Interactive effects of elevated CO_2 and temperature on water transport in ponderosa pine[1]

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Many studies report that water flux through trees declines in response to elevated CO_2, but this response may be modified by exposure to increased temperatures. To determine whether elevated CO_2 and temperature interact to affect hydraulic conductivity, we grew ponderosa pine seedlings for 24 wk in growth chambers with one of four atmospheric CO_2 concentrations (350, 550, 750, and 1100 ppm) and either a low (15°C nights, 25°C days) or high (20°C nights, 30°C days) temperature treatment. Vapor pressure deficits were also higher in the elevated temperature treatment. Seedling biomass increased with CO_2 concentration but was not affected by temperature. Root : shoot ratio was unaffected by CO_2 and temperature. Leaf : sapwood area ratio (A_L/A_S) declined in response to elevated temperature but was not influenced by CO_2. Larger tracheid diameters at elevated temperature caused an increase in xylem-specific hydraulic conductivity (K_S). The increase in K_S and decrease in A_L/A_S led to higher leaf-specific hydraulic conductivity (K_L) at elevated temperature. Stomatal conductance (g_S) was correlated with K_L across all treatments. Neither K_S, K_L, nor g_S were affected by elevated CO_2 concentrations. High K_L in response to elevated temperature may support increased transpiration or reduce the incidence of xylem cavitation in ponderosa pine in future, warmer climates.

Key words: biomass allocation; CO_2; hydraulic conductivity; leaf : sapwood area ratio; Pinaceae; *Pinus ponderosa;* stomatal conductance; temperature; xylem anatomy.

Although there is considerable variation across studies, in many cases growth under elevated atmospheric CO_2 causes a reduction in stomatal conductance (g_S) in trees (Eamus and Jarvis, 1989; Field, Jackson, and Mooney, 1995; Curtis, 1996; Drake, Gonzàlez-Meler, and Long, 1997; Curtis and Wang, 1998). A conclusion drawn from this observation is that water flux through trees and uptake by roots will be reduced in a future high atmospheric CO_2 climate (Eamus and Jarvis, 1989; Field, Jackson, and Mooney, 1995; Drake, Gonzàlez-Meler, and Long, 1997). Stomatal conductance, however, is only one control of water flux through the soil-plant-atmosphere continuum. Another important factor regulating water flux is water conduction through the xylem relative to leaf area, defined as the leaf-specific hydraulic conductivity (K_L; Tyree and Ewers, 1991). Leaf-specific hydraulic conductivity and leaf-level transpiration are correlated, and the role of K_L in controlling leaf water supply is well defined (Meinzer and Grantz, 1990; Tyree and Ewers, 1991; Sperry and Pockman, 1993). Relatively little is known about how K_L responds to elevated atmospheric CO_2 in particular and climate change in general (Saxe, Ellsworth, and Heath, 1998). Measurements of both g_S and K_L in experimental studies may provide a greater understanding of how water flux and uptake by trees will respond to elevated atmospheric CO_2 concentrations.

Leaf-specific hydraulic conductivity is dependent on the conducting efficiency of xylem (specific hydraulic conductivity, K_S) and the relative allocation of biomass to xylem and leaves. Therefore, it represents the long-term effects of growth environment on plant water transport. For a shoot, K_L can be expressed as

$$K_L = \frac{K_H}{A_L} = \frac{[K_H/A_S]}{[A_L/A_S]} \qquad (1)$$

where K_H is the hydraulic conductivity of a stem, A_L is the leaf area, and A_S is the sapwood area. K_H/A_S is the specific hydraulic conductivity of xylem (K_S), and A_L/A_S is the leaf : sapwood area ratio. This relationship can be used to determine whether xylem function or biomass allocation is the primary factor controlling water transport through the shoot. For example, at a constant K_S, a decrease in leaf area would increase K_L. Higher K_L permits increased transpiration without a rise in the water potential gradient, and may be a common feature of plants grown in environments with high evaporative demand (Tyree and Ewers, 1991; Mencuccini and Grace, 1995; Maherali, DeLucia, and Sipe, 1997).

The rise in atmospheric CO_2 concentration is expected to force a temperature increase of 1.5°–4.5°C in North America (Kattenberg et al., 1996; Schimel et al., 1996). This temperature increase will also raise the evaporative power of the air (Gregory, Mitchell, and Brady, 1997), as measured by the atmospheric vapor pressure deficit (VPD). Although elevated CO_2 may reduce leaf-level transpiration (Field, Jackson, and Mooney, 1995; Drake, Gonzàlez-Meler, and Long, 1997), exposure to high temperatures and increased evaporative demand may have

the opposite effect (Kolb and Robberecht, 1996). The pattern of aboveground biomass allocation, which alters K_L, varies substantially in response to CO_2 concentration, temperature, and evaporative demand (Waring and Schlesinger, 1985; Callaway, DeLucia, and Schlesinger, 1994; Callaway et al., 1994; Margolis et al., 1995; Mencuccini and Grace, 1995; Maherali, DeLucia, and Sipe, 1997; Curtis and Wang, 1998). Elevated CO_2 may also affect xylem anatomy (Conroy et al., 1990; Tyree and Alexander, 1993; Atkinson and Taylor, 1996; Saxe, Ellsworth, and Heath, 1998), which alters K_S. The integrated response of shoot hydraulic properties to the interaction of elevated atmospheric CO_2 and temperature is not well understood.

To examine the interactive effects of temperature and CO_2 on tree water transport, we grew ponderosa pine (*Pinus ponderosa* L.) seedlings in a four by two factorial experiment with four levels of atmospheric CO_2 and two levels of temperature. Our objectives were to determine (1) whether growth in elevated CO_2 affects the hydraulic conductivity and biomass allocation of ponderosa pine and (2) whether these effects were modified by exposure to elevated temperatures and associated increases in atmospheric evaporative demand.

METHODS

Plant material and treatment conditions—Ponderosa pine seeds of a single half-sib family were obtained from the Institute of Forest Genetics in Placerville, California, USA. Following stratification at 4°C for 6 wk, seeds were germinated in ''rootainer'' pots (Hummert International, Earth City, Missouri, USA). After 6 wk in a greenhouse under natural light, 80 similar-sized seedlings were transplanted into 3.14-L PVC (polyvinyl chloride) tubes (40-cm deep) containing a mixture of quartz sand and soil loam (10:3 v/v). The top 10-cm layer of each pot consisted of an equal mixture of the potting soil and forest litter collected underneath a ponderosa pine stand at the Institute of Forest Genetics. Litter was applied to inoculate seedlings with appropriate mycorrhizae. Seedlings were assigned to one of eight growth chambers with one of four atmospheric CO_2 concentrations (350, 550, 750, and 1100 ppm) and either a low (15°C nights, 25°C days) or high (20°C nights, 30°C days) temperature treatment. There were ten seedlings in each treatment combination. Our selection of CO_2 concentrations approximated projections of ~575 and ~950 ppm by years 2050 and 2100, respectively, assuming a constant 2% per year increase in anthropogenic emissions (scenario IS92-e; Schimel et al., 1996). The low temperature treatment represents the mean minimum and maximum growing season temperatures for ponderosa pine forests in the western Sierra Nevada at an elevation of 1500 m. We selected elevated temperature treatment conditions based on predictions by current climate models that forecast a maximum 4.5°C increase in mean annual global temperature (scenario IS92-e; Kattenberg et al., 1996). Because atmospheric evaporative demand and temperature covary in nature, we did not control vapor pressure deficit independently of temperature. The low temperature treatment provided a VPD range of 0.7–1.3 kPa, whereas the high temperature treatment provided a VPD range of 1.3–2.4 kPa. Our growth chambers were not designed to control absolute humidity, therefore VPD levels were lower than that normally experienced by ponderosa pine during the growing season in the Sierra Nevada. To minimize a possible chamber effect, plants were rotated among chambers each week. Each set of plants experienced each chamber three times during the experiment. Seedlings were treated with 10 g of slow-release fertilizer (Osmocote, Sierra Chemical Co., Milpitas, California, USA) after transfer to growth chambers and watered to field capacity every 2 d. Seedlings were harvested after 24 wk in the growth cham-

bers, ensuring that the majority of foliage and secondary xylem developed under treatment conditions.

Growth chambers were constructed of aluminum frames with clear cellulose acetate walls and located inside a greenhouse room. Natural light was supplemented with halogen lamps suspended above each chamber to provide a 14-h photoperiod and to maintain minimum incident irradiance (photosynthetically active radiation, PAR) at the tops of the pine seedlings above 300 μmol photons · m^{-2} · s^{-1}. Carbon dioxide concentrations in the chambers were monitored by a SBA-1 IRGA (PP Systems, Haverhill, Massachusetts, USA). Air temperature was measured by a sheltered, copper-constantan thermocouple suspended above the seedlings in each chamber. Relative humidity was measured with a Hygro-M1 dew-point hygrometer (General Eastern Instruments, Watertown, Massachusetts, USA). Carbon dioxide concentration in each chamber was controlled with a custom-built relay control system interfaced with the IRGA (infra-red gas analyzer) that permitted the injection of pure CO_2 into the growth chambers via a solonoid valve. Air temperature was controlled using a closed loop pathway under constant cooling and controlled heat input. Chamber environmental conditions were monitored and controlled by a microcomputer running proprietary software.

Hydraulic conductivity—At harvest intact seedlings were brought to an air-conditioned laboratory, placed underwater, and a 3–5 cm long stem segment between the root collar and first leaf was excised and debarked. Stem segments were placed in a waterbath for 1 h to reduce the exudation of resin. This treatment has the effect of removing emboli from tracheids (Lewis, Harnden, and Tyree, 1994); therefore we could not reliably measure in situ hydraulic conductance in the seedlings. Maximum hydraulic conductance (K_H) was measured as described in Sperry, Donnelly, and Tyree (1988). After soaking, segments were cleared of any remaining air emboli by flushing them with a filtered (0.2 μm) weak HCl solution (pH = 2) under high pressure. Preliminary experiments showed that ponderosa pine reached maximum mass flow rate (Q, in kilograms per second) after 30 min at 170 kPa, so all segments were flushed for 1 h prior to measuring hydraulic conductance. Measurements of K_H were made at a regulated pressure of 45 kPa. Stem efflux was collected and weighed to calculate mass flow rate.

Hydraulic conductance was defined as the mass flow rate divided by the pressure gradient [$Q/(dP/dx)$]. Specific hydraulic conductivity (K_S) was calculated as K_H divided by the stem area of the segment and leaf-specific hydraulic conductivity (K_L) was calculated as K_H divided by the leaf area of the seedling. After measuring hydraulic conductivity, stems were perfused with filtered (0.2 μm) 0.01 basic fuschin solution under hydrostatic pressure (~10 kPa) to determine the functional xylem area of each segment. Dye infiltrations showed that the entire stem was functional xylem except for a very small portion of pith. Therefore stem cross-sectional area was considered equivalent to functional xylem or sapwood area.

Stomatal conductance—Prior to harvest, stomatal conductance to water vapor was measured on 3–5 seedlings per treatment combination with a LI-1600M null-balance porometer (LI-COR, Lincoln, Nebraska, USA) equipped with a 63.4-cm^3 cylindrical cuvette (LI-1600–07). Three measurements were made per plant. Pots were watered to field capacity and placed in the dark for 2 h to allow plants to reach equilibrium with soil water and then exposed to measurement conditions for 1 h. To determine whether an intrinsic reduction (Gunderson and Wullschleger, 1994) in stomatal conductance (g_S) had occurred we made measurements at common environmental conditions. Differences in g_S measured under common environmental conditions may reflect morphological changes in stoma aperture or stomatal density. Stomatal conductance was measured at 21°C, 35% RH, an incident irradiance of 300 μmol · m^{-2} · s^{-1}, and a CO_2 concentration of ~425 ppm.

Xylem anatomy—Measurements of tracheid diameter and length

were made on a subsample of stem segments used for hydraulic conductivity measurements. Stem cross sections (20 μm thick) were made with sliding microtome (American Optical Co., Buffalo, New York, USA) and stained with toluidine blue. We measured radial strips of cells on sectors spaced at 90° intervals in the outermost portion of each cross section. Fifty tracheids were measured for each stem segment. Measurements were made at 430× with a light microscope equipped with an ocular micrometer (Bausch and Lomb, Rochester, New York, USA). Lumen diameter (D) was calculated as: $D = 2ab/(a + b)$, where a and b are the short and long sides of the tracheid, respectively (Lewis and Boose, 1995). The percentage of tracheids in 1-μm diameter classes was calculated as in Sperry and Ikeda (1997).

Wood from the outer portions of the stem segments was used to measure tracheid length. Several 2-cm long slivers of wood were macerated by placing them in a 1:1 solution of 10% nitric acid and 10% chromic acid (Berlyn and Mischke, 1976). After 24 h, samples were washed with distilled water, placed in 70% EtOH, and vortexed with 3 mm diameter glass beads. Tracheids were mounted on a slide and stained with toluidine blue. The lengths of 35–50 tracheids per individual were measured with a light microscope and ocular micrometer as described above.

Biomass allocation—Following harvest seedlings were separated into roots, stems, and needles, oven dried to constant mass (60°C for 48 h) in a forced-convection oven and weighed. Specific leaf area (SLA; in centimetres squared per gram) was calculated on a subsample of needles from each seedling. All-sided leaf area (A) for individual needles was calculated as $A = L(C + 2NR)$, where L is the needle length, N is the number of needles per fascicle, C is the circumference of the fascicle, and R is the fascicle radius. Leaf area per seedling was calculated as the product of SLA and leaf biomass.

Statistical analyses—Because the CO_2 and temperature treatments were not applied independently to each seedling, the plants in each treatment combination are not true replicates (Hurlbert, 1984; Curtis and Wang, 1998). Therefore, we treated the mean of the ten seedlings in each treatment combination as a replicate. We used analysis of covariance (ANCOVA; Sokal and Rohlf, 1995) to determine the effects of CO_2 and temperature on total biomass, root:shoot ratio, K_S, A_L/A_S, K_L, g_S, tracheid diameter, and tracheid length. Temperature was defined as a categorical variable and CO_2 as a continuous variable in the model. A significant temperature by CO_2 interaction in the model indicates that the slopes between a given response variable and CO_2 differed across temperature treatments. If there was no temperature by CO_2 interaction (i.e., the slopes were homogeneous) we tested for a temperature main effect by comparing intercepts. Since responses to elevated CO_2 may be confounded by plant size, we used seedling biomass as a second covariate in our analyses. If plant size did not have a significant effect on the response variable, we removed it from the model. Data were log transformed when appropriate to meet assumptions for ANCOVA. Statistical analyses were performed using Systat 5.2.1 for the Macintosh (SPSS, Evanston, Illinois, USA).

RESULTS

Seedling biomass increased in response to elevated CO_2 (Fig. 1A; $P < 0.01$) and increased marginally in response to elevated temperature ($P = 0.06$). Root and shoot biomasses increased with elevated CO_2, primarily because plants were larger in elevated CO_2 (data not shown, $P < 0.05$). Elevated CO_2 did not directly alter the root:shoot ratio. Although the root:shoot ratio appeared to increase with elevated CO_2 (Fig. 1B), this effect was caused by increased seedling biomass ($P < 0.05$) and not by CO_2 concentration ($P > 0.05$). Root:shoot ratios were also unaffected by temperature ($P > 0.05$). Leaf mass
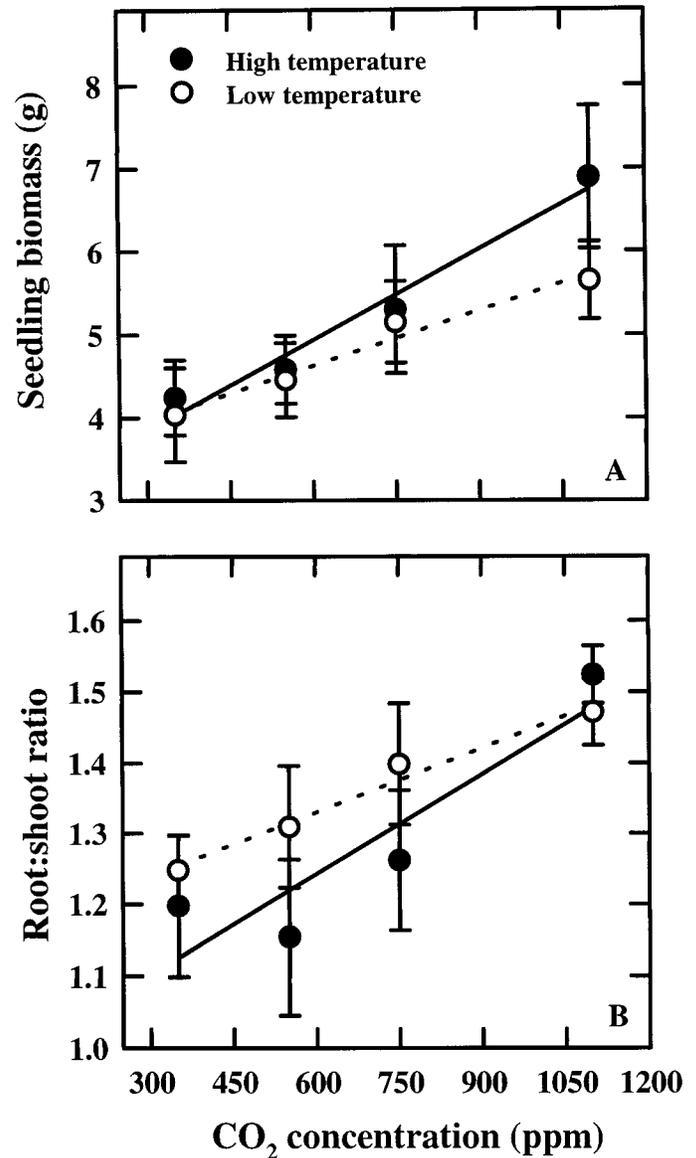
Fig. 1. The effect of atmospheric CO_2 concentration and air temperature on (A) total seedling biomass and (B) the root:shoot ratio for 30-wk-old ponderosa pine seedlings. Each data point is the mean of ($\pm$ 1 SE) of ten seedlings.

and leaf area increased with seedling biomass (data not shown, $P < 0.01$), but were not directly altered by CO_2 or temperature. Sapwood area increased with seedling biomass and elevated temperature (data not shown, $P < 0.05$), but was not directly affected by CO_2 concentration (data not shown, $P > 0.05$)

Specific hydraulic conductivity (K_S) increased in response to elevated temperature (Fig. 2A; $P < 0.01$), but was not affected by elevated CO_2 ($P > 0.05$). Leaf:sapwood (A_L/A_S) area ratio decreased in response to high temperature (Fig. 2B; $P < 0.05$), but was not affected by CO_2 concentration. The combination of higher K_S and lower A_L/A_S led to increased leaf-specific hydraulic conductivity (K_L) at high temperature (Fig. 2C; $P < 0.01$). K_L was not affected by elevated CO_2 concentrations (P
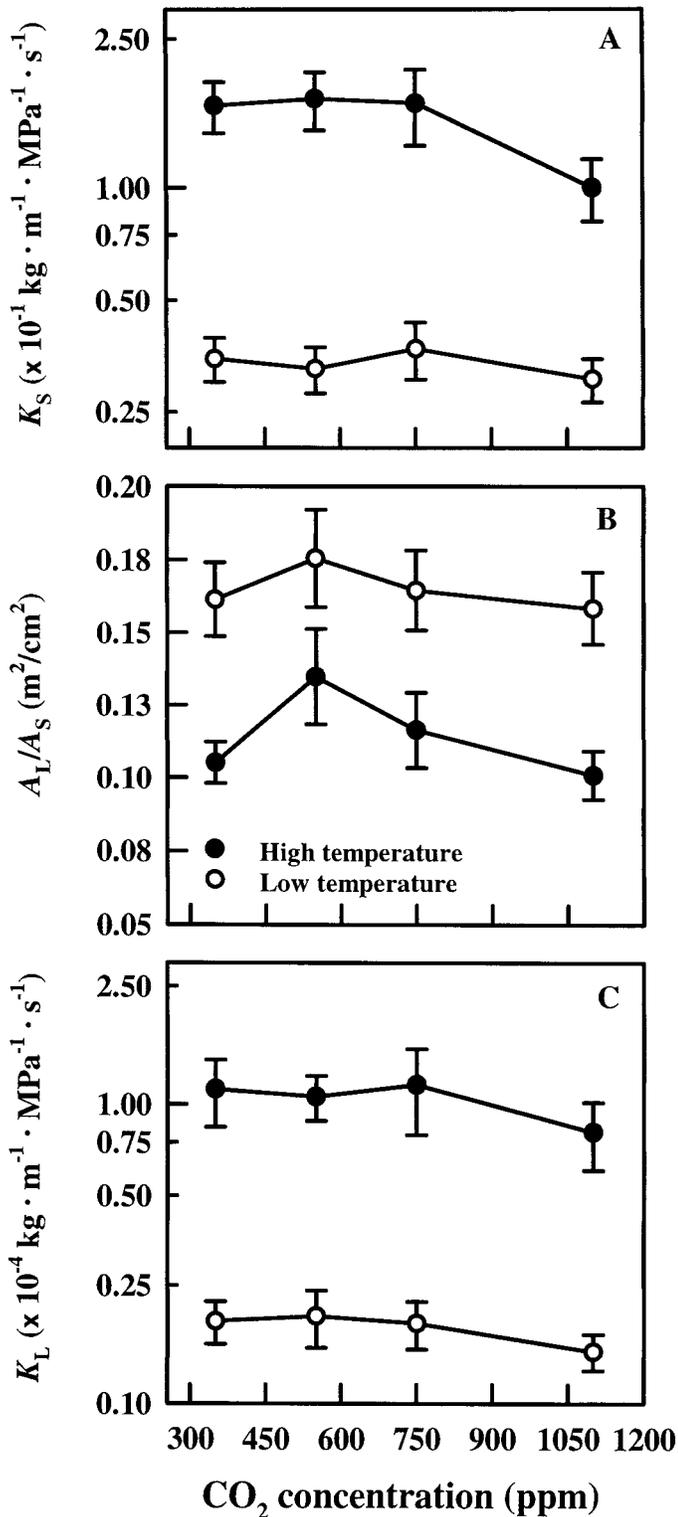
Fig. 2. The effect of atmospheric CO_2 concentration and air temperature on (A) specific-hydraulic conductivity (K_S), (B) leaf:sapwood area ratio (A_L/A_S), and (C) leaf-specific hydraulic conductivity (K_L) for 30-wk-old ponderosa pine seedlings. Each data point is the mean of ($\pm$ 1 SE) of ten seedlings.
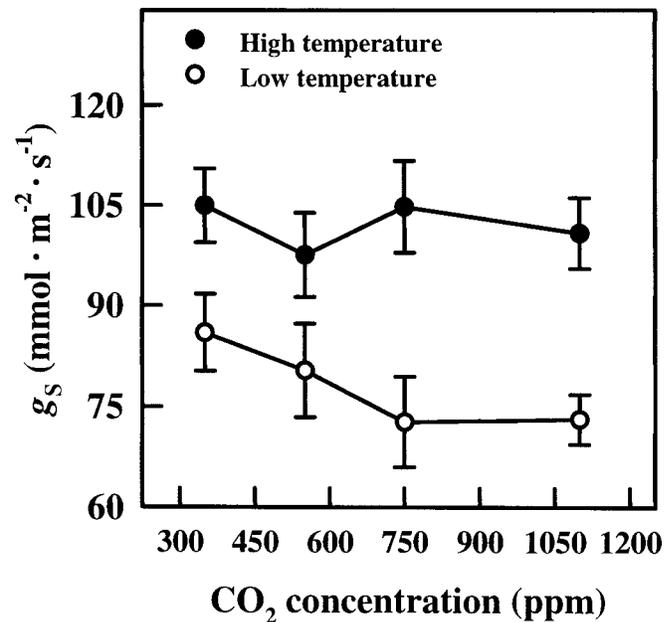
Fig. 3. The effect of atmospheric CO_2 concentration and air temperature on stomatal conductance (g_S) for 30-wk-old ponderosa pine seedlings. Each data point is the mean ($\pm$1 SE) of 3–5 seedlings.

> 0.05). Neither K_S, A_L/A_S, nor K_L were dependent on seedling size (data not shown, $P > 0.05$).

Stomatal conductance increased by 15% with elevated temperature (Fig. 3, $P < 0.01$). Although g_S appeared to decline with elevated CO_2 concentrations at low temperature, this response was not statistically significant ($P > 0.05$). Stomatal conductance was also correlated with leaf-specific hydraulic conductivity when expressed across all treatments (Fig. 4).

Mean ($\pm$1 SD) tracheid diameter increased significantly with elevated temperature (for high temperature, 11.51 ± 0.1 μm; for low temperature, 10.06 ± 0.2 μm; Fig. 5, $P < 0.05$), but was unaffected by elevated CO_2 concentrations ($P > 0.05$). Mean ($\pm$1 SD) wood density was unaffected by temperature (for high temperature, 0.42 ± 0.02 g/cm²; for low temperature, 0.42 ± 0.01 g/cm²) or CO_2 concentration ($P > 0.05$, data not shown).

DISCUSSION

Our results suggest that elevated CO_2 will have minimal effects on K_S and K_L, whereas elevated temperature and atmospheric evaporative demand will increase water transport capacity. The insensitivity of tracheid lumen diameter, and hence K_S, to elevated CO_2 may be common in trees. In experiments on young saplings ($\leq$2-yr-old), Donaldson et al. (1987) and Conroy et al. (1990) found that elevated CO_2 concentrations had no significant effect on tracheid diameter in *Pinus radiata* D. Don. Atkinson and Taylor (1996) found that elevated CO_2 had no effect on the vessel element diameter of 2-mo-old *Prunus avium* L. × *pseudocerasus* Lind seedlings. Although we found no effects of seedling size on tracheid dimension in ponderosa pine, xylem conduit dimensions are generally correlated with tree size and age (Gartner, 1995). Therefore, tree seedlings exposed to elevated CO_2 may have larger
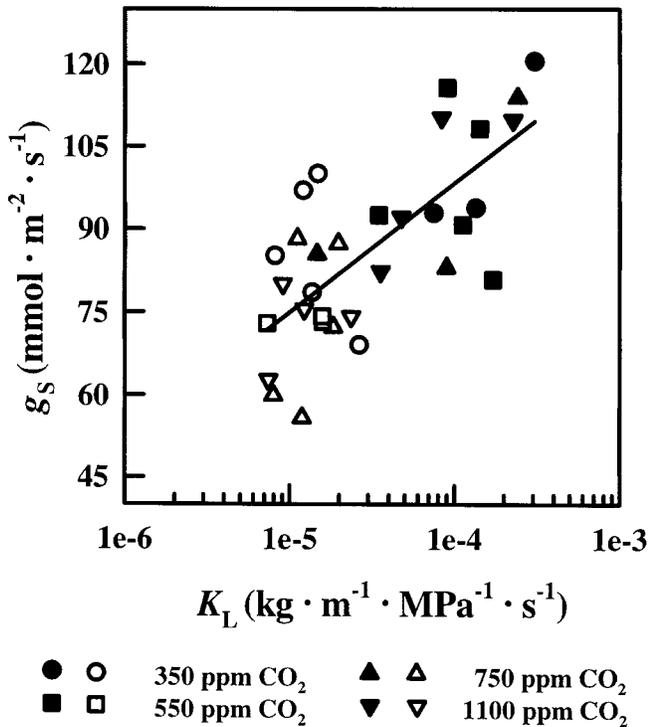
Fig. 4.   Stomatal conductance (g_S) as a function of leaf-specific hydraulic conductivity (K_L) for ponderosa pine grown in one of four CO_2 concentrations (350, 550, 750, and 1100 ppm) and two temperature treatments (20°C nights, 30°C days; or 15°C nights, 25°C days). The data were fit with least-squares regression, where $g_S = 23.25$ (log K_L) + 191.30, $r^2 = 0.52$, $P < 0.05$. Open symbols represent plants grown in low temperatures and closed symbols represent plants grown in high temperatures.

Fig. 5.   The effect of growth in low and high air temperature on the fraction of tracheids in 1-μm tracheid diameter classes for 30-wk-old ponderosa pine seedlings. There were no effects of elevated CO_2 concentration on tracheid diameter, so temperature data were pooled across CO_2 levels. Each data point is the mean (±1 SE) of 20 seedlings (five seedlings per treatment combination).

tracheid or vessel diameter than control trees simply because of larger size. For example, Atkinson and Taylor (1996) reported that 10-mo-old *Quercus robur* L. seedlings grown at elevated CO_2 had larger vessel elements than control trees, but could not separate the effects of elevated CO_2 from the effects of plant size and development. Size- and age-independent effects of elevated CO_2 on xylem anatomy may also become apparent with longer term exposure (Conroy et al., 1990; Atkinson and Taylor, 1996).

   The increase in K_S at high temperature was caused primarily by significantly larger tracheid lumen diameters in seedlings grown at high temperature (Fig. 5). Because conductance increases as a function of the fourth power of the lumen radius, small increases in tracheid diameter can lead to large increases in hydraulic conductance (Zimmermann, 1983). For example, with the assumption that tracheids are ideal capillaries, we calculated that the 14% increase in mean tracheid diameter of seedlings exposed to high vs. low temperature (Fig. 5) would drive a 75% increase in hydraulic conductance. However, the anatomy of bordered pits connecting adjacent tracheids (Pothier et al., 1989) and the number of tracheids per unit sapwood area (Atkinson and Taylor, 1996) also control water transport in conifers. Although not measured in this study, an increase in bordered pit permeability and tracheid numbers may have contributed to higher K_S in ponderosa pine seedlings exposed to elevated temperature.

The larger tracheid diameters observed in ponderosa pine seedlings may be caused by exposure to both elevated temperatures and VPD. Larger tracheid lumen diameter was associated with higher temperatures in *Pinus radiata* (Richardson, 1964; Jenkins, 1975) and *P. sylvestris* (Antanova and Stasova, 1993), although these studies did not control for VPD. Whitehead, Sheriff, and Greer (1983) found that *P. sylvestris* seedlings grown in daytime VPDs of 2.0 kPa had marginally larger tracheid lumen diameters than seedlings grown in daytime VPDs of 1.0 kPa or below. We did not manipulate VPD independently from temperature; therefore we could not directly determine whether ponderosa pine seedlings responded specifically to high temperatures, high VPD, or to an interaction between both factors. However, transpiration is driven primarily by VPD in conifers (Sanford and Jarvis, 1986) and is coordinated with stem hydraulic conductivity (Meinzer and Grantz, 1990; Tyree and Ewers, 1991; Sperry and Pockman, 1993). Stem hydraulic conductivity, in turn, is dependent on xylem anatomy (Zimmermann, 1983). Thus, the most probable explanation for larger tracheid diameter at high temperature is high VPD.

   Wood hydraulic conductance and anatomical properties were unaffected by CO_2 concentration in this study, therefore differences in K_L could only occur if the A_L/A_S was altered by exposure to elevated CO_2. We observed no differences in A_L/A_S in response to increasing CO_2 concentration. Similar to our results, elevated CO_2 did not alter A_L/A_S in 3-yr-old *P. taeda* saplings grown in open-top chambers (Pataki, Oren, and Tissue, 1998). We also found no intrinsic reduction of g_S in response to elevated CO_2 (Fig. 3). Other greenhouse and open-top chamber studies (Surano et al., 1986; Hollinger, 1987; Conroy et al., 1988; Grulke, Homand, and Roberts, 1993; Pataki, Oren, and Tissue, 1998) suggest that conifers may not reduce stomatal conductance and leaf-level transpiration in response to elevated CO_2, possibly because of a general insensitivity of conifer stomata to atmospheric CO_2 (Tyree and Alexander, 1993; Wang and Kellomaki, 1997;

Will and Teskey, 1997). The overall reduction of g_S in response to elevated atmospheric CO_2 concentrations across woody plant genera may also be small (Curtis and Wang, 1998). However, because g_S remained unchanged and plant biomass increased with CO_2 in our study, whole-plant transpiration may have been higher in the elevated CO_2 treatment.

As with the response of g_S in woody plants (e.g., Eamus and Jarvis, 1989; Field, Jackson, and Mooney, 1995; Curtis, 1996; Drake, Gonzàlez-Meler, and Long, 1997; Curtis and Wang, 1998), the effects of elevated atmospheric CO_2 on K_L may be variable and species-specific. For example, Heath, Kierstens, and Tyree (1997) found that growth in ambient + 250 ppm CO_2 concentrations reduced K_L in *Quercus robur* L. but not in *Fagus sylvatica* L. shoots. Atkinson and Taylor (1996) found that growth in 700 ppm CO_2 concentrations increased K_L in *Q. robur* but not in *Prunus avium* L. × *pseudocerasus* stems. Our results suggest that elevated CO_2 has no effect on K_L in ponderosa pine.

By combining the Penman-Montieth equation (which describes transpiration from a forest canopy) and Darcy's law (which describes water transport through tree stems), Whitehead and Jarvis (1981) developed a relationship to predict A_L/A_S in response to atmospheric evaporative demand. The relationship states

$$\frac{A_L}{A_S} = \frac{K_S \times \Delta\Psi}{VPD \times g_S} \quad (2)$$

where $\Delta\Psi$ is the water potential gradient. Based on this relationship, A_L/A_S should decline in response to increased atmospheric evaporative demand. This prediction has been supported by several studies that compared the biomass allocation of mature trees growing in contrasting climates (Waring, Schroeder, and Oren, 1982; Callaway, DeLucia, and Schlesinger, 1994; Margolis et al., 1995; Mencuccini and Grace, 1995; E. H. DeLucia, H. Maherali, and E. V. Carey, unpublished data). Our observation that A_L/A_S declined in response to elevated temperature and evaporative demand is also consistent with the Whitehead and Jarvis (1981) theory. The combination of increased K_S and reduced A_L/A_S led to significantly higher K_L in seedlings grown at high temperature. High K_L permits higher transpiration in response to increased evaporative demand without a rise in the water potential gradient (Tyree and Ewers, 1991; Sperry and Pockman, 1993; Mencuccini and Grace, 1995; Maherali, DeLucia, and Sipe, 1997). Coordination between transpiration and K_L (e.g., Meinzer and Grantz, 1990; Sperry and Pockman, 1993) is also supported by the observation that K_L and g_S were correlated for plants grown across all treatment conditions (Fig. 4). High K_L may reduce susceptibility to drought-induced cavitation (Meinzer and Grantz, 1990; Sperry and Pockman, 1993) and be an adaptive response for ponderosa pine in xeric environments.

As in other studies (Norby, 1994; Curtis and Wang, 1998), we found that allocation to roots was not significantly affected by elevated CO_2 independently of plant size. Conifer roots may have higher hydraulic conductivity and be more vulnerable to xylem embolism than stems (Sperry and Ikeda, 1997), suggesting that roots and stems may play different roles in controlling water transport in

trees. Because aboveground K_L was correlated with g_S and hence transpiration in our study, it is possible that root hydraulic conductivity also increased in response to elevated temperature.

Most predictions of the response of forest ecosystems to climate change suggest that dry-mesic forests, such as ponderosa pine, may experience reduced water stress because of lower transpiration or enhanced water use efficiency in response to elevated CO_2 (Eamus and Jarvis, 1989; Field, Jackson, and Mooney, 1995; Drake, Gonzàlez-Meler, and Long, 1997). Elevated CO_2 did not alter K_S, A_L/A_S, or K_L of ponderosa pine seedlings in this experiment, whereas elevated temperature increased hydraulic conductivity. Similar to the responses observed in seedlings, mature ponderosa pine trees growing in warm and dry climates in the field also had higher K_S, lower A_L/A_S, and higher K_L than similar-sized trees growing in cool, moist climates (Callaway, DeLucia, and Schlesinger, 1994; H. Maherali and E. H. DeLucia, unpublished data). We conclude that elevated temperatures and VPD are the primary factors influencing water transport in ponderosa pine. A shift to a warmer, drier climate in the future may increase tree hydraulic conductivity. This change may increase leaf-level transpiration or decrease susceptibility to drought-induced xylem embolism, but may also reduce leaf area development.

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