{-1} were included. Mean predawn shoot water potentials (Ψ_P) for desert and montane trees are shown for each measurement period

Two other factors that may potentially contribute to increased K_L in desert relative to montane trees can be ruled out in this study. First, a temperature-dependent decrease in water viscosity in desert trees could increase hydraulic conductance (Cochard et al. 2000). However, the sapwood temperature difference between sites was small (ca 3°C; H. Maherali, unpublished data), and only reduced the difference in J_S between desert and montane trees by 7.5%. Temperature-corrected K_L in desert trees was still more than twice that of montane trees (Fig. 4C, D). Second, higher atmospheric evaporative demand at the desert site suggests that differences in J_S and E_L could be driven by D. However, maximum canopy-averaged stomatal conductance (g_C) over the growing season was two to four times as high in desert relative to montane trees across the range of D (Fig. 6). These data corroborate observations of the nearly twofold higher stomatal conductance in desert relative to montane trees reported previously (DeLucia and Schlesinger 1991), and support the conclusion that there are substantial differences in hydraulic architecture between desert and montane trees. In an earlier study at the same sites, Carey et al. (1998) found that foliage on desert trees had higher photosynthetic capacity than similar-aged needle cohorts on montane trees. Thus, a greater degree of stomatal opening may also facilitate higher photosynthetic rates in desert relative to montane trees.

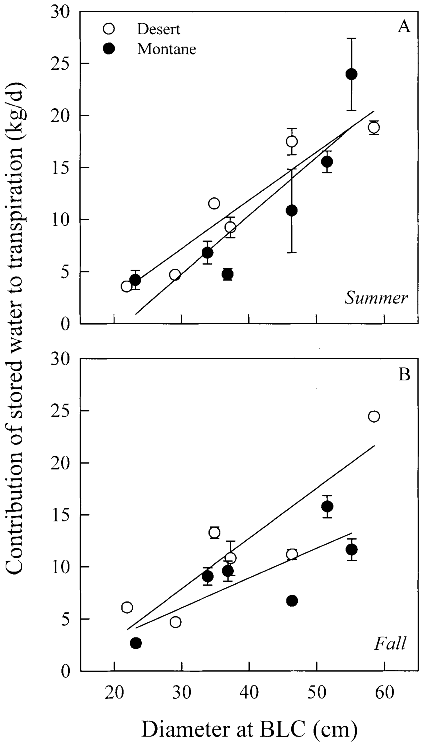

Fig. 7 Mean (±1 SE) contribution of stored water to transpiration measured over the course of 5 days as a function of tree diameter at the base of the live crown for desert and montane sites during the summer (**A**) and fall (**B**). Desert and montane trees did not differ in stored water use at either measurement period

The functional significance of climate-related variation in tree structure between desert and montane ponderosa pine (Table 1) can be evaluated using a simple hydraulic model proposed by Schäfer et al. (2000), in which g_C is proportional to the product of A_S/A_L, the water potential gradient, K_S, and the inverse of tree height, (e.g., Ryan et al. 2000). In the absence of a shift in the water potential gradient between climates (Fig. 4A), a 1.83-fold increase in A_S/A_L (Callaway et al. 1994), a 1.19-fold increase in K_S (Maherali and DeLucia 2000b), and a 1.61-fold increase in the inverse of tree height yields a predicted 3.48 times higher g_C for desert relative to montane trees. This value is similar to the 3.91-fold higher g_C we observed for desert relative to montane trees averaged over the measurement periods (Fig. 6). However, the 12% difference between observed and predicted values of g_C suggests that that other components of the soil-to-leaf hydraulic pathway may have also adjusted to climate. Recent models and experiments (Sperry et al. 1998; Hacke et al. 2000) indicate that adjustments in the root:leaf area ratio (A_R/A_L) have substantial implications for water uptake and transport. For example, Ewers et al. (2000) reported that K_L increased proportionately with A_R/A_L in *P. taeda* spanning a fertilization and irrigation treatment. Because roots are inaccessible (DeLucia et al. 1988) in our experimental system, we could not assess their contribution to g_C in desert and montane trees. However, we suggest that an increase in A_R/A_L may have also contributed to higher g_C in desert relative to montane trees.

Although g_C declined with increased evaporative demand in desert and montane ponderosa pine, transpiration continues at relatively high rates in the desert environment because of extreme atmospheric vapor pressure deficits (4–6 kPa). This observation suggests that stomatal closure may not be the only mechanism that prevents xylem tensions from decreasing to levels that cause cavitation (Tyree and Sperry 1988). For example, despite differences in stomatal opening and transpiration rates, desert and montane trees reached similar minimum xylem tensions at midday (Fig. 4A) and did not differ in their vulnerability to cavitation (Table 1; Maherali and DeLucia 2000b). Sapwood relative water content over the growing season also did not differ between desert and montane trees, suggesting that trees in different climates had similar amounts of embolism induction. These results are consistent with the interpretation that high K_L, caused by shifts in biomass allocation and K_S, represents a long-term response to high atmospheric evaporative demand that allows desert trees to avoid incurring the cost of increased xylem cavitation.

On average, stored water provided between 11–17% of daily transpiration (Table 2) during the summer and fall, an amount consistent with that of other species (ca 10–25% of daily transpiration; Schulze et al. 1985; Loustou et al. 1996; Goldstein et al. 1998; Wullschleger et al. 1998). In woody plants, water storage has three components: capillary storage, elastic storage, and cavitation release (Tyree and Yang 1990; Holbrook 1995). Capillary storage and cavitation release are the two largest water storage pools (Tyree and Yang 1990; Holbrook 1995). However, they are unlikely to have contributed substantial water to transpiration in ponderosa pine during the growing season for two reasons. First, capillary water storage occurs in intercellular spaces and the lumens of cavitated xylem elements (Zimmermann 1983; Tyree and Yang 1990; Holbrook 1995) and does not persist in wood at xylem tensions less than –0.5 MPa (Tyree and Yang 1990; Holbrook 1995). Desert and montane trees never reach predawn water potentials higher than –0.5 MPa, even in early May (e.g., DeLucia et al. 1988), suggesting that capillary water is unlikely to be available. Second, the minimum water potential in desert and montane trees was stable during the growing season and did not drop below –2.05 MPa (Fig. 2A), a level that does not induce substantial (<20%) xylem cavitation in these ponderosa pine populations (Maherali and DeLucia 2000b).

The relatively small amount of stored water available for diurnal transpiration (Table 2) suggests that elastic storage provides the majority of stored water in ponderosa pine. Elastic storage represents water that is liberated when cell volume decreases because of elastic contraction (Tyree and Yang 1990). Because sapwood is composed of inelastic and lignified tracheids, this storage pool is relatively small (Tyree and Yang 1990). Although the amount of transpiration withdrawn from water storage pools in desert and montane trees is small, it may still be important for carbon assimilation. For example, storage provides enough water for 1–2 h of transpiration per day, permitting stomata to open well before sap flow starts in the morning (Table 2). Given that stomata are nearly closed by midday (when D>3.5 kPa; Fig. 6), photosynthesis during this extra period of high stomatal conductance provided by storage could account for a substantial portion of daily carbon fixation.

Large differences in sapwood:leaf allocation did not translate into differences in the amount of stored water contributed to E between desert and montane trees, in either absolute terms (Fig. 7), or as a percentage of total transpiration (Table 2). If water storage capacity during the growing season in ponderosa pine is determined primarily by tissue elastic properties, both sapwood and foliar water storage pools could be physiologically important for transpiration in desert and montane trees. For example, water storage per unit mass of ponderosa pine foliage (0.076 kg H_2O kg^{-1} foliage MPa^{-1}; H. Maherali, unpublished data) in the –0.5 to –2.0 MPa water potential range is nearly twice that for conifer sapwood (Tyree and Yang 1990). This pattern, coupled with the observation of 70% higher allocation to foliage in montane than in desert trees (Table 1) may result in significantly higher needle storage in the former. Higher water storage in needles could effectively compensate for decreased sapwood water storage capacity caused by lower sapwood mass (e.g., Tyree 1988), resulting in similar water storage capacities for desert and montane trees during the growing season.

In contrast to other studies (Ryan and Yoder 1997; Hubbard et al. 1999; Ryan et al. 2000), our results suggest that large desert and montane ponderosa pine trees do not incur hydraulic limitations of photosynthesis relative to smaller trees. We found that E_L and K_L increased or remained constant with tree size in desert and montane trees, respectively (Figs. 3C, D, 5C, D). Using the same study populations, Carey et al. (1998) found that the size-dependent pattern of photosynthetic capacity in desert and montane trees paralleled our observations for hydraulic conductance. Photosynthetic capacity increased with size in desert trees, but decreased slightly or remained constant with size in montane trees. These results are also not unique to our experimental system, as leaf water supply increases (Köstner et al. 1992; Dawson 1996; Martin et al. 1997) or remains constant (Vertessy et al. 1995; Arneth et al. 1996; Teskey and Sherriff 1996; Becker et al. 2000) with increasing tree size in several other species. Variation in size-related patterns of leaf water supply may be accounted for by factors that influence the leaf:sapwood area ratio of trees, such as stocking density and climate. For example, high density in young stands suppresses A_L/A_S relative to larger trees growing in older and less dense stands, resulting in higher K_L in small trees (e.g., Alsheimer et al. 1998). In our experiments, a climate-related decrease in A_L/A_S for desert trees was associated with higher K_L, and with a positive relationship between tree size and K_L. We suggest that differences in A_L/A_S caused by stand density or climate may contribute to the apparent conflict between our results and those of others for ponderosa pine.

Our results are consistent with the hypothesis that pines alter biomass allocation patterns and sapwood permeability in response to rising atmospheric evaporative demands in order to avoid xylem cavitation (Maherali and DeLucia 2000b; Piñol and Sala 2000). In the absence of intraspecific variation for vulnerability to xylem cavitation among these populations (Maherali and DeLucia 2000b), a rise in K_L caused by reduced A_L/A_S in an arid environment would be necessary to prevent xylem tensions reaching levels that cause catastrophic embolism induction. This pattern may be broadly applicable to pine-dominated forests because reduced A_L/A_S in response to rising atmospheric evaporative demands occurs in several North American and European pine species (Mencuccini and Grace 1995; DeLucia et al. 2000). A cavitation avoidance strategy of constraining leaf area to increase K_L could have substantial implications for ecosystem processes such as net biomass production (Carey et al. 1998) and the transfer of water from the soil to the atmosphere.

Acknowledgements This research was supported by grants from the International Arid Lands Consortium (96R-08) and the National Science Foundation (Dissertation Improvement Grant, IBN-9800932). We thank the Desert Research Institute (Reno, Nev.) for providing laboratory space and logistical support. We are particularly indebted to J.T. Ball, J.S. Coleman, K.L. Griffin, and L. Piehl of DRI for their efforts on our behalf. Climate data were provided by the Western Regional Climate Center (Reno, Nev.) and the Utah Climate Center (Logan, Utah). This manuscript was improved by comments from C.M. Caruso, W.T. Pockman, three anonymous reviewers, and members of the physiological ecology group at the University of Illinois.

References

Alsheimer M, Köstner B, Falge E, Tenhunen JD (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

Arneth A, Kelliher FM, Bauer G, Hollinger DY, Byers JN, Hunt JE, McSeveny TM, Ziegler W, Vygodskaya NN, Milukova I, Sogachov A, Varlagin A, Schulze ED (1996) Environmental regulation of xylem sapflow and total conductance of *Larix gmelinii* trees in eastern Siberia. Tree Physiol 16:247–255

Becker P, Meinzer FC, Wullschleger SD (2000) Hydraulic limitation of tree height: a critique. Funct Ecol 14:4–11

Billings WD (1950) Vegetation and plant growth as affected by chemically altered rocks in the western Great Basin. Ecology 31:62–74

Callaway RM, DeLucia EH, Schlesinger WH (1994) Biomass allocation of montane and desert ponderosa pine: an analog for response to climate change. Ecology 75:1474–1481

Carey EV, Callaway RM, DeLucia EH (1998) Increased photosynthesis offsets costs of allocation to sapwood in an arid environment. Ecology 79:2281–2291

Cochard H, Martin R, Gross P, Bogeat-Triboulot MB (2000) Temperature effects on hydraulic conductance and water relations of *Quercus robur* L. J Exp Bot 51:1255–1259

Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. Tree Physiol 16:263–272

DeLucia EH, Schlesinger WH (1991) Resource use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. Ecology 72:51–58

DeLucia EH, Schlesinger WH, Billings WD (1988) Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. Ecology 69:303–311

DeLucia EH, Maherali H, Carey EV (2000) Climate-driven changes in biomass allocation in pines. Global Change Biol 6:587–593

Ewers BE, Oren R, Albaugh TJ, Dougherty PM (1999) Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. Ecol Appl 9:513–525

Ewers BE, Oren R, Sperry JS (2000) Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant Cell Enivron 23:1055–1066

Farrar JF (1999) Acquisition, partitioning and loss of carbon. In: Press MC, Scholes JD, Barker MG (eds) Physiological plant ecology. Blackwell, Oxford, pp 25–43

Goldstein G, Meinzer FC, Monasterio M (1984) The role of capacitance in the water balance of Andean giant rosette species. Plant Cell Environ 7:179–186

Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. Plant Cell Environ 21:397–406

Goulden ML, Field CB (1994) Three methods for monitoring the gas exchange of individual tree canopies: ventilated-chamber, sap-flow and Penman-Monteith measurements on evergreen oaks. Funct Ecol 8:125–135

Grace J (1997) Towards models of resource allocation by plants. In: Bazzaz FA, Grace J (eds) Plant resource allocation. Academic Press, New York, pp 279–291

Granier A (1985) Une nouvelle methode pour la mesure de flux de seve brute dans le tronc des arbres. Ann Sci For 42:193–200

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

Granier A, Loustau D (1994) Measuring and modeling the transpiration of a maritime pine canopy from sap flow data. Agric For Meteorol 71:61–81

Hacke UG, Sperry JS, Ewers BE, Ellsworth DS, Schafer KVR, Oren R (2000) Influence of soil porosity on water use in *Pinus taeda*. Oecologia 124:495–505

Holbrook NM (1995) Stem water storage. In Gartner BL (ed) Plant stems: physiology and functional morphology. Academic Press, New York, pp 151–174

Holbrook NM, Sinclair TR (1992a) Water balance in the arborescent palm, *Sabal palmetto*. I. Stem structure, tissue water release properties and leaf epidermal conductance. Plant Cell Environ 15:393–399

Holbrook NM, Sinclair TR (1992b) Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and stem water storage. Plant Cell Environ 15:401–409

Hubbard RM, Bond BJ, Ryan MG (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol 19:165–172

Köstner BMM, Schulze ED, Kelliher FM, Hollinger DY, Byers JN, Hunt JE, McSeveny TM, Meserth R, Wier PL (1992) Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. Oecologia 91:350–359

Kravka M, Krejzar T, Cermak J (1999) Water content in stem wood of large pine and spruce trees in natural forests in central Sweden. Agric For Meteorol 98–99:555–562

Loustau D, Berbigier P, Roumagnac P, Arruda-Pacheco C, David JS, Ferreira MI, Pereira JS, Tavares R (1996) Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. Oecologia 107:33–42

Maherali H, DeLucia EH (2000a) Interactive effects of elevated CO_2 and temperature on the water transport of ponderosa pine. Am J Bot 87:243–249

Maherali H, DeLucia EH (2000b) Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. Tree Physiol 20:859–867

Margolis H, Oren R, Whitehead D, Kaufmann MR (1995) Leaf area dynamics of conifer forests. In: Smith WK, Hinckley TM (eds) Ecophysiology of conifer forests. Academic Press, New York, pp 181–223

Martin TA, Brown KJ, Cermák J, Ceulemans R, Kucera J, Meinzer FC, Rombold JS, Sprugel DG, Hinckley TM (1997) Crown conductance and tree and stand transpiration in a second-growth *Abies amabilis* forest. Can J For Res 27:797–808

Mencuccini M, Grace J (1995) Climate influences the leaf area/sapwood area ratio in Scots pine. Tree Physiol 15:1–10

Oren R, Zimmermann R, Terborgh J (1996) Transpiration in upper Amazonia floodplain and upland forests in response to drought-breaking rains. Ecology 77:968–973

Pallardy SG, Cermak J, Ewers FW, Kaufmann MR, Parker WC, Sperry JS (1995) Water transport dynamics in trees and stands. In: Smith WK, Hinckley TM (eds) Resource physiology of conifers. Academic Press, New York, pp 301–389

Pearcy RW, Schulze ED, Zimmermann R (1991) Measurement of transpiration and leaf conductance. In: Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW (eds) Plant physiological ecology: field methods and instrumentation. Chapman & Hall, New York, pp 137–160

Phillips N, Nagchaudhuri A, Oren R, Katul G (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sap flow. Trees 11:412–419

Piñol J, Sala A (2000) Ecological implications of xylem cavitation for several Pinaceae in the Pacific northern USA. Funct Ecol 538–545

Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. Bioscience 47:235–242

Ryan MG, Bond BJ, Law BE, Hubbard RM, Woodruff D, Cienciala E, Kucera J (2000) Transpiration and whole-tree conductance in ponderosa pine trees of different heights. Oecologia 124:553–560

Schäfer KVR, Oren R, Tenhunen JD (2000) The effect of tree height on crown level stomatal conductance. Plant Cell Environ 23:365–375

Schlesinger WH, DeLucia EH, Billings WD (1989) Nutrient-use efficiency of woody plants on contrasting soils in the western Great Basin, Nevada. Ecology 70:105–113

Schulze ED, Cermàk J, Matyssek R, Penka M, Zimmermann R, Vasicek F, Gries W, Kucera J (1985) Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees – a comparison xylem flow, porometer and cuvette measurements. Oecologia 66:475–483

Siau JF (1971) Flow in wood. Syracuse University Press, Syracuse, NY

Sokal RR, Rohlf J (1995) Biometry, 3rd edn. Freeman, New York

Sperry JS, Adler FR, Campbell GS, Comstock JP (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant Cell Environ 21:347–359

Tan CS, Black TA, Nnyumah JU (1978) A simple model of transpiration applied to a thinned Douglas-fir stand. Ecology 59:1221–1229

Teskey RO, Sherriff DW (1996) Water use by *Pinus radiata* trees in a plantation. Tree Physiol 16:273–279

Tyree MT (1988) A dynamic model for water flow in a single tree: evidence that models must account for hydraulic architecture. Tree Physiol 4:195–217

Tyree MT, Ewers FW (1991) The hydraulic architecture of trees and other woody plants. New Phytol 119:345–360

Tyree MT, Sperry JS (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. Plant Physiol 88:574–580

Tyree MT, Yang S (1990) Water storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms: the contribution of capillary water and cavitation. Planta 182:420–426

Vertessy RA, Benyon RG, O'Sullivan SK, Gribben PR (1995) Relationships between stem diameter sapwood area, leaf area and transpiration in a young mountain ash forest Tree Physiol 15:559–567

Waring RH, Running SW (1978) Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. Plant Cell Environ 1:131–140

Waring RH, Schlesinger WH (1985) Forest ecosystems: concepts and management. Academic Press, New York

Waring RH, Whitehead D, Jarvis PG (1979) The contribution of stored water to transpiration in Scots pine. Plant Cell Environ 2:309–317

Whitehead D, Jarvis PG (1981) Coniferous forests and plantations. In: Kozlowski TT (ed) Water deficits and plant growth. Academic Press, New York, pp 49–152

Whitehead D, Edwards WRN, Jarvis PG (1984) Relationships between conducting sapwood area, foliage area and permeability in mature *Picea stichensis* and *Pinus contorta* trees. Can J For Res 14:940–947

Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in trees. Tree Physiol 18:499–512

Zimmerman MH (1983) Xylem structure and the ascent of sap. Springer, Berlin Heidelberg New York