

Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine

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ABSTRACT

Relationships between tree size and physiological processes such as transpiration may have important implications for plant and ecosystem function, but as yet are poorly understood. We used a process-based model of the soil–plant–atmosphere continuum to investigate patterns of whole-tree sap flow in ponderosa pine trees of different size and age (36 m and ~250 years versus 13 m and 10–50 years) over a developing summer drought. We examined three different hypothetical controls on hydraulic resistance, and found that size-related differences in sap flow could be best explained by absolute differences in plant resistance related to path length (hypothesis 1) rather than through different dynamic relationships between plant resistance and leaf water potential (hypothesis 2), or alterations in rates of cumulative inducement and repair of cavitation (hypothesis 3). Reductions in sap flow over time could be best explained by rising soil–root resistance (hypothesis 1), rather than by a combination of rising plant and soil–root resistance (hypothesis 2), or by rising plant resistance alone (hypothesis 3). Comparing hourly predictions with observed sap flow, we found that a direct relationship between plant resistance and leaf water potential (hypothesis 2) led to unrealistic bimodal patterns of sap flow within a day. Explaining seasonal reduction in sap flow purely through rising plant resistance (hypothesis 3) was effective but failed to explain the observed decline in pre-dawn leaf water potential for small trees. Thus, hypothesis 1 was best corroborated. A sensitivity analysis revealed a significant difference in the response to drought-relieving rains; precipitation induced a strong recovery in sap flow in the hypothetical case of limiting soil–root resistance (hypothesis 1), and an insignificant response in the case of limiting plant resistance (hypothesis 3). Longer term monitoring and manipulation experiments are thus likely to resolve the uncertainties in hydraulic constraints on plant function.

INTRODUCTION

Recent experiments have identified connections between physiology and size of plants (Dunn & Connor 1993), and linked these to age-related declines in forest productivity (Yoder *et al.* 1994; Hubbard, Bond & Ryan 1999), but mechanistic explanations are, at present, lacking. One hypothesis proposes that critical plant processes, such as carbon assimilation and evapotranspiration, are significantly constrained by the hydraulic pathway from soil to leaf, the nature of which varies according to growth-related changes in plant morphology (Mencuccini & Grace 1996; Ryan & Yoder 1997). If hydraulic constraints on plant function are ultimately shown to be significant, this may have considerable relevance to models of forest productivity (Landsberg & Waring 1997), watershed hydrology, carbon sequestration and biogeochemistry (Rastetter *et al.* 1991), and vegetation dynamics (Running & Gower 1991). Currently most models of plant processes do not take explicit account of plant hydraulics.

The nature of hydraulic constraints on plant function is partially understood (Fig. 1). Leaf water potential varies according to differences between rates of water loss from leaf to atmosphere, and rates of water re-supply from soils through the vascular system. Rates of water loss are determined by the vapour pressure gradient from leaf to atmosphere and resistance generated by the stomata and leaf boundary layer. Water supply is determined by the water potential gradient from soil to leaf, and the resistance and capacitance of the hydraulic pathway. Stomata apparently close to maintain leaf water potential above a critical level that would cause destructive cavitation and impairment of the vascular system (Sperry & Tyree 1988; Tyree & Sperry 1989; Jones 1992). Because of gravity, the height of leaves above the reference plane diminishes leaf water potential by approximately 0.01 MPa m⁻¹. Resistance to liquid flow through the vascular system is dependent on the number, radius and length of the component tracheids or vessels (Poiseuille's Law). Thus, all other things being equal, in longer stems the rate of flow declines. To maintain flow rates over longer distances, larger trees tend to compensate by widening tracheids or vessels (West, Brown & Enquist 1999). However, this compensation may come at a cost,

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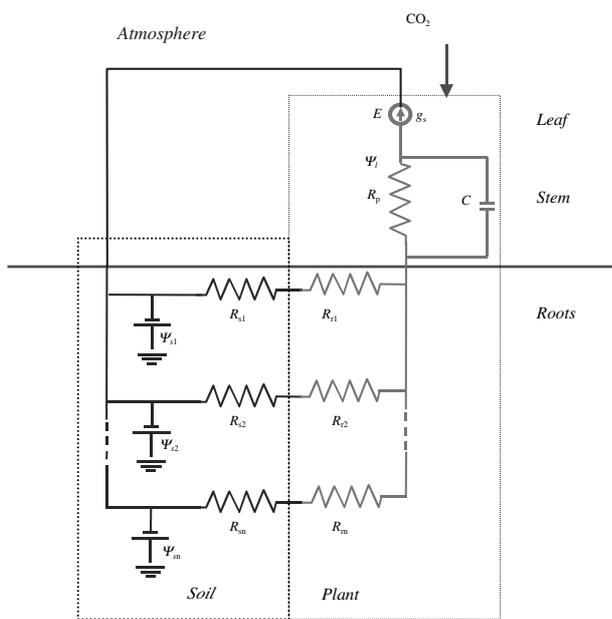


Figure 1. The resistance network for sap flow through the soil–plant–atmosphere system. Multiple (n) root layers are shown in parallel, each with specific resistance (R_b) comprised of both soil and root resistance components in series. The plant stem has a single resistance (R_p) but also a capacitance (C_p). Current is generated by transpiration.

perhaps via diminished structural strength or increased vulnerability to embolism (Tyree & Ewers 1991).

The development of techniques to measure sap flow (Wullschlegel, Meinzer & Vertessy 1998) has allowed *in situ* studies of plant water use, and has revealed significant differences in hydraulic resistance between large and small trees (Hubbard *et al.* 1999; Ryan *et al.* 2000). Analysis of both sap flow studies and latent energy flux data from eddy covariance systems (Williams *et al.* 1998) has indicated that hydraulic resistance can also vary seasonally. However, detailed understanding is lacking of how hydraulic constraints vary according to changes in the local physical environment (soil water feed-backs) and in the biological environment (size-related feed-backs). There are three particular areas of uncertainty that confuse interpretation of sap flow data. Firstly, the location of the greatest hydraulic resistance to flow is unclear. Is it within the plant vascular

system, or in the soil or soil–root interface? Secondly, how dynamic is plant resistance in comparison with soil resistance? In some plants there is evidence of a close coupling between leaf water potential and plant resistance, but there is also a clear physical relationship between soil moisture content and soil hydraulic resistance; which of these feed-backs is more important? Thirdly, it is unclear whether plant resistance is related to the length of flow path. West *et al.* (1999) suggest that vessel tapering avoids any increase in resistance in longer flow paths, whereas Tyree & Ewers (1991) suggest that most of the resistance to water transport is actually located in the final metre or so of flow into the transpiring leaves, while the bole is highly conductive.

We used a mechanistic model of the soil–plant–atmosphere continuum (Williams *et al.* 1996) to investigate patterns of hydraulic resistance in an open-grown ponderosa pine stand in central Oregon. Our purpose was to use three different model parametrizations to explore the three areas of uncertainty in tree hydraulics set out above, comparing measured sap flow with predicted values, for both large and small trees, and through a summer season of low precipitation. The parametrizations were based on alternate hypotheses of hydraulic sensitivity and dynamics, emphasizing different constraints and/or feed-backs on whole-tree sap flow (Table 1). The three hypotheses are based on the following precepts:

Constant plant resistance hypothesis. In moist soils, plant and soil resistance are of roughly equal magnitude. Plant resistance is a function purely of path length, and changes only with height of each canopy layer, not with plant or soil water status. Soil resistance is strongly linked to soil water status. This hypothesis is encapsulated in the soil–plant–atmosphere model (Williams *et al.* 1996; Williams *et al.* 1998; Williams *et al.* 2001).

Dynamic resistance-potential hypothesis. In moist soils, plant resistance is initially slightly greater than soil resistance. Plant hydraulic resistance is a function of leaf water potential, and stomata operate to maximize sap flow, following the hypothesis of Sperry *et al.* (1998). Thus, plant resistance varies on an hourly basis, whereas soil resistance is strongly linked to soil water status, and thus varies seasonally. Larger trees are increasingly vulnerable to cavitation as vessel/tracheid sizes increase, but there is no difference in vulnerability for leaves at different heights within a single tree.

Table 1 Hypotheses for dynamic hydraulic conductance

Hypothesis	1	2	3
Soil–root resistance	High	Medium	Low
Plant resistance	Proportional to path length	Vulnerability curve	A function of time spent stressed or at rest
Critical LWP	Constant	Variable	Constant
Size effect	Increased path length	Increased vulnerability	Increased vulnerability
Drought effect	Increased soil–root resistance	Increased plant and soil–root resistance	Increase plant resistance

LWP, leaf water potential.

Cumulative cavitation inducement/repair hypothesis. In moist soils, plant hydraulic resistance is significantly greater than soil resistance. Plant resistance varies depending on the balance between cavitation inducement and repair, governed, respectively, by the time spent at the critical leaf water potential and the time spent at a resting state. Seasonal changes in sap flow are a function of rising plant hydraulic resistance. Larger trees are subject to more rapid cavitation inducement. Soil–root resistance is a minor component of the hydraulic pathway and is only weakly responsive to soil drying.

We tested the three hypotheses against sap flow data from young (short) and older (tall) ponderosa pine at a stand in central Oregon, and judged whether any or all of the hypotheses provided consistent mechanisms to explain the observed patterns of water dynamics in trees (i.e. patterns of sap flow) and leaves (leaf water potential) in both young and old stands.

MATERIALS AND METHODS

Field site

We measured water use of individual ponderosa pine (*Pinus ponderosa* Laws.) trees at a site near Black Butte, Oregon, USA (44°24' N, 121°40' W) during May–September 1996 (days 161–280). The stand is open, individual trees are well illuminated, and there are both old, tall trees (36 m, 250 years) and young, short trees (3–16 m, 10–50 years), with a sparse bitterbrush (*Purshia tridentata* L.) and bunchgrass understorey. The climate is typified by warm, dry summers and cool, wet winters. Mean annual precipitation (1960–90) was 360 mm (at Sisters, OR, 15 km east of the site), and approximately 17% of annual precipitation falls between May and September. Precipitation for 1996 at Sisters was 132% of the 1960–90 mean. Precipitation for the soil recharge period (the preceding September to May) was 411 mm. The soil is a sand loam (73% sand, 6% clay), derived from volcanic ash and is classified as a light-coloured andic inceptisol. Based on the root systems of some wind-toppled trees, the rooting depth is greater than 1.5 m. For more details see Ryan *et al.* (2000).

Sap flow measurements

We sampled five trees in each of two size classes, from 9 to 16 m height, and from 31 to 41 m height. We measured sap flow through the xylem of each tree using a heat-balance approach (EMS, Brno, Czech Republic, Cermak *et al.* 1995). Tree leaf area was determined using site-specific allometric relationships between branch diameter and leaf mass and between leaf mass and leaf area for each size class (Ryan *et al.* 2000). Soil moisture was measured every 7–14 d using time-domain reflectometry. For a complete description of all the measurements and methods, see Hubbard *et al.* (1999) and Ryan *et al.* (2000).

Model description

Simulating sap flow

Water travels from soil to atmosphere through a network of resistances, down a gradient of water potential (Fig. 1). Leaves draw moisture from multiple soil layers, which are assumed to act as resistors in parallel; within each soil layer, root and soil resistance act in series. The large store of water in tree stems acts to buffer sap flow and is represented as a capacitor. The current through the resistance network is generated by transpiration, itself initiated by stomatal opening (Williams *et al.* 1996).

The principle behind stomatal dynamics is that C assimilation is maximized within the limitations of the hydraulic system, so stomatal resistance is adjusted to balance atmospheric demand for water with rates of water uptake and supply from soils. Atmospheric demand is governed by the vapour pressure difference between leaf internal air spaces and the atmosphere, and vapour phase exchange (E) is determined using the Penman–Monteith equation. Water loss ($= E$) is linked to changes in leaf water potential (Ψ_l), according to the water potential gradient between leaf and soil, liquid-phase hydraulic resistances [in the rhizosphere (R_s), plant stems (R_p) and roots (R_r)] and the capacitance (C) of the pathway that links soil to leaf. Stomatal resistance is varied to maintain evapotranspiration (E) at the rate that keeps Ψ_l from falling below a critical threshold value (Ψ_{lmin}), below which potentially dangerous cavitation of the hydraulic system may occur. Thus, once $\Psi_l = \Psi_{lmin}$, E is set so that $d\Psi_l/dt = 0$, where

$$\frac{d\Psi_l}{dt} = \frac{\Psi_s - \rho_w gh - E(R_s + R_r + R_p) - \Psi_l}{C(R_s + R_t + R_p)}. \quad (1)$$

The gravitational component of leaf water potential is determined by the density of water (ρ_w), acceleration due to gravity (g), and the height above the reference plane (h), set to the soil surface.

Capacitance is the change in stem water content (W) for a given change in water potential

$$C = \frac{dW}{d\Psi}, \quad (2)$$

where W varies as the difference between the sap flow into the stem (J) and the flux out (E)

$$\frac{dW}{dt} = J - E. \quad (3)$$

Thus, the sap flow at the base of the tree stem can be determined from evapotranspirative losses as

$$J = E + C \frac{\Delta\Psi}{\Delta t}. \quad (4)$$

Radiative transfer in open canopy forests and radiation absorption by individual trees

In traditional canopy models the equations for radiative transfer tend to assume a statistical uniformity in the dis-

tribution and characteristics of canopy elements. This assumption is generally reasonable, but is not justifiable in open canopies. We modified the multiple layer radiative transfer scheme in the soil–plant–atmosphere model to: (1) take account of the highly clumped foliage and open canopy of the ponderosa pine stand; and (2) to simulate light absorption by individual trees. The model uses two leaf area distributions; one, for the overall stand, to determine radiation attenuation, and another, for the individual tree, to determine radiation absorption. Light is attenuated by the overall canopy (LAI), so that for a canopy layer x , irradiance penetrating through that layer (I_x) is a function of the irradiance incident from the layer above (I_{x+1}), attenuated by the light extinction coefficient (k) and the canopy leaf area density of the layer (L_x):

$$I_x = I_{x+1} \exp(-kL_x). \quad (5)$$

The absorption of light by leaves of the *individual tree* in the layer (A_x) is determined by the *tree* leaf area density in that layer (L'_x):

$$A_x = I_{x+1} [1 - \exp(-kL'_x)]. \quad (6)$$

If $L'_x \gg L_x$, then the canopy is open and clumped, self-shading of the individual tree is reduced, and the lower canopy is relatively well-illuminated.

Because the approach we used to model radiation absorption by trees in open stands is a new and untested development of the model, we examined sensitivity of sap flow to variations in density of the canopy LAI. We undertook simulations with canopy LAI set to tree LAI (Table 2) and then with canopy LAI set to 0.3, a very low value.

Soil–water relations

The soil–plant–atmosphere model simulates soil surface energy balance, coupled soil heat and water transport, root distribution and water uptake, and the interception and evaporation of water on canopy surfaces (Williams *et al.* 2001). The volume of soil accessed by roots is critical to water supply in drought-prone systems, so the individual tree model parametrization must define the exploited soil volume for the simulated tree. In an open stand, we assume that individual trees extend their rooting zone beyond their crown radii. Rooting area is estimated as a multiple of crown area, where the multiple is set by the ratio of tree LAI (Table 2) to stand LAI (approximately 1.5). This assumes that while the canopy is open, the soil surface layers are exploited uniformly by roots.

Model parametrization and application

We undertook a series of simulations over a period of 200 d of the growing season of 1996 (Julian days 100–300) to compare sap flow predictions with mean measured values for large and small trees collected over the period from day 160–280 (8 June to 6 October 1996). We set the initial conditions on day 100 so that water content was 22% by volume in all soil layers (approximately field capacity). In all cases, parametrization consisted of setting descriptors of the soil–plant system, such as root resistivity, that were then *constant* through each simulation. The model was applied with time-varying forcing variables of meteorology and foliar phenology.

Most model parameters were defined by independent measurements at the study site or a site close by (Williams *et al.* 2001). We first used a null hypothesis to demonstrate significant model–data discrepancies in simulations lacking differences in soil and plant hydraulic resistance. We then developed parametrizations for each of the hypotheses heuristically; that is, we adjusted parameters in an attempt to best match predictions to the observed daily sap flow. For each hypothesis, we examined what parameter changes were required to explain differences in behaviour between small and large trees, and over time. Only a specific and limited set of variables were adjusted (Table 3).

Soil characteristics

The soil was defined structurally by sand and clay content. We used a relationship between pre-dawn leaf water potential (measured by pressure bomb) and soil water content (time domain reflectometry) developed over 2 years at a nearby site to estimate relationships between soil water potential and soil water content (B. Law, Oregon State University, personal communication). Empirical equations (Saxton *et al.* 1986) related soil structure to the relationship between soil water content and soil hydraulic conductivity. Soil thermal conductivity and volumetric heat capacity were also related to soil structure through empirical relationships (Hillel 1998).

Canopy characteristics

We used measurements and empirical relationships to determine total leaf area and mean leaf area index for large and small trees (Table 2). For the simulated mean large tree, we distributed 96% of foliage uniformly in eight layers

Table 2. The mean characteristics of large and small trees at Black Butte

ID	Height (m)	Height to base of live crown (m)	Leaf area (m ²)	Crown cross-sectional area (m)	Leaf area index (m ² m ⁻²)
Small	13.2	2.40	68.08	14.89	4.58
Large	37.2	11.72	204.30	51.17	4.18

Table 3. Parametrizations and corroboration statistics for the three hydraulic hypotheses (1–3) and the null hypothesis (0) for both large and small tree applications. RMSE is the root-mean-square-error derived from comparison of predicted versus observed daily sap flow for 94 d (large trees) or 95 d (small trees); r^2 quantifies the proportion of observed day-to-day variation explained by the model; the slope and intercept describe the linear regression of observed on modelled sap flow

Hypothesis	0		1		2		3	
	Large	Small	Large	Small	Large	Small	Large	Small
Root resistivity (MPa s g mmol ⁻¹)	100	100	100	100	100	100	100	100
Root biomass (g m ⁻²)	900	900	900	900	900	900	1500	1500
Rooting depth (m)	2.0	2.0	2.0	2.0	2.0	2.0	2.4	2.4
K_1' (mmol m ⁻² s ⁻¹ MPa ⁻¹)	4	4			20	20	3.5	5.0
G_p (mmol m ⁻¹ s ⁻¹ MPa ⁻¹)			100	100				
v							0.25	0.20
c					2.8	4.0		
d					2.4	3.0		
RMSE	155	30	58	22	72	19	69	16
r^2	0.64	0.56	0.90	0.89	0.70	0.87	0.74	0.89
slope/intercept	0.71/–31	0.81/10	1.04/–56	1.05/14	0.90/–22	0.98/13	1.18/–76	0.99/9

between 10 and 36 m, and the remainder in two layers between 5 and 10 m. For the simulated small tree, the foliage was uniformly distributed in four layers between 5 and 13 m. Leaf area allometric relationships were determined on 18 August 1996, Julian day 230. Temporal variation in leaf area over the study period was estimated using time series data from Law *et al.* (2000) on canopy light transmission at a nearby ponderosa pine stand. Canopy capacitance was set to 7.0 mol m⁻² leaf area MPa⁻¹ (Landsberg, Blanchard & Warrit 1976; Schulze *et al.* 1985).

Root characteristics

Root hydraulic resistance (R_r) is proportional to total root biomass and root resistivity (specific resistance); soil hydraulic resistance (R_s) is governed by root surface area and soil hydraulic conductivity (Williams *et al.* 2001). At a nearby ponderosa pine site (Law *et al.* 2000) fine root (< 1 mm radius) biomass varied between 1272 and 2078 g m⁻³ in the top 0.2 m. We assumed an exponential decay in root biomass with depth, with surface values based on measurement data. In hypotheses 1 and 2 we set total root biomass to 900 g m⁻²; in hypothesis 3 we examined the effects of increasing root biomass to 1500 g m⁻², to explore the possibility that hydraulic resistance was concentrated in the plant stem rather than the roots. We determined root surface area based on an assumption of a root radius of 0.5 mm. We found that a minimum rooting depth of 2.0 m was required to avoid intense late season drought stress, especially in small trees. To examine the effect of reduced soil hydraulic stress, we increased rooting depth to 2.4 m in hypothesis 3.

Soil–plant hydraulic parameters

Hypothesis 1

Stomatal resistance was regulated to ensure that Ψ_l never fell below a minimum value, Ψ_{lmin} . From pressure chamber

measurements of mid-day Ψ_l , we set $\Psi_{lmin} = -1.8$ MPa. Leaf-level plant hydraulic resistance (R_p) varied with estimated path-length, using a constant hydraulic conductivity (G_p), thus

$$R_p = h/G_p, \quad (7)$$

where h is height of the canopy layer above the ground. Apart from increased hydraulic resistance in taller trees, R_p also increased with height within an individual tree. Root resistivity was set so that soil–root resistance ($R_s + R_r$) was of similar magnitude to plant resistance in moist soils (Table 3).

Hypothesis 2

We defined a relationship between Ψ_l and plant hydraulic resistance so that critical leaf water potential (Ψ_{lmin}) was dynamic rather than constant (Fig. 2, upper panel). We set maximum plant conductance (K_1') constant, irrespective of tree size or path-length, and calculated a loss of conductance based on Ψ_l :

$$R_p = 1/[K_1' \times \exp[-(-\Psi_l/d)^c]], \quad (8)$$

where the parameters c and d define a Weibull function that controls the conductance vulnerability curve (Fig. 2, lower panel). For each canopy layer and each time-step, we estimated Ψ_{lmin} by finding Ψ_l that maximized evapotranspiration. The difference between large and small trees was parametrized through changes in the form of eqn 8 (i.e. through c and d).

The Weibull parameters for hypothesis 2 (Table 3) were selected to ensure that the initial stable leaf water potential was close to the constant value set in hypothesis 1. The vulnerability curves described by these Weibull functions (Fig. 2) are significantly different from measured curves for ponderosa pine stem segments (Hubbard *et al.* 2001). Our parametrization results in a 50% loss in total conductance at –2.7 MPa in small trees and at –2.1 MPa in large trees,

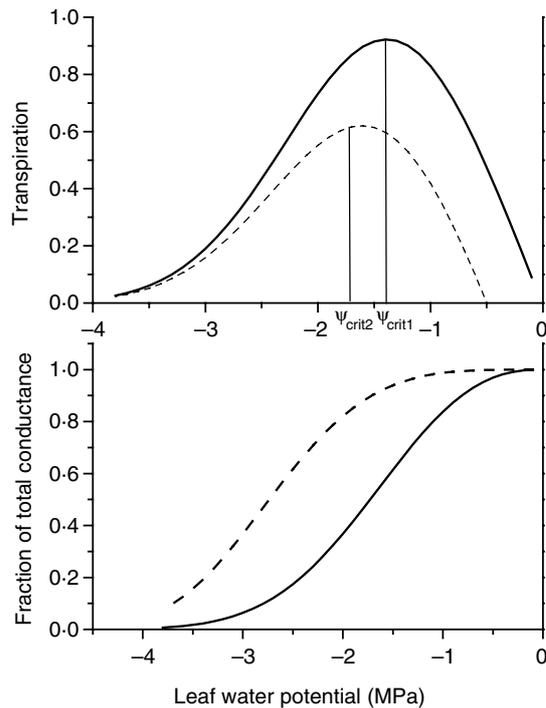


Figure 2. Upper panel: the relationship between leaf water potential and transpiration rate due to the link between resistance and potential in hypothesis 2. The solid line is for a plant in a well-watered soil ($\Psi_s = 0$ MPa) and the dashed line is for the same tree but with reduced soil water availability $\Psi_s = -0.5$ (MPa). Lower panel: the relationship between fractional loss of hydraulic conductance and leaf water potential characterized by Eqn 8. The relationships for both large (solid line) and small (dashed line) trees are shown.

whereas in stem segment experiments this loss occurs only at or below a leaf water potential of -4 MPa. However, the increased vulnerability in the parametrization may be a reasonable description of vulnerability in the whole tree, in comparison with the isolated segments used in direct measurements.

Hypothesis 3

Plant hydraulic resistance was assumed to increase according to the length of time the leaf spent at Ψ_{\min} , and to decrease in proportion to time spent in a fully recharged and resting state ($E = 0$ and $d\Psi_l/dt = 0$). We set a constant maximum conductance (K'_l) for all canopy layers in a tree, with a larger value for small trees (Table 3). The actual conductance for each canopy layer was a fraction F of the maximum; F was decremented by ν according to time spent at Ψ_{\min} and incremented by ν according to time spent at rest. The only difference between large and small trees was the maximum plant conductance (K'_l) and the vulnerability of the hydraulic system to stress, determined by the parameter ν , which characterized the response time of the hydraulic system.

$$\text{If } E = 0 \text{ and } d\Psi_l/dt = 0, F = F + \nu. \quad (9)$$

$$\text{If } \Psi_l = \Psi_{\min}, F = F - \nu,$$

$$0 < F < 1,$$

$$K_l = K'_l F,$$

$$R_p = 1/(K'_l F).$$

Soil-root resistance was set low for all tree sizes by increasing root biomass and rooting depth. Seasonal variation in total hydraulic resistance was hypothesized to originate largely in the plant vascular system.

Hypothesis 0

We compared these three hypotheses to a 'null' hypothesis. In this there were no differences in plant resistance between large and small trees, plant conductance was not varied according to path-length, and soil-root hydraulic resistance was de-coupled from soil moisture, and held constant (Table 3). Daily changes in soil water potential were prescribed from pre-dawn leaf water potential measurements (for data see lower left panel in Fig. 4). Thus, the simulations were purely responsive to measured changes in atmospheric forcing and soil water potential, while hydraulic resistance was static.

RESULTS

In the absence of hydraulic differences

Observed variations in atmospheric forcing and soil water potential were only able to explain some of the patterns in daily sap flow recorded in large and small trees (Fig. 3). Simulated daily sap flow for small trees closely matched observations from the first 50 d of measurements. But after day 215, predictions overestimated sap flow, except during cloudy and cold periods (e.g. day 260). Predicted sap flow for large trees was overestimated throughout the 120 d test period (Fig. 3), apart from some cold and cloudy days. The predicted sap flow per leaf area was similar for large and small trees, indicating that gravitational differences (see Eqn 1) were relatively insignificant. Changes in atmospheric conditions and soil water potential alone were not enough to explain the seasonal decline in sap flow in both large and small trees, nor could differences in light regime and gravitational effects explain the differences in sap flow observed between small and large trees. These results are suggestive that hydraulic resistance differs according to tree size, and is dynamic rather than static.

Hypothesis testing: comparison against daily data

Statistical analyses (Table 3) indicated that each of the three hypotheses was able to reduce prediction errors and explain a larger fraction of variability in daily sap flow than the null hypothesis, for large and small trees. In all cases, there was no significant difference at the 1% level between the linear regression of observed on modelled sap flow (Table 3), and the 1 : 1 line. Hypothesis 1 was the best pre-

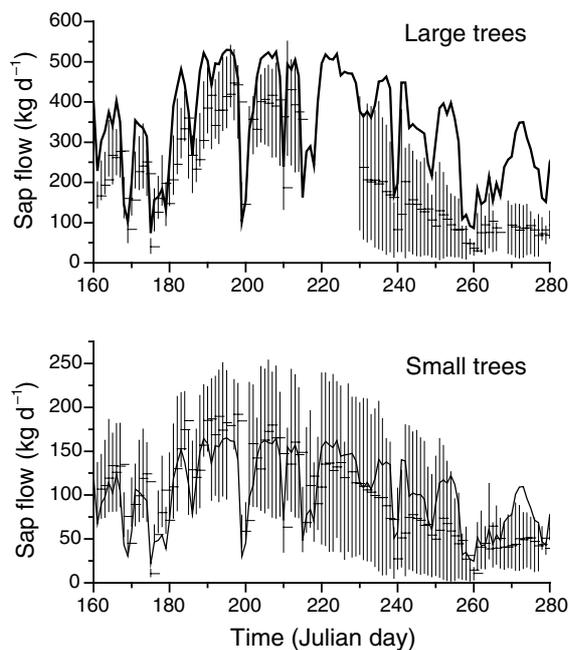


Figure 3. Predictions of daily sap flow with the null hypothesis for large (upper panel) and small (lower panel) Ponderosa pine during the summer of 1996. The simulations were purely responsive to measured changes in atmospheric forcing and soil water potential, while plant and soil hydraulic resistance were static. Mean measured sap flow for five trees, and the maximum and minimum flows of the five individuals (normalized for differences in tree leaf area), are shown as ticks and bars. Simulated sap flow (lines) uses parameters for the mean tree (Table 2).

dictor of large tree behaviour, but there was little difference among the hypotheses in ability to predict small tree activity.

In hypothesis 1, relating plant resistance to path-length allowed for a relative decline in flows in large trees compared with small (Fig. 4 upper panels). Because plant water abstraction was tied to soil moisture, the lack of summer precipitation led to an exponential increase in soil-root resistance (Fig. 4, middle panels). The increase in the resistance, coupled with a reduced potential gradient as soil water potentials declined (Fig. 4, lower panels), resulted in a steady drop in sap flow following day 210 in large and small trees. With the onset of drought stress, day-to-day variability in sap flow was reduced as supply controls dominated over demand, closely matching the data. The maximum value of Ψ_l dropped steadily as soils dried (Fig. 4, lower panels), in good agreement with the observations, especially for large trees. Given the likely errors on water potential measurements, the simulated values are reasonable (most simulations are within 0.1 MPa of corresponding data for large trees and 0.2 MPa for small trees). On days with reduced atmospheric demand (cloudy, humid days), Ψ_l remained above the minimum value.

In hypothesis 2, predictions were also improved over the null hypothesis by incorporating dynamics in both soil and plant components of the hydraulic pathway. Although hourly changes in plant resistance were driven by Eqn 8, the seasonal increase in plant resistance and decline in Ψ_{lmin} (Figs 2 & 5) were driven by increased soil resistance and declining soil water potential resulting from soil water

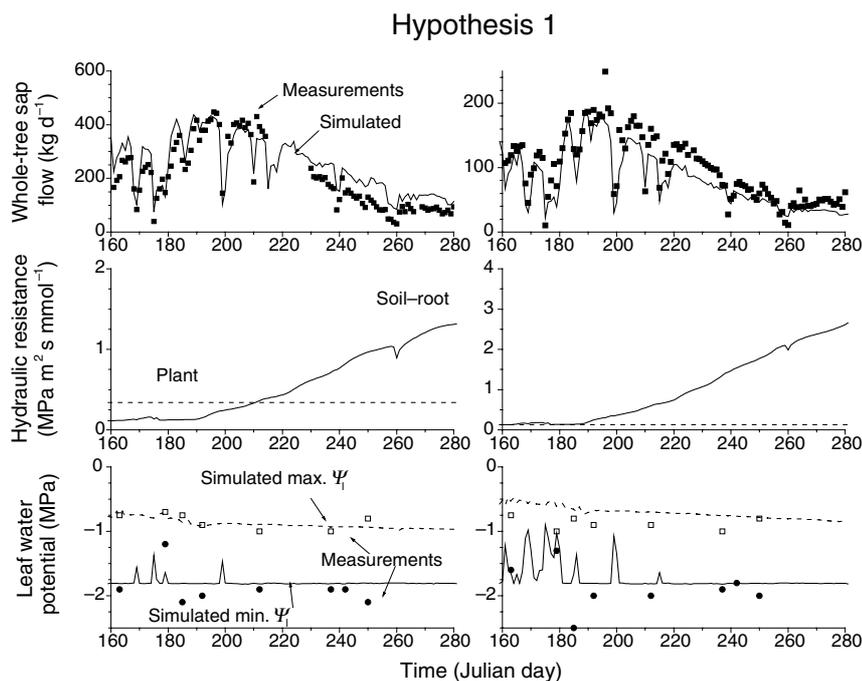


Figure 4. Daily predictions of tree hydraulics over a 120 d period in the summer of 1996 for hypothesis 1, with plant resistance tied to path length. The left and right panels are for a representative large and small tree, respectively. The top panels show simulated (lines) and measured (symbols) total tree sap flow. The middle panels show the hydraulic resistance for leaves in the uppermost canopy layer, originating in the plant (dashed line) and at the soil-root interface (solid line). The lower panels show the daily minimum (solid line) and maximum (dashed line) leaf water potential for the uppermost leaves in the canopy. Also shown are measured pre-dawn Ψ_l (open symbols) and mid-day values (solid symbols).

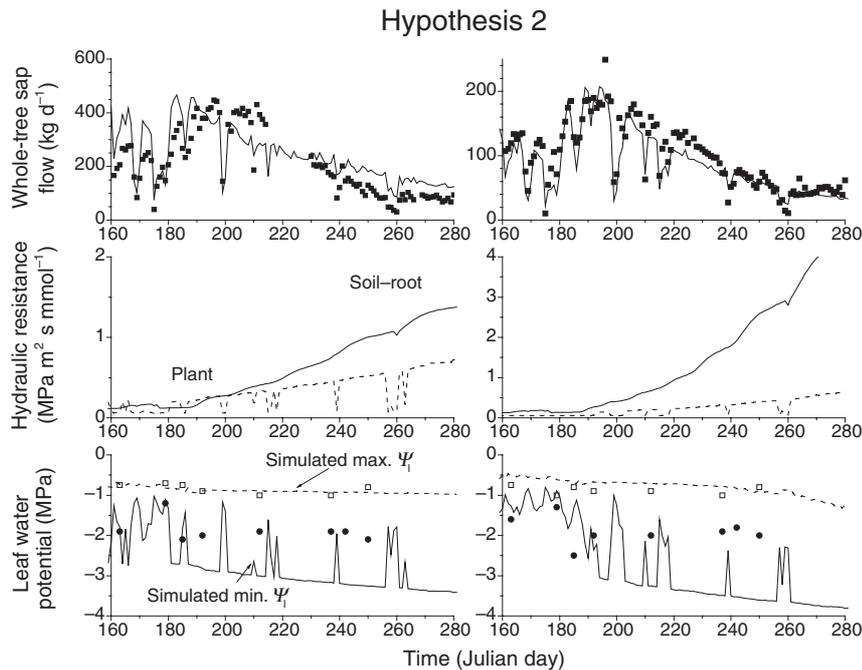


Figure 5. Daily predictions of tree hydraulics over a 120 d period in the summer of 1996 for hypothesis 2. See Fig. 4 for explanation of panels.

abstraction. The coupling between soil-root resistance and plant resistance caused a decline in large tree sap flow after Julian day 190, earlier than suggested by the observations. For small trees, predicted sap flow corresponded better with data (Table 3). Predicted hydraulic resistance rose rapidly during the drought, and by late season the total resistance in small trees was large enough to eliminate day-to-day variability in sap flow seen in the null hypothesis predictions. For both size simulations, predicted daily maximum Ψ corresponded closely with data. However, simu-

lated Ψ_{\min} fell steadily and there was little evidence for such a decline (Fig. 5 lower panel).

Hypothesis 3 (Fig. 6) explained size-related differences through an increase in vulnerability to cavitation and reduction in maximum conductance in large trees (Table 3). The development of increased plant resistance over time, a result of strong atmospheric demand for water, was able to explain the observed decline in sap flow over the summer in small trees, but was less successful for large trees. Soil-root resistance remained low throughout the

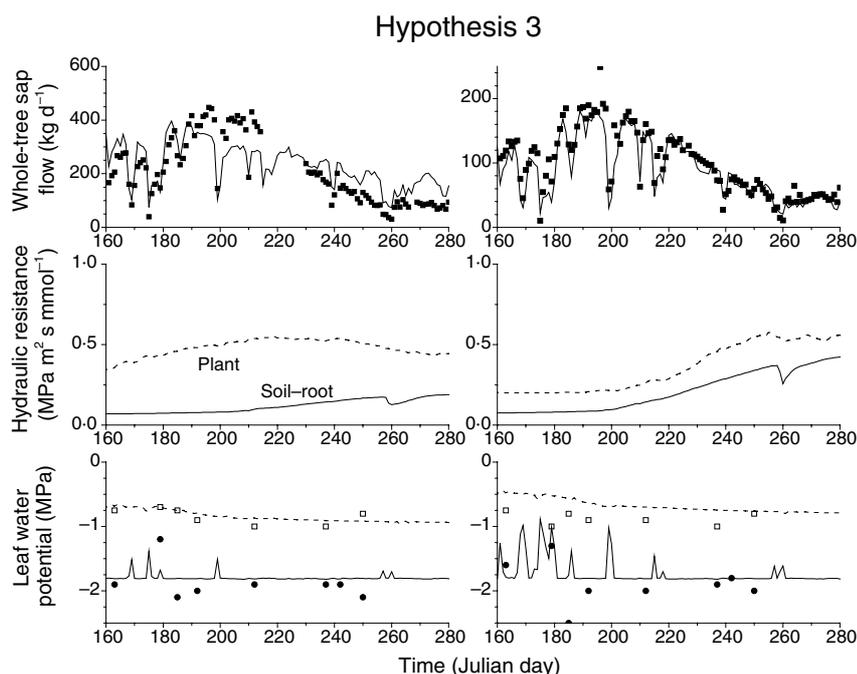


Figure 6. Daily predictions of tree hydraulics over a 120 d period in the summer of 1996 for hypothesis 3. See Fig. 4 for explanation of panels.

simulation. Because of differences in cavitation vulnerability, the predicted increase in plant resistance began around 70 d earlier in large trees, peaked around day 230 (large trees) or day 270 (small trees), and then slowly declined. These behaviours are in stark contrast with the dynamics in soil–root resistance predicted by hypotheses 1 and 2; in these cases, soil–root resistance continued to rise until rains around day 290 initiated a very steep decline. Predicted maximum and minimum Ψ_1 tracked measurements closely in large trees (Fig. 6, bottom panel). The decline in maximum Ψ_1 was delayed in small trees, and led to some discrepancies with the data.

Hypothesis testing: comparison against hourly data

The three hypotheses were parametrized to match daily observations of sap flow; differences between size classes and over time were used to set the key hydraulic parameters. Thus, examination of behaviour at finer, subdiurnal time-scales provides a useful check on the hypotheses. We examined hourly predictions of sap flow (i.e. water movement at the base of the tree trunk), transpiration (water loss from the canopy) and leaf water potential from two 4 d periods, before and after the onset of soil water stress, in mid–late July and early–mid September.

In July, the interaction of Ψ_1 and plant resistance under hypothesis 2 ensured that hourly changes in Ψ_1 lagged those under the other hypotheses for large and small trees (Fig. 7), but the evening recovery and stabilization of Ψ_1 were more rapid once initiated. Transpiration was similar for hypotheses 1 and 3, reaching a peak around midday and being diurnally symmetrical. Hypothesis 2, however, had a distinct morning peak in transpiration on some days, followed by a steep decline. Sap flow predictions under

hypotheses 1 and 3 were similar and symmetrical, and both matched the data closely. Hypothesis 2 had a morning peak, but also a sharp, short-lived evening peak on some days, which was linked to the rapid recovery of Ψ_1 in these simulations as plant resistance declined. Both hypotheses 1 and 3 tended to track the evening decline in sap flow more accurately than hypothesis 2; in the latter case sap flow fell off very rapidly after the simulated evening peak, and ceased before the indications in the data.

In September, the dynamics of Ψ_1 recovery each night was altered from July, recovering most quickly in hypothesis 3 and most slowly in hypothesis 2 (Fig. 8). These differences were most noticeable for small trees, and were related to the relative magnitude of total hydraulic resistance in late season (hypothesis 2 > 1 > 3). Hypothesis 1 predicted that peak transpiration occurred in the morning with a gradual decline thereafter. Hypothesis 2 had a steeper peak in transpiration each morning, and rates were nearly halved, but steady, by afternoon. Hypothesis 3 had a morning peak, but then a second peak of a magnitude similar (large trees) or greater (small trees) each afternoon, close to the period of maximum atmospheric demand. Diurnal patterns of sap flow were relatively symmetrical for hypotheses 1 and 3, and while both sets of predictions for large trees exceeded observations (Fig. 7), the overall forms were similar, matching the observed tail of evening recharge. For small trees, predicted sap flow from hypothesis 3 most closely matched observed sap flow, both in magnitude and the very rapid cessation of sap flow each evening. Small tree sap flow was underestimated by hypothesis 1 during most of each day. However, hypothesis 1 predicted a sustained evening tail to sap flow as Ψ_1 recharged, whereas the data suggest a much more rapid refilling. For large and small trees, hypothesis 2 predicted both morning and evening peaks in sap flow, coinciding with the periods

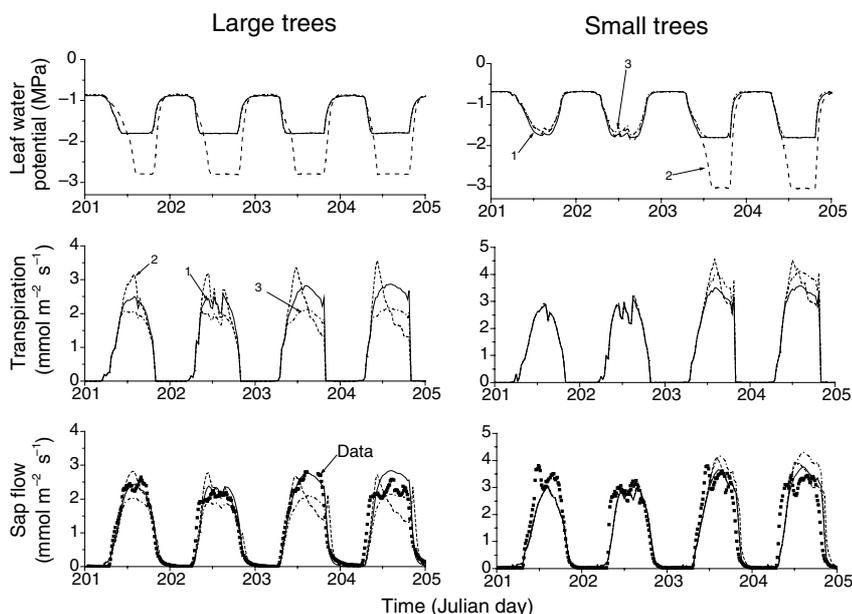


Figure 7. Hourly changes in leaf water potential, transpiration and sap flow over a 4 d period, 19–22 July 1996, for large trees (left panels) and small trees (right panels). Lines show predictions for the three hypotheses: 1, solid line; 2, dashed line; 3, dashed-dotted line. Symbols show measured sap flow.

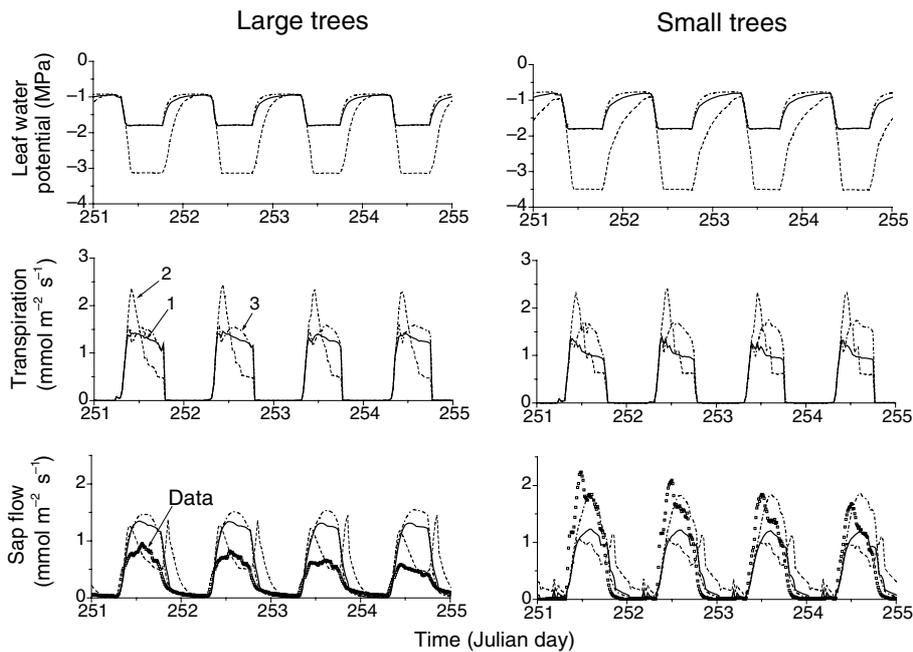


Figure 8. Hourly changes in leaf water potential, transpiration and sap flow over a 4 d period, 7–10 September 1996, for large trees (left panels) and small trees (right panels). Lines show predictions for the three hypotheses: 1, solid line; 2, dashed line; 3, dashed-dotted line. Symbols show measured sap flow.

of greatest change in leaf water potential, although there was no supporting evidence in the data. Small trees under hypothesis 2 failed to recharge Ψ_l by dawn, and sap flow continued throughout each night; again, these predictions were at odds with observations.

DISCUSSION

The purpose of this study was to develop a model to explain and predict patterns of whole-tree water use, accounting for both dynamic coupling with soils, and differences related to tree size. An effective model based on underlying mechanisms can then be used to predict behaviour outside observed conditions. However, model corroboration is prone to subjectivity, especially if the parametrization process is not completely independent of any corroboration data set. Models are not unique solutions, and interpretation must proceed cautiously; good corroboration may be serendipitous. Recognizing these intrinsic problems, we have modified the orthodox approach of testing a single hypothesis against a null model, and instead sought a more detailed insight and greater objectivity through an inter-comparison of three different models, representing alternative hypotheses, with a variety of observational data.

Comparison of measured sap flow with predicted sap flow in the absence of soil–plant hydraulic feed-backs, and with similar hydraulic characteristics for all tree sizes (Fig. 3), revealed that there are important differences in water use both with tree size and over time. On a leaf area basis, sap flow in large trees is less than in small trees, confirming the overall conclusions from an initial study of this data (Ryan *et al.* 2000). This confirmation was worthwhile, because the modelling took into account potentially confounding factors such as the distribution of light in large

versus small tree crowns, changes in soil water potential, and gravitational effects on sap flow.

Although each hypothesis could be parametrized to improve on the null hypothesis, hypothesis 1 provided the most effective, consistent explanation for observed size-related and time-dependent variation in sap flow (Table 3) and patterns of leaf water potential (Fig. 4). We recognize that other possible explanations, such as differences in root biomass, have not been considered, and that the technique of heuristic parametrization was not a comprehensive approach to model testing. It is possible that better parametrizations could be developed for each hypothesis. However, the overall forms of simulations are unlikely to change, given the governing equations, and the forms shown here provide a reasonable basis for judgement, and for developing ideas for further, corroborative measurements.

Examination of the hourly sap flow predictions revealed differences between the hypotheses. The predicted dynamics of stem sap flow under hypothesis 2 showed considerable discrepancies with measured values; predictions of an evening peak in sap flow and sustained flow each night in small trees during the late season were not supported by the data. The asymmetry of transpiration in hypothesis 2 is also at odds with eddy covariance studies that suggest a relatively constant latent energy flux from late morning to afternoon (B.E. Law, Oregon State University, personal communication), which is in closer agreement with patterns predicted by hypotheses 1 and 3. The exponential increases in soil–root resistance incorporated in hypotheses 1 and 2 led to unrealistically long tails in evening sap flow as drought developed, whereas the more gradual increase in plant resistance proposed by hypothesis 3 generated sap flow that corresponded more closely with data. Predictions of maximum Ψ_l were well corroborated under all scenarios,

the only possible exception being small trees under hypothesis 3.

The differing dynamics of hourly transpiration predicted by hypotheses 1 and 2 were particularly interesting in terms of potential interactions with local meteorology and boundary layer dynamics. Hypothesis 2 suggests that the forest transports significantly more moisture into the atmosphere in the early morning, whereas hypothesis 1 predicts a more even addition. Although it seems that hypothesis 1 is the more suitable description for this site, it is possible that other tree species behave in a manner closer to hypothesis 2, and this could lead to important differences in vegetation feed-backs on atmospheric processes.

Sensitivity analyses revealed that sap flow predictions were sensitive to changes in radiation incident on tree crowns. However, the parametrization for radiation transfer in open canopies used in the analyses was more effective at explaining the observed sap flow than schemes with increased or reduced incident radiation. When hypothesis 1 was applied to large trees, sap flow predictions for more open or closed canopies had RMSE values (83.5 and 63.3, respectively) greater than for the standard case. Likewise, the sparser and denser canopy parametrizations explained less of the day-to-day variation in sap flow (r^2 values were 0.71 and 0.78, respectively) than the standard case. We found that sap flow predictions were more sensitive to variations in canopy LAI prior to day 200. After this point, soil moisture levels became the primary limiting factor on sap flow.

This study has provided additional information on the uncertainties outlined in the introduction. First we have shown that an assumption that plant resistance is linearly related to path length can explain differences between large and small tree sap flow, and that increased resistance in the upper canopy does not lead to unrealistic predictions of total sap flow. We have been unable, however, to quantify the relative size and dynamism of plant and soil hydraulic resistance from the data available. Although hypothesis 1 was the most effective model, we cannot rule out hypothesis 3, given the variability in the observational data (Fig. 3). However, there is an important difference in the dynamics of the two hypotheses, related to their response to late season, drought-relieving precipitation. We developed new simulations with 100 mm additional precipitation between day 240–250 (Fig. 9). Predicted daily sap flow in hypotheses 1 and 2 responded strongly to this moisture input, increasing by around 30–50%. However, sap flow under hypothesis 3 showed a minimal response, rising by less than 1%, because hydraulic limitation was concentrated in the plant rather than the soil. This sensitivity analysis suggests that resolving uncertainties about the nature of dynamic resistance is of considerable significance for understanding hydrological controls on forest processes, and their sensitivity to climate change, because the hypotheses show important differences under an external forcing. Testing the actual response of trees by experimental water additions or removals would be highly illuminating, in conjunction with further modelling. Longer term monitoring of sap flow

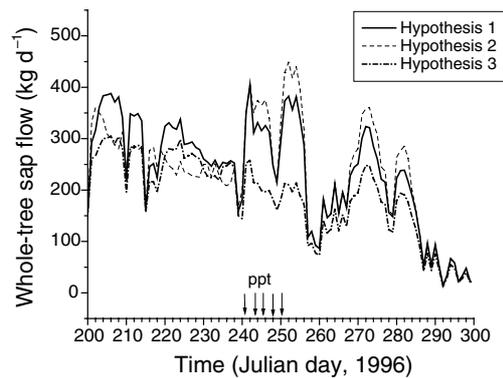


Figure 9. Predicted sap flow for a large tree. The results of the three hypotheses are shown, but the site meteorology has been altered so that 105 mm of additional precipitation occurred between days 240 and 250.

would also resolve some of the uncertainty, by measuring trees under a variety of climatic conditions, and so increasing the constraints on modelling. Multiple instantaneous data, such as sap flow, eddy covariance, soil moisture and catchment discharge, would assist model corroboration and eliminate alternative hypotheses.

In conclusion, these simulations confirm important differences in the hydraulic characteristics of small and large trees. The modelling has served to remove the complications posed by the dynamic environment and time-dependent nature of plant–water interactions, and has allowed a more precise quantification of hydraulic effects. We were best able to explain observed patterns in sap flow as the consequences of rising plant resistance with increasing tree height, and increased soil–root resistance with drying soils – hypothesis 1. The effect of increased resistance in large trees has important consequences for sap flow. Under hypothesis 1, the overall reduction in water use from the null hypothesis was greater for large (–23%) than for small trees (–18%), and small trees had a relatively larger peak sap flow and a stronger decline in the late season. Such changes in water usage could have significant impacts on local hydrology. The effects of individual tree physiology need ultimately to be examined in the community, ecosystem and catchment contexts. Other important uncertainties that need to be resolved concern seasonal dynamics of root growth and rooting depth, especially in response to developing drought, and more detailed studies of cavitation vulnerability within plants *in situ*. The next focus of research is to examine implications for carbon cycling. Whether these conclusions hold for other species and in other climatic zones is also of considerable interest.

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data soil water content and leaf water potential and on phenology of leaf area index and meteorology.

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