

# Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential

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Received October 28, 1997

**Summary** Midday stomatal closure is mediated by the availability of water in the soil, leaf and atmosphere, but the response to these environmental and internal variables is highly species specific. We tested the hypothesis that species differences in stomatal response to humidity and soil water availability can be explained by two parameters: leaf-specific hydraulic conductance ( $K_L$ ) and a threshold leaf water potential ( $\Psi_{\text{threshold}}$ ). We used a combination of original and published data to estimate characteristic values of  $K_L$  and  $\Psi_{\text{threshold}}$  for four common tree species that have distinctly different stomatal behaviors: black cottonwood (*Populus trichocarpa* Torr. & Gray.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), red alder (*Alnus rubra* Bong.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). We used the values to parameterize a simple, nonelastic model that predicts stomatal conductance by linking hydraulic flux to transpirational flux and maintaining  $\Psi_{\text{leaf}}$  above  $\Psi_{\text{threshold}}$ . The model successfully predicted fundamental features of stomatal behavior that have been reported in the literature for these species. We conclude that much of the variation among the species in stomatal response to soil and atmospheric water deficits can be explained by  $K_L$  and  $\Psi_{\text{threshold}}$ . The relationship between  $\Psi_{\text{threshold}}$  and xylem vulnerability to cavitation differed among these species.

**Keywords:** black cottonwood, Douglas-fir, hydraulic conductance, hydraulic model, red alder, soil water potential, stomatal conductance, vapor pressure deficit, western hemlock.

## Introduction

Plants commonly experience partial or complete stomatal closure during the middle of the day. When light is not limiting, stomatal closure is mediated by humidity in the atmosphere at the leaf surface (e.g., Lange et al. 1971, Raschke 1975, Kaufmann 1976, Sandford and Jarvis 1986, Ball et al. 1987) as well as water availability to roots (e.g., Lopushinsky and Klock 1976), although there is much debate about the mechanisms of these responses (e.g., Aphalo and Jarvis 1991, Tardieu and Davies 1993, Monteith 1995, Bunce 1997, Fort et al. 1997, Franks et al. 1997). Stomatal responses to water availability in the soil, leaf, and atmosphere are highly interactive: as soil water decreases, stomatal conductance also decreases at any particular level of evaporative demand (e.g., Raschke and Kuhl

1969, Hinckley et al. 1978, Whitehead and Jarvis 1981).

There are striking differences among species in stomatal response to soil and atmospheric water deficits (e.g., Running 1976, Sandford and Jarvis 1986). In the western United States, stomatal conductance of gymnosperms tends to be more sensitive to vapor pressure deficit than that of angiosperms (Marshall and Waring 1984), and riparian angiosperms have greater stomatal sensitivity to soil water deficits than gymnosperms. Furthermore, experimental manipulations such as transverse cuts in xylem (Sperry and Pockman 1993), root pressurization (Saliendra et al. 1995, Fuchs and Livingston 1996), or shading portions of a canopy (Whitehead et al. 1996) can alter stomatal conductance in a particular set of environmental conditions.

Stomatal behavior can be described mathematically to account for the interactive effects of soil and atmospheric water deficits, species differences in these responses, and responses to experimental manipulations to the hydraulic system by assuming that (1) stomatal behavior is dependent on the water supply capacity of the vascular system, and (2) stomata regulate transpirational water flux to prevent xylem water potential from falling below a threshold value. Assuming the simplest case of an unbranched, inelastic (i.e., no capacitance) hydraulic system, stomatal conductance to water vapor ( $g_s$ ) can be expressed as:

$$g_s = K_L(\Psi_{\text{soil}} - \Psi_{\text{leaf}})/\Delta W, \quad (1)$$

where  $K_L$  is leaf-specific conductance,  $\Psi_{\text{soil}}$  and  $\Psi_{\text{leaf}}$  are water potential of soil and leaf, respectively, and  $\Delta W$  is leaf-to-air vapor pressure gradient.

Similar formulations have been presented previously (Jones and Sutherland 1991, Dewar 1995, Sperry 1995, Williams et al. 1996, Whitehead 1998). This equation predicts a functional linkage among  $g_s$ ,  $\Psi_{\text{soil}}$  and  $\Delta W$ , and the linkage is directly related to  $K_L$ , which varies among species (e.g., Tyree and Ewers 1991) and with plant size and age (Yoder et al. 1994, Hubbard et al. 1999).

In Equation 1,  $K_L$  and  $(\Psi_{\text{soil}} - \Psi_{\text{leaf}})$  are not independent. As  $\Psi_{\text{leaf}}$  decreases, so will the water potential of the xylem ( $\Psi_{\text{xylem}}$ ), and tension in the water column will eventually cause xylem cavitation, thereby reducing xylem conductivity and  $K_L$ . Unless the transpirational flux of water is reduced by

stomatal closure, “runaway embolism” may occur (Tyree and Sperry 1988, Tyree and Ewers 1991). Tyree and Sperry (1988) suggested that woody plants routinely operate at the brink of catastrophic xylem failure, thereby maximizing carbon assimilation relative to the costs of constructing and maintaining hydraulic support for foliage.

Our objective was to determine whether stomatal behavior in field conditions conforms to predictions of Equation 1, constrained so that  $\Psi_{\text{leaf}}$  would not fall below a species-specific threshold value,  $\Psi_{\text{threshold}}$ . For our test, we used four tree species common in the western United States. Two were gymnosperms, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and two were mesic angiosperms, red alder (*Alnus rubra* Bong.) and black cottonwood (*Populus trichocarpa* Torr. & Gray.). We used a combination of original and previously published data to derive parameter values for Equation 1 and species-specific, minimum leaf water potential ( $\Psi_{\text{threshold}}$ , which is maintained except in extreme drought) and then compared predictions of  $g_s$  at varying soil and atmospheric water deficits with measured responses, also derived from the literature. We also examined  $\Psi_{\text{threshold}}$  values in relation to xylem vulnerability curves to determine whether there is a consistent relationship between  $\Psi_{\text{threshold}}$  and vulnerability to xylem cavitation for these species.

## Materials and methods

### The model

Stomatal conductance was modeled as follows:

(1) A preliminary value of  $\Psi_{\text{leaf}}$  was estimated using an empirically derived, species-specific value for maximum stomatal conductance ( $g_{s-\text{max}}$ ) in a reorganized version of Equation 1:

$$\Psi_{\text{leaf}} = \Psi_{\text{soil}} - (g_{s-\text{max}} \Delta W / K_L). \quad (2)$$

(2) If  $\Psi_{\text{leaf}} \geq \Psi_{\text{threshold}}$ , then  $g_s = g_{s-\text{max}}$  (in these simulations, we did not consider the case where  $\Psi_{\text{soil}} < \Psi_{\text{threshold}}$ ).

(3) If  $\Psi_{\text{leaf}} < \Psi_{\text{threshold}}$ , then: (a)  $\Psi_{\text{leaf}} = \Psi_{\text{threshold}}$ ; (b) based on the vulnerability function of hydraulic conductivity to  $\Psi_{\text{xylem}}$ ,  $K_L$  is adjusted to account for loss of hydraulic conductivity, if any, at the current  $\Psi_{\text{leaf}}$ ; and (c)  $g_s = K_L(\Delta\Psi/\Delta W)$ .

### Data for model parameterization

To estimate “representative” values of  $K_L$  for each species, we used diurnal measurements of  $g_s$ ,  $\Psi_{\text{leaf}}$  and  $\Delta W$  along with a predawn measurement of  $\Psi_{\text{leaf}}$  (used as an estimate of  $\Psi_{\text{soil}}$ ) in a reorganized version of Equation 1. Values of  $K_L$  calculated this way generally vary during the day because of the time lag between transpirational flux from foliage and hydraulic flux from stems caused by capacitance (e.g., Landsberg et al. 1976, Waring and Running 1978). We used the mean of values calculated hourly between 1000 and 1400 h.

For Douglas-fir and western hemlock, we used field measurements obtained from 22- to 27-year-old trees. The Douglas-fir site is in the Willamette Valley, near Corvallis, OR (44°38' N, 123°17' W), elevation 317 m. The western hemlock

site is on the west slope of the Cascade Range, east of Scio, OR (44°40' N, 122°36' W), elevation 730 m. Details concerning these sites are in Runyon et al. (1994) and Matson et al. (1994). Both study locations had scaffold towers allowing canopy access to at least three trees; all measurements were taken near canopy tops.

We conducted measurements on August 10, 1994 (for Douglas-fir) and August 24, 1994 (for western hemlock) with an LI-6200 photosynthesis system (Li-Cor, Inc., Lincoln, NE) with a 0.25-l cuvette for hourly measurements of  $g_s$ . A pressure chamber (PMS systems, Corvallis, OR) was used simultaneously to measure  $\Psi_{\text{leaf}}$  of adjacent small twigs and also before dawn (the measurement of the twig was used to approximate leaf water potential). Projected leaf area was determined with a video image recorder and AgVision software (Decagon Devices, Inc., Pullman, WA). Air temperature and humidity were measured with the LI-6200 by placing the sensor in a shaded location, turning off the dry air flow, allowing the system to equilibrate for at least ten minutes, and waiting until measurements were constant over two minutes.

For red alder and black cottonwood, we estimated  $K_L$  from data published by Pezeshki and Hinckley (1982) for July 31, 1980, near the end of a pre-drought period. (Values of  $g_s$  were converted from  $\text{cm s}^{-1}$  to  $\text{mol m}^{-2} \text{s}^{-1}$  following the equations in Percy et al. (1991). We made educated guesses of temperature and pressure, which were not provided in the report. The conversion is not sensitive to these values; an error of no more than 2–3% could result from differences between actual and measured temperature and pressure. A somewhat larger error is possible as a result of estimating data values from published figures.) For red alder,  $K_L$  was also estimated from data published by Shainsky et al. (1994).

Parameter values for  $g_{s-\text{max}}$  and  $\Psi_{\text{threshold}}$  for all species were estimated from maximum values of  $g_s$  and minimum values of  $\Psi_{\text{leaf}}$  reported in the literature (Lopushinsky 1969, Running 1976, Tan et al. 1977, Pezeshki and Hinckley 1982, Shainsky et al. 1994, Yoder and Waring 1994, Harrington and Yoder, unpublished data).

### Vulnerability to cavitation

For red alder, we measured xylem vulnerability to cavitation following methods described by Kavanagh et al. (1999). One- to three-year-old stems were collected in early morning in June 1997 from three trees near Knappa, OR (46°10' N, 123°32' W), and one tree near Astoria, OR (46°10' N, 123°50' W) and immediately wrapped in moist towels and placed on ice; measurements were completed that afternoon. Trees ranged in age from five to ten years old, and stems ranged in diameter from 0.4 to 0.7 cm. For the other species, we used xylem vulnerability responses reported by Kavanagh and Zaerr (1997), Kavanagh et al. (1999) and Jed Sparks (University of Colorado, Boulder, CO, personal communication).

## Results

### Parameter estimates

Calculated values for  $K_L$  and estimated values for other pa-

parameters are summarized in Table 1. Each species showed a consistent  $\Psi_{\text{threshold}}$  that was apparent in diurnal patterns of  $\Psi_{\text{leaf}}$  across a wide variety of environmental conditions and in a number of studies. For Douglas-fir and western hemlock,  $\Psi_{\text{leaf}}$  generally dropped quickly to about  $-2.0$  MPa, then remained between  $-2.1$  and  $-2.5$  MPa through midday, and recovered at the end of the day (e.g., Lopushinsky 1969, Running 1976, Tan et al. 1977, data not shown from this study). The pattern was similar for red alder except that  $\Psi_{\text{leaf}}$  began to plateau at about  $-1.0$  MPa, remaining between  $-1.1$  and  $-1.5$  MPa during midday (Pezeshki and Hinckley 1982, Shain-sky et al. 1994, Harrington and Yoder, unpublished data). For cottonwood, midday minimum  $\Psi_{\text{leaf}}$  typically ranged between  $-0.7$  and  $-1.0$  MPa (Pezeshki and Hinckley 1982). These patterns suggest a  $\Psi_{\text{threshold}}$  range rather than a discrete point. However, for the sake of simplicity, we chose  $\Psi_{\text{threshold}}$  values near the point when midday  $\Psi_{\text{leaf}}$  first began to level off, because stomatal closure must have been reducing transpiration at this point.

#### Vulnerability to cavitation in relation to $\Psi_{\text{threshold}}$

For coastal seed sources, which are similar to the Douglas-fir trees used in the current study, xylem vulnerability curves for the main stems of seedlings indicated no loss of conductivity when  $\Psi_{\text{xylem}}$  was greater than  $-2.0$  MPa and complete loss below  $-7.5$  MPa (Figure 1a). Cochard (1992) reported similar vulnerability curves for mature Douglas-fir, with no loss of hydraulic conductivity for  $\Psi_{\text{xylem}}$  greater than  $-2.5$  MPa. Western hemlock is somewhat more vulnerable to cavitation than Douglas-fir; however, western hemlock seedlings also showed little loss of conductivity when  $\Psi_{\text{xylem}}$  was greater than  $-2.0$  MPa (Kavanagh and Zaerr 1997). The vulnerability functions indicate that for both Douglas-fir and western hemlock, less than 5% loss of hydraulic conductivity is expected if  $\Psi_{\text{xylem}}$  is above the  $\Psi_{\text{threshold}}$  value of  $-2.1$  MPa ( $\Psi_{\text{xylem}}$  is greater than  $\Psi_{\text{leaf}}$  when leaves are transpiring, so even this is a high estimate). Therefore, we omitted Step 3b of the model (adjusting to account for hydraulic loss caused by cavitation) for Douglas-fir and western hemlock.

Xylem vulnerability for young red alder from the NW Oregon coast (Figure 1b) showed approximately 6% loss of hydraulic conductivity at the  $\Psi_{\text{threshold}}$  of  $-1.1$  MPa, with slightly less than 10% loss at  $-1.5$  MPa (again, these estimates are high because  $\Psi_{\text{xylem}}$  is greater than  $\Psi_{\text{leaf}}$  when transpiration occurs). Therefore, we also ignored the small loss of hydraulic conductivity for red alder that is expected as  $\Psi_{\text{xylem}}$  approached  $\Psi_{\text{threshold}}$ . Black cottonwood trees from coastal regions lost about 30% of their hydraulic conductivity when  $\Psi_{\text{xylem}}$  reached

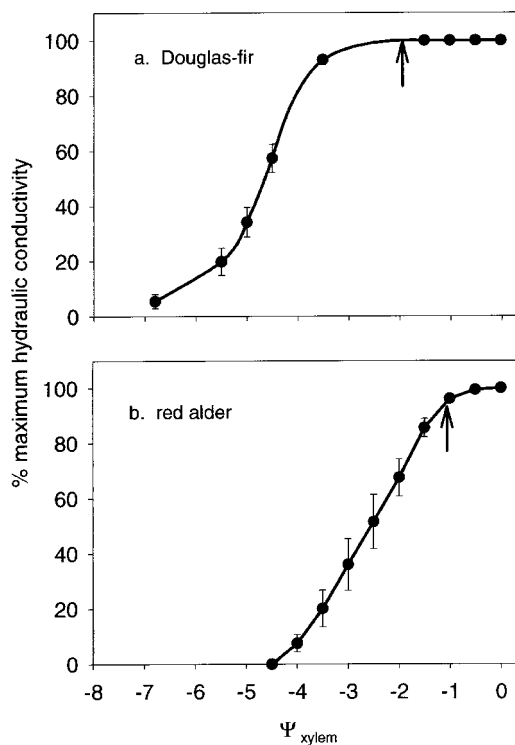


Figure 1. Xylem vulnerability to cavitation as a function of stem water potential for (a) coastal Douglas-fir seedlings ( $n = 10$ ) and (b) young red alder trees ( $n = 4$ ). Error bars are standard errors. Arrows denote  $\Psi_{\text{threshold}}$  for each species from field observations. Data for Douglas-fir are adapted from Kavanagh et al. (1999). See text for more explanation of the vulnerability curve for red alder and for a discussion of vulnerability of western hemlock and black cottonwood to xylem cavitation.

the  $\Psi_{\text{threshold}}$  of  $-0.8$  MPa (Jed Sparks, personal communication). We ran two simulations with black cottonwood, first assuming no loss of hydraulic conductivity as  $\Psi_{\text{xylem}}$  approached  $\Psi_{\text{threshold}}$ , and second assuming 10% loss at  $\Psi_{\text{xylem}} = -0.5$  MPa scaling to 30% loss at  $\Psi_{\text{xylem}} = -0.8$  MPa, as indicated by Sparks' unpublished data.

#### Effects of soil water potential on daily maximum $g_s$ in Douglas-fir

Field observations with conifers have shown that maximum  $g_s$  during any day is directly proportional to  $\Psi_{\text{soil}}$  over a broad range of  $\Psi_{\text{soil}}$  (e.g., Running 1976). A generalized representation of this response for Douglas-fir is shown in Figure 2a. To determine whether the hydraulic model can explain

Table 1. Species and parameters used in the model (see text for derivation of values).

Species	$g_{s-\text{max}}$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$K_L$ ( $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ )	$\Psi_{\text{threshold}}$ (MPa)
Douglas-fir	0.15	1.1	-2.1
Western hemlock	0.20	0.7	-2.1
Red alder	0.30	7.9	-1.1
Black cottonwood	0.30	8.4	-0.8

this relationship, we predicted  $g_s$  for Douglas-fir over a matrix of  $\Delta W$  and  $\Psi_{\text{soil}}$  values (Figure 2b). The generalized response from field measurements in Figure 2a is likely to be biased such that measurements with high soil water also had high humidity, and low soil water corresponded to low humidity. Simultaneous conditions of high soil water with very low humidity, and vice versa, rarely occur in the field. With this caveat, the modeled and measured responses of Douglas-fir looked quite similar.

#### Interactive effects of humidity and soil water potential on $g_s$

Figure 3a shows interactive effects of  $\Psi_{\text{soil}}$  and  $\Delta W$  on  $g_s$  of Douglas-fir based on the data of Tan et al. (1977). Modeled values of  $g_s$  for Douglas-fir (Figure 3b) demonstrated similar trends, although the modeled data indicated less sensitivity to both  $\Delta W$  and  $\Psi_{\text{soil}}$  than the measured values. This difference could result from comparatively low  $K_L$  values for the trees measured by Tan et al. (1977), which were from the east side of Vancouver Island, B.C., Canada. When the simulation was performed with lower  $K_L$  values, the  $g_s$  versus  $\Delta W$  response closely mimicked the results of Tan et al. (1977).

#### Differences in stomatal behavior between western hemlock and Douglas-fir

Stomatal conductance of western hemlock is more sensitive to humidity compared with Douglas-fir (Figure 4a illustrates data adapted from Waring and Schlesinger 1985; also see Running 1976, Minore 1979). To determine whether the hydraulic

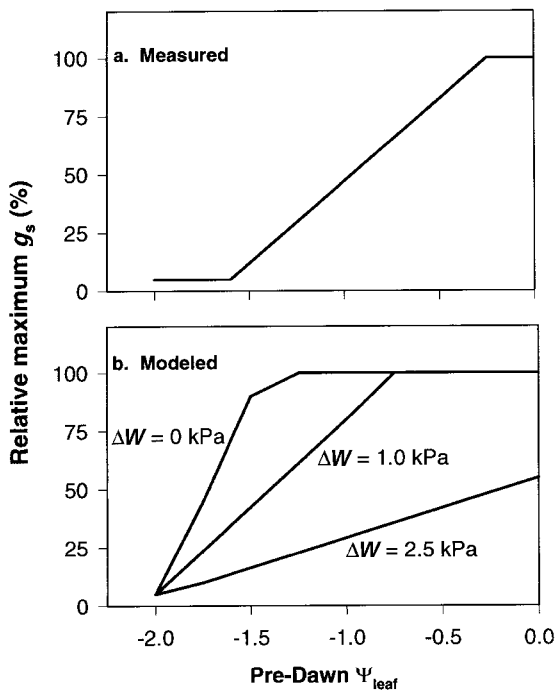


Figure 2. Measured (a) and modeled (b) maximum daily  $g_s$  of Douglas-fir in response to soil water deficit. Measured data are adapted from Waring and Schlesinger (1985), based on measurements reported in Waring et al. (1981). Modeled data are based on the parameters in Table 1.

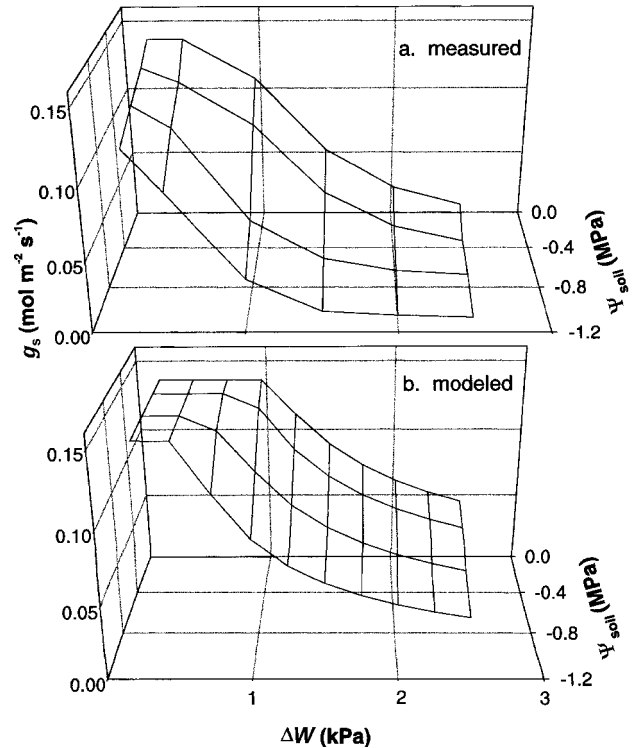


Figure 3. Measured (a) and modeled (b) responses of  $g_s$  of Douglas-fir to simultaneous variations in  $\Psi_{\text{soil}}$  and  $\Delta W$ . Measured data are adapted from Whitehead and Jarvis (1981), based on data originally reported by Tan et al. (1977). Modeled data are based on the parameters in Table 1.

model can account for these differences, we applied it using the parameter values in Table 1 with  $\Psi_{\text{soil}} = 0$  over a range of  $\Delta W$  (Figure 4b). Because of the low  $K_L$  for western hemlock, maximum stomatal conductance was only possible for  $\Delta W$  values less than 0.5 kPa. As a result, simulated  $g_s$  for Douglas-fir was greater than for western hemlock except at very low evaporative demand. Over the  $\Delta W$  range of 0.5 to 2.5 kPa,  $g_s$  of western hemlock declined by more than 75%, whereas  $g_s$  of Douglas-fir was reduced by only 50%, as also shown in field measurements. However, modeled  $g_s$  values were unable to reproduce slightly higher  $g_s$  reported for western hemlock than for Douglas-fir at very high evaporative demand. Our current hydraulic model does not account for minimum  $g_s$ , and it is possible that cuticular as well as residual stomatal conductance after complete stomatal closure are greater for western hemlock than for Douglas-fir.

#### Comparisons of Douglas-fir, western hemlock, red alder, and black cottonwood

In general, stomata of angiosperm trees in western Oregon show less sensitivity to vapor pressure deficit than those of gymnosperms (Marshall and Waring 1984). Figure 5a illustrates the difference under conditions of high soil water based on data from published reports. The curves for the gymnosperms are derived from a compilation of data reported by Marshall and Waring (1984) and Waring and Schlesinger

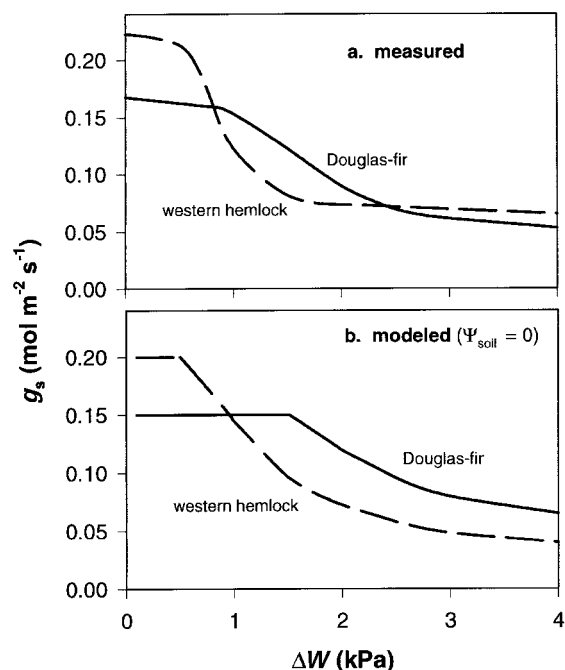


Figure 4. Measured (a) and modeled (b) responses of  $g_s$  of Douglas-fir and western hemlock to  $\Delta W$ . Measured data are adapted from Waring and Schlesinger (1985). Modeled data are based on the parameters in Table 1.

(1985), and are slightly different from the  $g_s$  versus  $\Delta W$  curves in Figure 4a. The curves for alder and cottonwood are derived from data reported by Pezeshki and Hinckley (1982).

The simulated responses of  $g_s$  to  $\Delta W$  in saturated soil conditions (Figure 5b) showed the same species ranking as the measured data. Western hemlock initiated stomatal closure at the highest humidity, followed by Douglas-fir, black cottonwood and red alder. The relative stomatal sensitivity of the species to humidity did not rank in the same order as their  $K_L$  values. The  $K_L$  for cottonwood was higher than for alder, but the higher  $\Psi_{\text{threshold}}$  value for cottonwood triggered stomatal closure at a lower  $\Delta W$ .

With the introduction of a moderate soil water deficit ( $\Psi_{\text{soil}} = -0.5$  MPa), the model predicted large changes in stomatal behavior of the angiosperms compared with the gymnosperms (Figure 5c). For all results shown with a solid line, we assumed no loss of hydraulic conductivity as  $\Psi_{\text{leaf}}$  approached  $\Psi_{\text{threshold}}$ . Nevertheless, for the angiosperms the change in  $\Psi_{\text{soil}}$  from 0 to  $-0.5$  MPa reduced the soil-to-leaf water potential gradient by more than 50% because of their comparatively high  $\Psi_{\text{threshold}}$ . Thus, the moderate soil water deficit had a large impact on modeled transpiration rate and stomatal conductance of red alder and black cottonwood. Because of the lower  $\Psi_{\text{threshold}}$  for the two gymnosperms, the reduced  $\Psi_{\text{soil}}$  had much less impact on  $\Delta\Psi$ , so they showed less stomatal sensitivity to reduced soil water. When hydraulic loss due to cavitation was considered for the cottonwood (dashed line in Figure 5c), the trees could not sustain maximum stomatal conductance with  $\Psi_{\text{soil}} = -0.5$  MPa even at high humidity. Cottonwood typically grows only in conditions of high soil

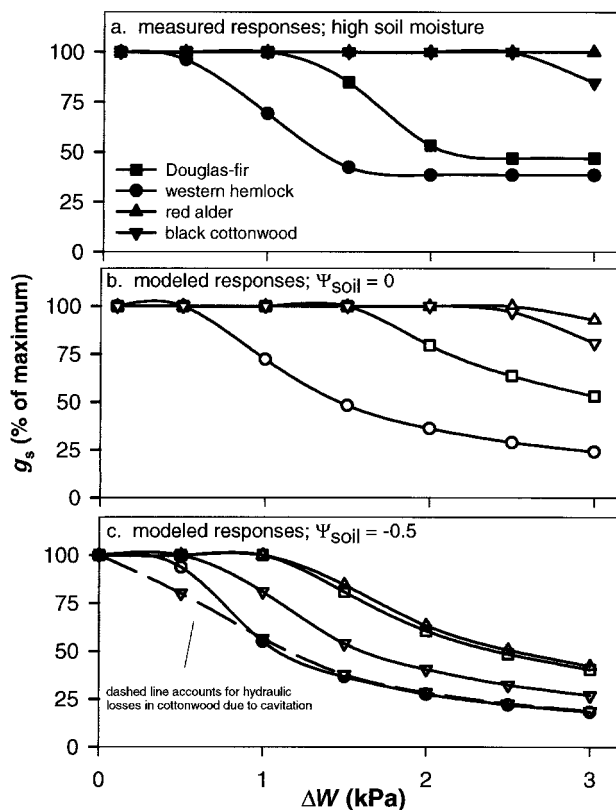


Figure 5. Measured (a) and modeled (b and c) responses of  $g_s$  (expressed as a percent of the maximum possible for each species) of Douglas-fir (■), western hemlock (●), red alder (▲) and black cottonwood (▼) to  $\Delta W$ . Measured responses for the angiosperms are adapted from Pezeshki and Hinckley (1982) and for the gymnosperms from Marshall and Waring (1984). Modeled data are based on parameters in Table 1, assuming no soil water deficit (b) or  $\Psi_{\text{soil}} = -0.5$  MPa (c). The dashed line in (c) indicates the modeled response for black cottonwood if losses in  $K_L$  are considered, based on xylem vulnerability measurements by Jed Sparks (personal communication).

water. The simulation illustrates why low soil water contents might be especially deleterious to these trees, although they tolerate high vapor pressure deficits when soil water availability is high.

## Discussion

The concept that stomatal behavior is coordinated with internal leaf water status and hydraulic properties of the vascular system has been discussed previously by many investigators (e.g., Landsberg et al. 1976, Running 1976, Hinckley et al. 1978, Waring and Running 1978, Whitehead and Jarvis 1981, Teskey et al. 1983, Tyree and Sperry 1988, Jones and Sutherland 1991, Meinzer and Grantz 1991, Saliendra et al. 1995, Williams et al. 1996). Nevertheless, there remains much controversy about the role of hydraulic signals in controlling stomatal behavior. In species comparisons, differences in stomatal responses to humidity and soil water deficit are almost always discussed and modeled as though these traits were independent of characteristics of the vascular system (but see Williams et al. 1996).

Our analysis implies strong linkages, although these relationships do not imply causality. We now take a closer look at some of the assumptions, implications and limitations of the hydraulic model.

*Do stomata regulate transpiration to maintain a threshold water potential?*

Many, if not most, woody species have a characteristic threshold water potential for stomatal closure (reviewed in Hinckley et al. 1978). An implication of the concept of a threshold water potential is that stomata respond to subtle variations in leaf water status, and that the mesophyll signals that trigger responses in guard cells are somehow related to the water potential of the supplying xylem. There is ample experimental evidence that stomata respond directly to hydrostatic signals (Teskey et al. 1983, Saliendra et al. 1995, Fuchs and Livingston 1996, Whitehead et al. 1996). However, there is no known mechanism for such a “feedback” response (e.g., Sinclair and Ludlow 1985, see Whitehead 1998 for a recent review).

Thirty years ago, Hodges (1967) determined that variation in leaf water potential was a primary influence on gas exchange in Douglas-fir, and Lopushinsky (1969) added further evidence shortly thereafter. However, many investigators in the 1970s and early 1980s concluded that  $\Psi_{\text{leaf}}$  is not related to stomatal conductance of Douglas-fir or other woody species (e.g., Brix 1972, Schulze et al. 1975, Watts et al. 1976, Tan et al. 1977, Leverenz 1981). Interestingly, one would reach the same conclusion from a correlation analysis of  $g_s$  and  $\Psi_{\text{leaf}}$  predicted in this study, although the model explicitly limits  $g_s$  on the basis of  $\Psi_{\text{leaf}}$ . Furthermore, a statistical analysis of the modeled data showed much closer correlation between  $g_s$  and  $\Delta W$  than between  $g_s$  and  $\Psi_{\text{leaf}}$ , even though the model includes no direct response of  $g_s$  to  $\Delta W$ . This is because transpiration rate is constrained by the water supply; to control transpiration, stomatal conductance must vary inversely with evaporative demand. The conclusion that  $g_s$  is unrelated to  $\Psi_{\text{leaf}}$  may result, in part, from data analysis procedures.

*What happens if  $\Psi_{\text{leaf}}$  is less than  $\Psi_{\text{threshold}}$ ?*

A problem with assuming that  $\Psi_{\text{leaf}}$  controls  $g_s$  is that  $\Psi_{\text{leaf}}$  can fall well below the threshold value associated with stomatal closure. For example, although many studies document  $\Psi_{\text{leaf}}$  values for Douglas-fir that “bottom-out” between  $-2.0$  and  $-2.4$  MPa (e.g., Lopushinsky 1969, Running 1976, Tan et al. 1977), values lower than  $-3.0$  MPa have been recorded when soils are very dry, especially with seedlings. In the current model, hydraulic flux, stomatal conductance and transpiration all approach zero as  $\Psi_{\text{soil}}$  approaches  $\Psi_{\text{threshold}}$ ; when  $\Psi_{\text{soil}}$  is less than  $\Psi_{\text{threshold}}$ , the model predicts “negative” stomatal conductance. Thus, the current model is not appropriate for severe soil water stress. One way to account for lower  $\Psi_{\text{leaf}}$  values would be to quantify cuticular conductance and minimum stomatal conductance to account for water vapor flux after complete stomatal closure. It is probably the cuticular and residual stomatal conductances that allow leaf and twig water potentials to fall well below  $\Psi_{\text{threshold}}$  after complete stomatal closure.

*Is  $\Psi_{\text{threshold}}$  for stomatal closure related to xylem vulnerability to cavitation?*

Based on detailed models of hydraulic architecture, Tyree and Sperry (1988) concluded that nearly all woody species operate near the edge of catastrophic xylem failure. However, they also noted that under normal field conditions, drought rarely induces catastrophic loss of hydraulic conductance. Most plants do not maintain their maximum possible transpiration rate in the face of incipient hydraulic failure. Instead, as Tyree and Sperry (1988) concluded, stomatal closure maintains transpiration below a critical rate.

Jones and Sutherland (1991) considered two extreme alternatives concerning stomatal control of cavitation. (1) Stomata regulate transpiration to avoid hydraulic loss. According to this scenario, stomatal closure should occur as  $\Psi_{\text{xylem}}$  approaches the point of incipient cavitation. (2) Stomatal conductance is optimized to ensure the maximum flux of water (i.e., maximizing  $K_L \Delta \Psi$ ) and therefore maximum photosynthesis, even at the expense of some loss of hydraulic conductance. Our analyses indicate that leaf water potentials of mature Douglas-fir and western hemlock generally do not fall below a value that would induce more than 5% loss of xylem conductivity. By combining information from vulnerability curves and  $K_L$  values, we estimate that “optimum”  $\Delta \Psi$  for Douglas-fir and western hemlock would require  $\Psi_{\text{leaf}}$  values of less than  $-3.5$  MPa; such low values are unusual for these species. We conclude that Douglas-fir and western hemlock are “conservative,” *sensu* Jones and Sutherland (1991), and do not routinely function near the edge of catastrophic cavitation in stems, although significant hydraulic losses might occur in roots. In contrast, our literature review suggests that black cottonwood and red alder may routinely operate closer to the edge of xylem safety, although our data for these species are more limited.

Jones and Sutherland (1991) and Sperry (1995) noted that plants with a very steep hydraulic loss versus  $\Psi_{\text{xylem}}$  function (i.e., vulnerability curve) are more likely to follow a “conservative” strategy because they have a smaller margin of safety. Jones and Sutherland (1991) also noted that, for some species, conservative use of soil water in the short term may be beneficial by providing for a longer growing season. Another important consideration is the cost of losing leaves or larger plant parts as a result of hydraulic loss. The long-lived foliage of evergreens represents a greater investment compared with deciduous foliage, which in any event is discarded at the end of a growth season. From this perspective, there may be a selective advantage for plants with long leaf life spans to have xylem that is resistant to cavitation and to regulate transpiration in a way that minimizes risk of cavitation. This could be one of the sources of convergent evolution that results in an inverse relationship between leaf life spans and relative growth rates (Reich et al. 1997).

## Conclusions

We tested the hypothesis that species differences in stomatal responses to soil and atmospheric water deficits can be explained by two parameters, (1) leaf-specific conductance of the

vascular system, and (2) a threshold value of leaf water potential. For four woody species, a simple hydraulic model based on these two parameters predicted stomatal behaviors that were similar to published reports. A physiological mechanism for such a response awaits future investigators.

### Acknowledgments

We gratefully acknowledge financial support for this research to B.J. Bond from NASA (NAGW-3870) and the USDA NRI Competitive Grants Program (94-37101-1214). Drs. Tom Hinckley, Richard Waring, Michael Ryan and Joe Zaerr provided many constructive comments on drafts of the manuscript. We thank Blake Farnsworth, Matthew Radosevich, and Michelle Fischler for help with field measurements and Steve McKenna, Eric Hanson, and Bob Shula for help with construction of access towers.

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