New Phytologist

Research

Compression wood has little impact on the water relations of Douglas-fir (*Pseudotsuga menziesii*) seedlings despite a large effect on shoot hydraulic properties

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Received: *9 October 2001*
Accepted: *4 February 2002*

Summary

- Compression wood has been shown to reduce stem permeability, but it is not known to what extent it affects leaf-level processes. Here, we report whole-plant hydraulic properties of Douglas-fir (*Pseudotsuga menziesii*) seedlings induced to form varying amounts of compression wood.
- Seedlings were grown under three bending treatments to assess the impact of compression wood on hydraulic properties, including stomatal conductance (g_s), above-ground shoot conductance ($K_{l(abg)}$), and both specific and leaf area-specific conductivity (k_s and k_l, respectively).
- $K_{l(abg)}$ was significantly lower (50% reduction) in severely bent seedlings than in controls. Similarly, both k_s and k_l of the main axis were significantly reduced (by 52% and 46%, respectively) in severely bent seedlings relative to controls. Seedlings in the moderate bending treatments had k_s and k_l that were intermediate between controls and severe bending.
- Despite clear differences in above-ground shoot hydraulic properties, severely bent seedlings maintained the same water potentials as controls and had similar diurnal patterns of g_s. This suggests that when the entire soil–plant–atmosphere continuum is considered, even a severe reduction in stem k_s caused by compression wood has little impact on leaf-level processes.

Key words: compression wood, reaction wood, stomatal conductance, hydraulic conductivity, hydraulic architecture.

Introduction

Continuing advances in the field of tree hydraulic architecture suggest that consideration of the entire tree system is critical to assess hydraulic efficiency. Although the permeability of xylem is a key physical property determining resistance to the flow of water through axes, woody plants have many design options with which to compensate for increased resistance. Such compensation may occur at the level of the shoot through a reduction in the ratio of leaf area to conducting xylem area, as was found in shrubs relative to lianas in *Toxicodendron* (Gartner, 1991), and in self-supported relative to staked *Pinus* seedlings (Dean, 1991). Similarly, woody hemi-epiphytes typically support more leaf area per unit xylem area than free-standing trees (Zotz *et al.*, 1997a). A reduction in the ratio of leaf area to conducting xylem area is also found with increasing tree height, and may compensate for the increased resistance associated with a greater path length in tall trees (Schäfer *et al.*, 2000). At the whole-plant level, adjustments in allocation patterns among vegetative components of varying resistance may compensate for increased resistance at the shoot level. For example, recent work has shown that although conifer seedlings have lower conductivity (normalized by either cross-sectional area or leaf area) than angiosperms at the branch level, soil-to-leaf hydraulic conductance (normalized by leaf area) did not differ (Becker *et al.*, 1999). It is therefore important to look beyond properties of shoots when assessing hydraulic efficiency.

Compression wood (CW) is specialized to function in mechanical support in gymnosperms, forming regularly on the undersides of branches and in stems that have been displaced from a vertical orientation. CW forms in response to a gravitational stimulus, and effects repositioning by generating an upward bending force within the xylem as tracheids with modified secondary walls mature (Wardrop & Davies, 1964; Wilson & Archer, 1977; Wilson, 1981). We have shown that the wide bands of dense wood characteristic of CW are composed of narrow-diameter tracheids that can reduce the conductive capacity of the xylem (Spicer & Gartner, 1998a,b). This increased resistance to flow could put trees that are subject to mechanical stress at a hydraulic disadvantage and subsequently limit gas exchange through stomatal closure. Although CW reduces the specific (expressed per unit cross-sectional area) and leaf area-specific (expressed per unit leaf area) conductivity of stems (Spicer & Gartner, 1998a), its effect in whole branches is less clear (Spicer & Gartner, 1998b). Further, the stem is only one component of the total resistance along the soil–plant–atmosphere continuum. Substantial evidence indicates that the soil, roots, petioles and leaves make up the bulk of resistance to flow (Tyree *et al.*, 1975, 1983; Ikeda & Suzaki, 1984; Edwards *et al.*, 1986; Sellin, 1988, 1990; Tyree & Alexander, 1993; Yang & Tyree, 1994; Hacke *et al.*, 2000), suggesting that the presence of CW may have minimal impact on whole-plant water relations. In contrast, stomatal conductance has been shown to decrease in response to a reduction in shoot conductance brought about by cavitation (Sperry & Pockman, 1993; Sperry *et al.*, 1998), increased path length (Hubbard *et al.*, 2001; Schäfer *et al.*, 2000) and xylem notching (Sperry *et al.*, 1993; Saliendra *et al.*, 1995). The extent to which CW might affect gas exchange would then depend on the contribution of the main shoot axis (where significant CW formation occurs) to total shoot conductance.

At the heart of this question is whether CW formation requires a trade-off between xylem mechanical and hydraulic functions. Xylem typically functions in both water conduction and mechanical support, and this dual role is particularly evident in gymnosperms, where a single cell type (the tracheid) is responsible for both functions. Structural modifications in gymnosperms that increase mechanical support (e.g. increased cell wall thickness) are likely to decrease permeability (or specific conductivity), but these modifications may or may not affect the supply of water to the leaves. This trade-off may be less clear in angiosperms, in which different cell types are specialized to function in mechanical support (fibers) and water conduction (vessel elements).

We designed a controlled experiment to test the hypothesis that increased amounts of CW in conifer stems will cause a reduction in stomatal conductance, maintenance of lower water potentials, or both. The CW treatments were established by applying three levels of bending (mild and severe bending, and unbent controls) to the main stem of 3-yr-old Douglas-fir seedlings and allowing the leaders (distal portions) to return to a vertical position over the course of a full growing season. By monitoring the diurnal course of stomatal conductance and water potential, measuring above-ground shoot conductance and hydraulic conductivity normalized for both leaf and xylem cross-sectional area, we were able to assess the impact of varying degrees of CW on seedling hydraulic function.

Materials and Methods

Plant material

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) seedlings were grown outdoors in raised beds in Corvallis, OR, USA (latitude 44°39′34″, longitude 123°14′01″, elevation 130 m above sea level). Seedlings were grown from seed sown in April 1995 as part of a genetics trial and included a large amount of genetic variation, with 80 families from both Coast Range and Cascade Mountain seed sources (O'Neill *et al.*, 2001). Seedlings were grown in eight raised beds (1.3 × 4 m and 0.7 m deep) at the Forest Research Laboratory at Oregon State University with a spacing of about 8 × 10 cm at sowing. In the summer of 1996, seedlings in four randomly selected beds were subject to mild drought (e.g. soil water potential of −1.7 MPa) as part of the genetics trial (O'Neill *et al.*, 2000; O'Neill *et al.*, 2001). In all other years the seedlings were well-watered. In 1997, half of each bed (selected at random) was harvested for the genetics trial. The remaining seedlings were used for the current experiment. In March 1998, seedlings were thinned to 18 seedlings per half-bed, forming two rows, with approximate spacing of 0.25 × 0.25 m. Seedlings were therefore from both droughted and well-watered treatments and included a random distribution of seed source families.

Bending treatments

Bending treatments were applied before the start of cambial activity in March 1998, as seedlings were about to begin their fourth growing season. Treatments were assigned randomly to individuals in each bed to give six trees per treatment per bed, for a total of 48 trees per treatment. Seedlings were tethered via 2-m-long strings attached just beneath the first branch whorl from the top, and tied to a wooden support at the base of the raised beds. At the point of attachment around the stem, the string was laced through a piece of flexible tubing tied into a ring around the stem to prevent injury or girdling. The vertical midpoint of the second year's growth (second 'interwhorl' from the top) was marked with paint and used as the reference for determining the bending angle. Trees were bent until the angle of the reference stem region was at 25° or 50° from vertical, measured with a protractor fitted with a weighted string that hung vertically. Control trees were fitted with string but left straight.

The leaders (distal portions) of the seedlings had returned to a vertical position by the end of their fourth growing season by reorienting the preexisting stem (above the tether) through CW formation, and orienting the new shoot vertically. At the time of harvest, seedlings measured about 1.3 m vertical height and 4 cm basal diameter.

Stomatal conductance and water potential

In August 1998, stomatal conductance (g_s, mmol $\mathrm{m^{-2}\,s^{-1}}$) was measured on the control and 50° seedlings (48 per treatment) six times throughout the day with a LI-1600 M (Li-Cor, Inc., Lincoln, NE, USA). Extremely hot weather (maximum daily temperatures of 35–39°C over 4 d) made for abnormal conditions during these measurements, so they were repeated in April 1999 (before bud break and the start of cambial activity) on the control and 50° seedlings (24 per treatment) that remained following the harvest of above-ground shoots described later. Water potential was measured simultaneously in April five times throughout the day with a pressure bomb (PMS Instrument Co., Corvallis, OR, USA). Seedlings were well-watered throughout the experiment via drip irrigation and had predawn water potentials of about −0.1 MPa during the April measurements (measured on three randomly selected seedlings).

Above-ground shoot conductance

Above-ground shoot hydraulic conductance normalized for leaf area ($K_{\mathrm{l(abg)}}$, m $\mathrm{s^{-1}}$ $\mathrm{MPa^{-1}}$) was measured on 50° and control seedlings in February 1999. Seedlings from four beds were wrapped in black plastic at night and harvested early the next morning by cutting above the root–shoot collar. Seedlings were placed in buckets of 0.22 µm-filtered water and brought into the laboratory, where they were recut with a razor blade underwater at the base and attached to tubing and a supply of similarly filtered water. Three seedlings were attached to the water supply simultaneously and oriented vertically, supported by metal clamps attached to horizontal rods. The black plastic was removed from the seedlings and they were allowed to transpire for about 1 h before being measured for flow rate. Preliminary work showed that seedling transpiration under these conditions increased for 15–45 min (probably the amount of time required for the foliage to dry) but then remained constant for at least 5 h. Although $K_{\mathrm{l(abg)}}$ was measured only on 50° and control seedlings, seedlings from all three treatments transpired under these conditions for about 1 h before xylem and leaf area-specific conductivity were measured (see later).

Following equilibration, seedlings were attached to a filtered water source with an inline 0.1 ml graduated pipette. Flow rate was measured by timing the movement of the meniscus of a bubble introduced into the pipette. The pressure gradient was estimated assuming atmospheric pressure at the base of the seedling (the water source was kept level with the base; assuming negligible osmotic pressure, $\Psi_{\mathrm{base}} = 0$ MPa) and using the mean of two or three leaf water potential (Ψ_{l}) measurements made throughout the crown. The Ψ_{l} rarely differed by more than 0.1 MPa within a seedling, was similar among trees and did not differ by treatment (-0.87 ± 0.04 vs -0.98 ± 0.06, mean ± SE ($n = 24$) for 50° and control, respectively; $P = 0.1$ in a t-test). $K_{\mathrm{l(abg)}}$ was thus calculated as,

$$K_{\mathrm{l(abg)}} = \frac{Q}{A_{\mathrm{l}}\Delta P}$$

(Q, volume flow rate ($\mathrm{m^3\,s^{-1}}$); A_{l}, projected leaf area ($\mathrm{m^2}$); and ΔP, estimated as Ψ_{l} (leaf water potential, MPa). Fluid temperature measured with a thermometer was used to correct all values (for viscosity) to 20°C, including xylem and leaf area-specific conductivity. Estimation of projected leaf area is described later in this section.

We recognize that laboratory conditions are far from normal outdoor conditions, and represent extremely low photosynthetically active radiation (PAR) and different humidity levels. However, with the constant conditions of the laboratory we could compare easily across treatments over extended hours and therefore process large numbers of seedlings. In order to gauge the effect of these atypical conditions, we measured g_s and transpiration on a subsample ($n = 11$; six bent, five control) of seedlings in the laboratory, and $K_{\mathrm{l(abg)}}$ on seedlings outside in full sun ($n = 5$; three bent, two control) and inside ($n = 23$, 12 bent and 11 control) in June 1999.

Sapwood and leaf area-specific conductivity

Following measurement of $K_{\mathrm{l(abg)}}$ (or the equilibration period in the case of 25° seedlings), all branches were removed from the seedlings and the base and top were trimmed (by about 5 cm and 30 cm, respectively) and cut with a razor blade to leave a central segment about 1 m long. Stem segments were attached at the base (proximal end) to a source of 0.22 µm filtered oxalic acid (10 mol $\mathrm{m^{-3}}$) via tubing, and at the tip (distal end) to a graduated pipette. Branch stubs were wrapped in Parafilm to prevent leakage, and flow rate was measured under an applied pressure of about 0.02 MPa ($\Delta P/l$, see next equation). Sapwood cross-sectional area was taken as the mean of the area of the two ends minus the area of the pith. Conductivity normalized for sapwood area (k_s, $\mathrm{m^2\,s^{-1}\,MPa^{-1}}$) was thus calculated as

$$k_s = \frac{Ql}{A_s\Delta P}$$

(l, segment length (m); A_s, sapwood area ($\mathrm{m^2}$); and ΔP, the difference in pressure between the two ends of the segment (MPa).) Similarly, k_{l} is calculated as

$$k_{\mathrm{l}} = \frac{Ql}{A_{\mathrm{l}}\Delta P}$$

(A_l, projected fresh leaf area (m^2).) Following flow rate determination, segments were attached to a solution of safranin-O (0.5% w/v) under a pressure of 0.02 MPa for 1 h.

Leaf area estimation

In order to estimate leaf area, fresh foliage was sampled from three randomly selected twigs per seedling, which included needles from the previous 2 yr of growth. Current buds had not opened. All needles on the seedlings were between 1 yr and 3 yr old, and did not differ obviously in thickness among age classes. The projected fresh area of needles was determined with a video camera and image analysis system using NIH Image software (v.1.60; developed at the US National Institutes of Health and available at http://rsb.info.nih.gov/nih-image/). Needle dry weights were measured following 48 h in an oven at 60°C, and fresh area to dry weight ratios were calculated for each sample. The mean ratio for each seedling was used to determine a global mean (70 ± 4 cm^2 g^{-1}, mean ± SE; $n = 48$), which we then applied to the total foliar dry mass of each seedling (weighed following 48 h in an oven at 60°C). We applied a global conversion because (a) bending treatments did not differ in fresh area/dry weight, (b) there was no current-year foliage, which would likely have a significantly greater fresh area/dry weight, and (c) it was not feasible to sample each seedling thoroughly enough to produce accurate ratios for individual seedlings.

Per cent compression wood area (%CW)

The proportion of stem cross-sectional area occupied by CW was measured on 3-mm thick disks sawn from the samples about 5 cm from the base. Disks were viewed with a video camera and areas calculated using an image analysis system and NIH image software (v.1.60). The CW was distinguished visually by its dark color.

Data analysis

Hydraulic data and CW data were analysed with a one-way ANOVA in which raised beds were treated as blocks. $K_{l(abg)}$, k_s and k_l were log transformed to satisfy the assumption of constant variance. Multiple comparisons were made with Tukey–Kramer adjusted *P*-values. Linear regression was used to compare independent measures of flux, and to test for a relationship between %CW and $K_{l(abg)}$, k_s and k_l. Hydraulic data taken inside and outside were compared with a two-tailed *t*-test.

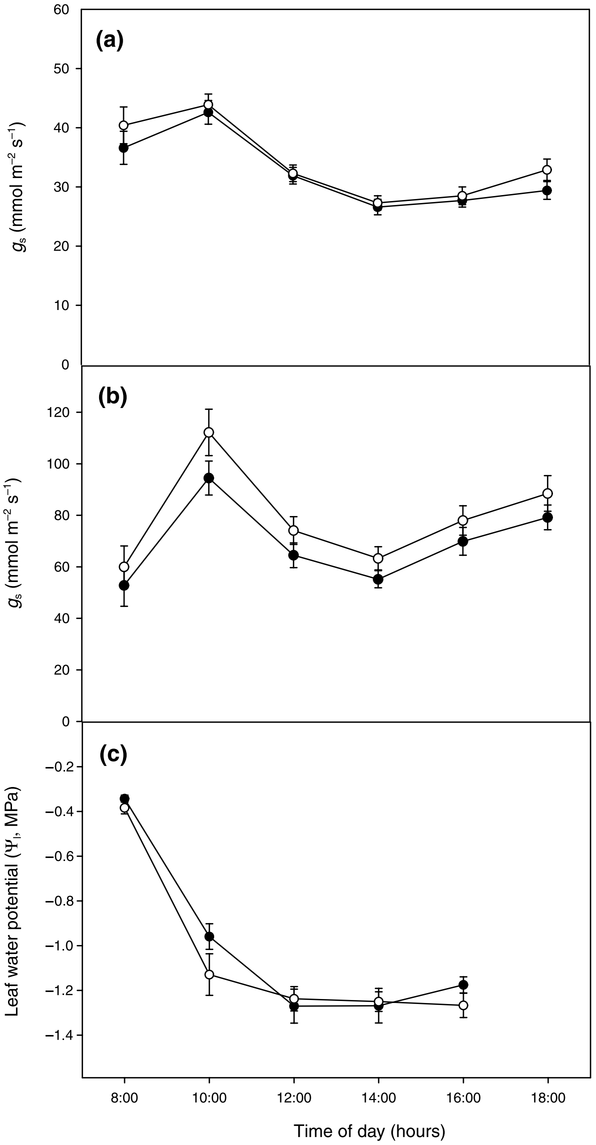

Fig. 1 Stomatal conductance (g_s) measured in (a) the summer (August 1998; $n = 48$) and (b) the following spring (April 1999; $n = 24$), and (c) leaf water potential (Ψ_l) measured in spring (April; $n = 24$) on severely bent (50° angle, closed circles) and unbent (control, open circles) Douglas-fir seedlings (mean ± SE).

Results

Stomatal conductance (g_s) did not differ between control and 50° (severe bending) seedlings under the extremely hot summer conditions (Fig. 1a). In the spring, control seedlings had only slightly higher g_s (Fig. 1b) and maintained the same Ψ_l (Fig. 1c) as 50° seedlings. During g_s measurements, both the temperature and relative humidity surrounding the foliage (from LI-100 M cuvette measurements) were higher throughout the day in summer 1998 than in spring 1999 (Table 1).

Above-ground shoot conductance normalized for leaf area ($K_{l(abg)}$) was significantly higher in controls than in 50° seedlings ($P = 0.04$, Table 2). Similarly, both k_l and k_s decreased with increasing degrees of bending. Differences in k_l and k_s were highly significant for controls vs 50° seedlings ($P = 0.003$ and 0.0002, respectively), marginally significant

Table 1 Estimates of air temperature and relative humidity surrounding foliage during stomatal conductance (g_s) measurements for sampling dates in summer and spring

	Time of day (hour)					
	08 : 00	10 : 00	12 : 00	14 : 00	16 : 00	18 : 00
Summer 1998						
Air temperature (°C)	20.2 ± 0.3	26.3 ± 0.4	30.3 ± 0.4	33.1 ± 0.4	33.4 ± 0.5	28.8 ± 0.2
Relative humidity (%)	57.0 ± 0.5	37.6 ± 0.4	28.9 ± 0.2	25.9 ± 0.2	25.0 ± 0.2	31.8 ± 0.4
Spring 1999						
Air temperature (°C)	15.8 ± 0.2	22.0 ± 0.1	27.4 ± 0.2	29.0 ± 0.1	27.4 ± 0.3	23.2 ± 0.3
Relative humidity (%)	54.0 ± 0.6	33.0 ± 1.6	21.2 ± 0.4	19.6 ± 0.1	20.9 ± 0.6	23.0 ± 0.3

Each value represents the mean (± SE) of *n* seedlings, but includes measurements made on different days (summer, $n = 96$, measured over 6 d; spring, $n = 48$, measured over 4 d). Maximum temperatures on 3 d during the summer sampling dates were as high as 40°C, with a mean maximum across all 6 d of 35°C.

Table 2 Hydraulic and anatomical properties of Douglas-fir seedlings across three bending treatments

	Control	25°	50°	*P*-value
$K_{l(abg)}$ (m s^{-1} MPa^{-1} × 10^{-8})	4.4 ± 1.4^a	–	2.2 ± 0.1^b	0.04
k_s (m^2 s^{-1} MPa^{-1} × 10^{-4})	2.5 ± 0.3^a	1.7 ± 0.2^{ab}	1.2 ± 0.1^b	0.0003
k_l (m^2 s^{-1} MPa^{-1} × 10^{-8})	11.1 ± 1.5^a	8.4 ± 1.0^{ab}	6.0 ± 0.9^b	0.004
SA : LA (m^2 m^{-2} × 10^{-4})	7.3 ± 0.5^a	8.2 ± 0.4^a	8.9 ± 0.6^a	0.08
% CW	5 ± 1^a	30 ± 3^b	45 ± 2^c	< 0.0001

Values are mean ± SE, $n = 24$. Means in the same row followed by the same letter are not significantly different (adjusted $P > 0.05$, one-way ANOVA, Tukey-Kramer adjustment). $K_{l(abg)}$, above-ground shoot conductance; k_s, specific conductivity; k_l, leaf area-specific conductivity; SA : LA, ratio of sapwood area to leaf area; %CW, per cent compression wood.

for 25° vs 50° seedlings ($P = 0.09$ and 0.06, respectively) and not significant for controls vs 25° seedlings ($P = 0.4$ and $P = 0.1$, respectively). Sapwood area per leaf area did not differ among bending treatments ($P = 0.08$ for ANOVA), although the average value increased from control to 25° to 50° (Table 2). Increased bending resulted in significant increases in compression wood formation in both 25° and 50° seedlings (Table 2), but there was no significant relationship between %CW and shoot hydraulic properties ($K_{l(abg)}$, k_l or k_s, linear regression; data not shown).

Flux rates derived from estimates of whole-plant leaf area and transpiration rates measured with the LI-1600 M ($n = 11$) agreed well with measurements of water uptake by cut seedlings in the laboratory (Fig. 2). Measurement of volume flux through cut seedlings outside in full sun produced values (both flux and $K_{l(abg)}$) similar to those observed in the laboratory ($P = 0.35$ and $P = 0.90$, respectively; *t*-test), but seedlings transpiring outside maintained slightly more negative water potentials than those in the laboratory ($P = 0.002$, *t*-test; Table 3).

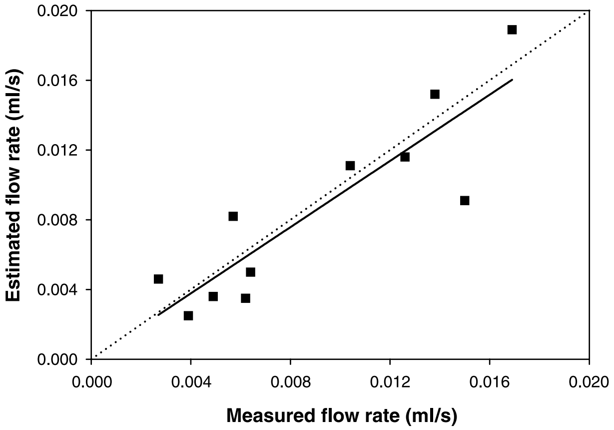

Fig. 2 Comparison of independent means of estimating flow through above-ground portion of seedlings. Estimated flow rate, derived from the measured transpiration rate extrapolated to total seedling leaf area, is shown vs measured flow rate, taken from volumetric uptake. Each point represents one seedling ($n = 11$, including six severely bent and five control seedlings). Solid line shows linear regression ($r^2 = 0.78$, model $P = 0.0003$, $y = 0.95x$). Dotted line shows 1 : 1 relationship.

Discussion

The formation of CW clearly affects shoot hydraulic properties by reducing the permeability of the main stem. Seedlings responding to severe (50°) and moderate (25°) bending had less than 50% and 70% the k_s of controls, respectively. This is in agreement with results we reported previously, in which branches that had grown vertically through the action of CW had about 45% the k_s of normal

Table 3 Volume flux (Q), leaf water potential (Ψ_l) and above-ground shoot conductance normalized for leaf area ($K_{l(abg)}$) measured inside the laboratory and outside in full sun

	Inside (*n* = 23)	Outside (*n* = 5)	*P*
Q (ml s^{-1})	0.010 ± 0.001	0.013 ± 0.003	0.35
Ψ_l (MPa)	−0.38 ± 0.02	−0.50 ± 0.02	0.002
$K_{l(abg)}$ (m s^{-1} $MPa^{-1} \times 10^{-8}$)	1.99 ± 0.13	1.95 ± 0.14	0.90

Mean ± SE, combining control and 50° bending treatments.

leaders (Spicer & Gartner, 1998a). Recovery from bending also reduced seedling k_l, suggesting that slight, nonsignificant increases in the ratio of sapwood area to leaf area (SA : LA) did not compensate for reductions in k_s. The increased SA : LA observed in bent seedlings is most likely the result of increased growth in the region of CW (Core *et al.*, 1961; Timell, 1986), rather than any compensation strategy, with the additional xylem having very low k_s.

Although k_s and k_l are useful in estimating the resistance imposed by the main stem, $K_{l(abg)}$ is more relevant to whole-plant function, in that it includes branch and foliar resistances, as well as diffusional resistance as water enters the gas phase (Tyree & Ewers, 1991; Tsuda & Tyree, 1997). $K_{l(abg)}$ was reduced by 50% in seedlings responding to severe bending, indicating that the presence of CW does reduce the ability of the entire above-ground shoot to supply the foliage with water. However, g_s was only slightly reduced in seedlings with large amounts of CW, and this difference disappeared under the large evaporative demand of days with a 35°C maximum air temperature (mean across 6 d; individual maximum leaf temperatures were in excess of 40°C). This result suggests that, at least in these seedlings, the collective resistance of the root system and soil–root interface dominates the total resistance of the soil–plant–atmosphere continuum. Values in the literature for the per cent of whole-plant resistance attributable to roots vary from 20 to 90%, but several reports suggest a high percentage in seedlings and small trees – over 66% in both *Acer saccharinum* (Tsuda & Tyree, 1997) and *Annona glabra* (Zotz *et al.*, 1997b), for example. Using a gross estimate of total resistance (R_t) for the soil–root–leaf pathway derived from transpiration (*E*, measured in April on seedlings growing in the raised beds), and the difference between predawn and midday water potentials ($\Delta\Psi$) (i.e. $1/R_t = E/\Delta\Psi$, following (Meinzer *et al.*, 1995) and reviewed in (Wullschleger *et al.*, 1998)), we estimate the soil/root component to account for about 60% of the total resistance (59 ± 3%, mean ± SE; *n* = 24). This estimate is likely an underestimate because it compares R_t derived from early spring (April) measurements of transpiration (before full foliage expansion and significant cambial activity) with above-ground shoot resistance ($1/K_{l(abg)}$) measured in summer (June). Seedling $K_{l(abg)}$ would be expected to decrease during this period. Applying these calculations we found no evidence for a difference in per cent soil/root resistance between bending treatments (58 ± 4% vs 59 ± 5% for severe bending vs controls, respectively; mean ± SE; *n* = 12), suggesting that any effect of bending treatments on root volume and/or architecture was minimal. It is therefore unlikely that additional root growth in response to bending (Stokes *et al.*, 1997; Goodman, 1998) was able to compensate for the hydraulic limitation imposed by CW.

The good agreement found between independent estimates of flux (volumetric uptake vs measured transpiration extrapolated to total leaf area) suggests that flow through seedlings had reached steady state and that capacitance did not preclude the use of uptake rates. In contrast, uptake rates in large trees may overestimate transpiration (Knight *et al.*, 1981). That g_s was similarly low for cut seedlings both in the laboratory and outside in full sun suggests several possibilities. First, partial stomatal closure may have occurred in response to stem cutting rather than simply in response to low light levels indoors. Second, stomatal conductance may have been limited in both locations by some other factor, such as cavitation. Safranin staining following k_s measurement showed occasional small regions (arcs) of cavitation within the first and second annual rings, but these were similar in frequency and extent for both bent and control seedlings. Although g_s was abnormally low during flux measurements for $K_{l(abg)}$, Ψ_l was typical for mid-morning, and given the expected relationship between flux, driving force and conductance, it is unlikely that more realistic rates of g_s would eliminate the difference in $K_{l(abg)}$ observed between bent and control seedlings. That k_s was more affected by CW (and the reduction more statistically significant) than $K_{l(abg)}$ is consistent with work in ponderosa pine by Hubbard *et al.* (2001), although they report that a 50% reduction in whole-plant conductance required a 90% reduction in stem k_s. Recent work demonstrates that whole-plant hydraulic conductance can affect both transpiration and assimilation (Schäfer *et al.*, 2000; Hubbard *et al.*, 2001; Williams *et al.*, 2001), but it is unlikely that conductance of the main axis within a stem will be the limiting factor.

The results of this experiment are clear: only the most severe CW formation is likely to negatively affect seedling growth through an impact on water relations and/or gas exchange. Other problems associated with seedling bending, such as shading due to reduced stature, are more likely to negatively affect growth. It may be worth considering in future research whether there are fundamental differences in the effect of CW on water relations (if any) between branches and main stems, noting that CW forms regularly in all gymnosperm branches, but only in response to perturbation in stems. It is also not known to what extent CW might affect the water relations of large trees, rather than seedlings, or whether it has the potential to affect vulnerability to embolism. This question of a trade-off between hydraulic and mechanical functions of xylem can also be applied to the reaction wood formed in angiosperms, termed tension wood (TW). The effect of TW on water relations may be even less than that of CW, because angiosperms have cell types specialized to function in water transport (vessel elements) and mechanical support (fibers). In *Quercus ilex*, bent seedlings (inclined 30° from vertical) had the same k_s as vertical controls (B. L. Gartner, J. Roy & R. Huc, unpublished), suggesting an effective decoupling of transport and support functions in this more recently evolved xylem type. Continued work in this field should clarify the role of the stem in whole-plant processes and may illustrate important evolutionary paths in the relationship between xylem structure and function.

Acknowledgements

The authors gratefully acknowledge funding from USDA CSREES 96-35103-3832 and 97-35103-5052. We also wish to thank G. O'Neill for use of the experimental seedlings and Armelle Bonnet for assistance in the field and laboratory.

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