

Predicting the decline in daily maximum transpiration rate of two pine stands during drought based on constant minimum leaf water potential and plant hydraulic conductance

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Summary The effect of drought on forest water use is often estimated with models, but comprehensive models require many parameters, and simple models may not be sufficiently flexible. Many tree species, *Pinus* species in particular, have been shown to maintain a constant minimum leaf water potential above the critical threshold for xylem embolism during drought. In such cases, prediction of the relative decline in daily maximum transpiration rate with decreasing soil water content is relatively straightforward. We constructed a soil–plant water flow model assuming constant plant conductance and daily minimum leaf water potential, but variable conductance from soil to root. We tested this model against independent data from two sites: automatic shoot chamber data and sap flow measurements from a boreal Scots pine (*Pinus sylvestris* L.) stand; and sap flow measurements from a maritime pine (*Pinus pinaster* Ait.) stand. To focus on soil limitations to water uptake, we expressed daily maximum transpiration rate relative to the rate that would be obtained in wet soil with similar environmental variables. The comparison was successful, although the maritime pine stand showed carry-over effects of the drought that we could not explain. For the boreal Scots pine stand, daily maximum transpiration was best predicted by water content of soil deeper than 5 cm. A sensitivity analysis revealed that model predictions were relatively insensitive to the minimum leaf water potential, which can be accounted for by the importance of soil resistance of drying soil. We conclude that a model with constant plant conductance and minimum leaf water potential can accurately predict the decline in daily maximum transpiration rate during drought for these two pine stands, and that including further detail about plant compartments would add little predictive power, except in predicting recovery from severe drought.

Keywords: *Pinus pinaster*, *Pinus sylvestris*, plant–soil interactions, water stress, water uptake.

Introduction

Soil water availability is an important determinant of forest productivity. The likely increase in frequency of summer droughts with climate change (Saxe et al. 2001) is driving interest in accurately quantifying effects of drought on forest water use. For this purpose, a large number of soil–plant–atmosphere models have been developed (Federer 1979, Molz 1981, Williams et al. 1996, Sperry et al. 1998) that describe the hydraulic pathway and predict stomatal closure with soil drying. Parameterization of these comprehensive models is often difficult, however, because of the number of parameters needed. Many plant traits are related to water uptake, including hydraulic conductance, resistance to embolism, leaf area to root area ratio and root distribution, and they vary across species and sites (Wullschlegel et al. 1998, Hacke et al. 2000, Piñol and Sala 2000, Martínez-Vilalta et al. 2004). In addition, variation in soil properties, such as texture, hydraulic conductivity and porosity, influence the availability of soil water to plants (Hillel 1980, Bristow et al. 1984). Thus, simple models that can accurately predict forest water use during droughts would be of great value.

In a simple one-dimensional steady-state representation of flow, Darcy's law relates leaf transpiration rate (E_L) to hydraulic conductance of the soil-to-leaf pathway (k_L) and leaf (Ψ_L) and soil water (Ψ_S) potentials (Whitehead and Jarvis 1981):

$$E_L = k_L(\Psi_S - \Psi_L) \quad (1)$$

During the day, E_L increases gradually with the evaporative demand of the atmosphere (e.g., Ewers et al. 2005), and reaches a maximum (E_{\max}), bringing about the daily minimum leaf water potential (Ψ_{\min}) (Jones and Sutherland 1991).

Many plants limit transpiration by stomatal closure before a serious loss of hydraulic conductance from embolism occurs at low negative xylem water potentials (Cochard et al. 1996,

Loustau et al. 1996, Irvine et al. 1998, Delzon et al. 2004a, Fisher et al. 2006). In the simple case of perfect isohydric behavior (Tardieu and Simonneau 1998), Ψ_{\min} is constant for a given plant, just above the critical threshold for embolism (Jones and Sutherland 1991, Bond and Kavanagh 1999). Many woody plants, *Pinus* species in particular, are thought to exhibit isohydric control of Ψ_L . Piñol and Sala (2000) showed that ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) was prone to xylem embolism formation, but that this tendency was limited by strong stomatal control, which prevents xylem pressure potentials falling below the threshold for catastrophic embolism formation. Likewise, Irvine et al. (1998) found that stomatal control in Scots pine (*Pinus sylvestris* L.) was sufficient to prevent embolization of xylem elements. From a practical modeling perspective, the assumption of a constant Ψ_{\min} sufficient to prevent embolism is attractive because it implies constant plant hydraulic conductance (k_p) and constant Ψ_L when E_{\max} occurs (see Figure 1), thereby simplifying the prediction of daily E_{\max} .

However, during drought, empirical evidence shows that k_L decreases, including in isohydric *Pinus* species (Loustau et al. 1996, Irvine et al. 1998, Delzon et al. 2004a). If there is successful isohydric control of Ψ_L above the critical threshold, this decrease in conductance must occur in the soil pathway. The effective conductance of the soil (k_s) decreases sharply when soil pores are emptied. For example, when volumetric soil water content (θ) drops from 0.25 to 0.1 in a typical sandy loam, k_s decreases by a factor of about 10^5 (Campbell 1974). Williams et al. (2001) found that the decrease in k_s during drought likely explains the decrease in tree sap flow of *Pinus ponderosa*, and evidence obtained by Fisher et al. (2006) for multiple species in a tropical rain forest supports this view. If the decrease in k_s alone can explain the major part of the decline in E_{\max} during soil drying, detailed plant representations, such as those used in the Sperry et al. (1998) model, could be avoided, aiding practical application.

Our model is based on the central assumptions that both daily Ψ_{\min} and k_p are constant during drought. These assumptions are not necessarily consistent with detailed empirical evidence, even for isohydric species. Oren et al. (1999) argued that the response to vapor pressure deficit (VPD) is consistent with some daily loss of conductance. At very high VPD, E_L may actually decrease (Pataki et al. 2000) rather than remain constant as our simple assumptions imply (Figure 1). However, if changes in Ψ_{\min} and k_p are relatively small during drought, these simple assumptions will lead to a practically useful model for predicting the decline in daily E_{\max} .

We developed a model for E_{\max} with variable conductance in only the soil-to-root pathway and tested it against measurements of E_L during drought for two pine stands, one boreal Scots pine stand (*Pinus sylvestris* L.), and one maritime pine stand (*Pinus pinaster* Ait.). To separate effects of soil water content (θ) from other environmental variables (evaporative demand and light availability in particular), we compared the model against the relative maximum transpiration rate by dividing daily E_{\max} by the maximum rate that would be obtained in wet soil with similar environmental variables ($E_{\max}|_{\Psi_S=0}$; cf. Sinclair 2005).

Methods

General framework

In a one-dimensional pathway, steady-state water flow can be described by Darcy's law:

$$J = K \frac{\partial \Psi}{\partial x} \quad (2)$$

where J is water flux ($\text{mol m}^{-2} \text{s}^{-1}$), K is conductivity ($\text{mol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$) and $\partial \Psi / \partial x$ is the gradient in water potential driving the flow. Under certain circumstances, Equation 2 may be integrated (Cowan 1965) over x to give:

$$J = k \Delta \Psi \quad (3)$$

where k is conductance ($\text{mol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$), and $\Delta \Psi$ is the water potential difference through some compartment that causes the flow (MPa). In this way, water flow from the bulk soil to the leaf can be written as:

$$E_L = k_L (\Psi_S - \Psi_L - \Psi_g) \quad (4)$$

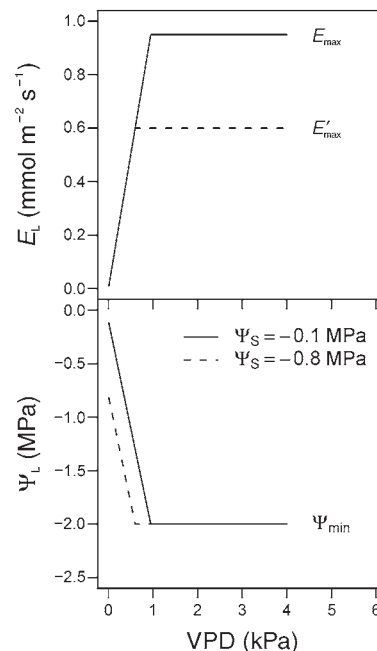


Figure 1. Response of leaf transpiration rate (E_L) and leaf water potential (Ψ_L) to vapor pressure deficit (VPD) and soil water potential (Ψ_S) with perfect isohydric behavior at the minimum Ψ_L (Ψ_{\min}) (see also Jones and Sutherland 1991, Bond and Kavanagh 1999). If Ψ_{\min} is reached, E_L reaches a maximum (E_{\max}) and does not depend on VPD, but only on Ψ_S and hydraulic conductance (Equation 1). At lower Ψ_S , Ψ_{\min} is reached at a lower VPD and a lower E_{\max} is reached (E'_{\max}). Before Ψ_{\min} is reached, E_L depends on the maximum stomatal conductance (g_{\max} ; Oren et al. 1999) as $E_L = (\text{VPD})g_{\max}$, and Ψ_L is related to E_L with hydraulic conductance (Equation 1). For simplicity, k_L is kept constant here (but in the model it depends on Ψ_S). Parameter values used were, $g_{\max} = 0.10 \text{ mol m}^{-2} \text{ s}^{-1}$, $k_L = 0.5 \text{ mmol m}^{-2} \text{ s}^{-1} \text{MPa}^{-1}$, $\Psi_{\min} = -2 \text{ MPa}$. We studied only the behavior of E_{\max} in relation to Ψ_S , not the relationship between VPD and E_L at low VPD.

where Ψ_g is gravitational potential ($\sim 0.01 \text{ MPa m}^{-1}$), which is subsumed in Ψ_L in subsequent equations. See Table 1 for a summary of symbols and their units. Because we assumed a one-dimensional pathway, k_L can be split into k_S and k_P :

$$\frac{1}{k_L} = \frac{1}{k_S} + \frac{1}{k_P} \quad (5)$$

Daily E_{\max} is reached at Ψ_{\min} . From Equation 4:

$$E_{\max} = k_L(\Psi_S - \Psi_{\min}) \quad (6)$$

Soil hydraulic conductance

Conductance of the soil-to-root path way can be estimated assuming that the root system consists of one long root that has access to a surrounding cylinder of soil (Gardner 1960, see also Newman 1969). The steady-state solution of k_S can be written as:

$$k_S = \frac{R_1}{\text{LAI}} \frac{2\pi K_S(\Psi_S)}{\log\left(\frac{r_{\text{cyl}}}{r_{\text{root}}}\right)} \quad (7)$$

where R_1 is root length index (m root m^{-2} soil surface), LAI is leaf area index, K_S is soil hydraulic conductivity ($\text{mol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$), r_{root} is root radius and r_{cyl} is the radius of a cylinder of soil to which the root has access. The soil can be divided into identical cylinders with a root along the middle axis, resulting in the radius of the cylinder (Newman 1969):

$$r_{\text{cyl}} = \frac{1}{\sqrt{\pi L_v}} \quad (8)$$

where L_v is root length density (m m^{-3}) of the roots that are active in water uptake (assumed to be all roots $< 2 \text{ mm}$ diameter). A simple equation relating K_S to Ψ_S is given by (Campbell 1974):

$$K_S(\Psi_S) = K_{\text{sat}} \left(\frac{\Psi_e}{\Psi_S}\right)^{2+\frac{3}{b}} \quad (9)$$

where K_{sat} is saturated conductivity ($\text{mol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$), Ψ_e is air entry water potential (MPa) and b is an empirical coefficient related to the clay content of the soil (Cosby et al. 1984). The parameters b and Ψ_e are estimated from a typical soil moisture release function (Campbell 1974):

$$\Psi_S = \Psi_e \left(\frac{\theta}{\theta_{\text{sat}}}\right)^{-b} \quad (10)$$

where θ_{sat} is soil volumetric water content at saturation (assumed equal to the total pore fraction of the soil). Clapp and Hornberger (1978) and Cosby et al. (1984) have summarized values of b , K_{sat} and Ψ_e for several soil type classes.

Relative transpiration rate

To separate the effects of θ from those of other environmental drivers (VPD, light, temperature) on daily E_{\max} , we normalized E_{\max} by $E_{\max}|_{\Psi_S=0}$, but all other variables were the same (cf. Sinclair 2005):

$$E_{\max}/E_{\max}|_{\Psi_S=0} = \frac{R_p(\Psi_S - \Psi_{\min})}{-\Psi_{\min}(R_p + R_S(\Psi_S))} \quad (11)$$

where R is resistance ($1/k$). The value of R_S is zero when Ψ_S is zero (Equation 9). This function varies between 0 (no water uptake possible) and 1 (no restriction caused by soil water deficit).

Model application

Boreal Scots pine stand

Shoot gas exchange, tree sap flow and soil measurements were carried out in a stand of 40-year-old Scots pine (*Pinus syl-*

Table 1. Definitions of abbreviations.

Symbol	Definition	Unit
E_L	Canopy average leaf transpiration	$\text{mol m}^{-2} \text{ s}^{-1}$
E_{\max}	Maximum transpiration rate	$\text{mol m}^{-2} \text{ s}^{-1}$
$E_{\max}/E_{\max} _{\Psi_S=0}$	Maximum transpiration rate relative to that in wet soil	–
θ	Soil volumetric water content	$\text{m}^3 \text{ m}^{-3}$
θ_{sat}	θ at saturation	$\text{m}^3 \text{ m}^{-3}$
$\theta_{\text{PWP}}, \theta_{\text{FC}}$	θ at permanent wilting point and field capacity, respect.	$\text{m}^3 \text{ m}^{-3}$
k_S	Leaf-specific soil hydraulic conductance	$\text{mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$
k_P	Leaf-specific plant hydraulic conductance	$\text{mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$
k_L	Leaf-specific conductance of the soil–leaf pathway	$\text{mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$
K_S	Soil hydraulic conductivity	$\text{mol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$
K_{sat}	Saturated soil hydraulic conductivity	$\text{mol m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$
b	Parameter of the soil water retention curve	–
LAI	Leaf area index (all-sided)	–
L_v	Root length density	m m^{-3}
R_1	Root length index	m m^{-2}
r_{cyl}	Radius of the modeled soil cylinder	m
r_{root}	Mean radius of water-absorbing roots	m
Ψ_S	Bulk soil water potential	MPa
Ψ_e	Soil water potential at saturation	MPa
Ψ_g	gravitational potential	$\sim 0.01 \text{ MPa m}^{-1}$
Ψ_L	Leaf water potential	MPa
Ψ_{\min}	Minimum leaf water potential	MPa
Z_{soil}	Rooting zone depth	m

vestris) trees at the SMEAR II measurement station (Station for Measuring Forest Ecosystem–Atmosphere Relations; Hari and Kulmala 2005) in Hyytiälä, southern Finland (61°51′ N, 24°18′ E, 180 m a.s.l.). Mean tree height was about 16 m. Mean annual temperature is 2.9 °C, and mean annual precipitation is 710 mm.

The soil water retention curve (Equation 10) was determined based on the data of Mecke et al. (2002), who collected 129 soil samples (small cylinders) throughout the soil profile (up to 90 cm depth) at soil pits distributed around the SMEAR-II station. Water retention curves (pF-curves) of these samples were generated by the standard pressure-plate technique at pressures of 1, 1.5, 1.8, 2, 2.8, 3 and 4.2 cm (hydraulic head). To compare these measurements with those of θ , the soil samples were grouped into three soil horizons, A (0–10 cm), B (10–40 cm), C (> 40 cm), and the data reanalyzed with a linear mixed-effects model to fit Equation 10 to log-transformed θ :

$$\log(-\Psi_s) = \log(-\Psi_e) + b \log\left(\frac{\theta}{\theta_{\text{sat}}}\right) \quad (12)$$

which yielded estimates of b and Ψ_e for each soil horizon (see Table 2).

Soil volumetric water content was measured with 26 time-domain reflectometry (TDR) sensors (TDR100, Campbell Scientific, Logan, UT) distributed over five soil pits. The permanently installed probes were connected to the TDR100 by multiplexers (SDMX50, Campbell Scientific). Measurements were grouped into three soil layers by depth and averaged across the soil pits.

Mecke and Ilvesniemi (1999) measured soil hydraulic conductivity at two sites close to the SMEAR-II station, under field conditions without disturbing the soil. The soil type and forest conditions were the same as those at the SMEAR-II station. The $K_s(\Psi_s)$ values obtained by Mecke and Ilvesniemi (1999) were used in Equation 9 to estimate K_{sat} with b and Ψ_e values obtained from the fitted soil water retention curves (Equation 10).

Ilvesniemi and Liu (2001) reported fine root mass by depth based on measurements in the same Scots pine stand, from which we calculated root length density (R_l) for each soil horizon separately based on the mean root radius for fine roots determined by Ilvesniemi and Liu (2001). We assumed that all roots < 2 mm were capable of water uptake. The total rooting zone depth (Z_{soil}) was assumed equal to the mean depth to bedrock, because fine roots occurred throughout the profile (Ilvesniemi and Liu 2001). Total depth to bedrock was estimated by averaging the depth of the seven soil pits that extended to bedrock. The profile was divided into three horizons as determined from the soil pits.

Gas exchange of three Scots pine shoots from the top of the canopy was measured with an automatic chamber system operating continuously throughout the year 2006, with three measurements per hour. This system, with various modifications, has been operating for a number of years and is de-

scribed in detail by Altimir et al. (2002). The flux calculation, system calibration and corrections for water adsorption on chamber walls have been presented by Hari et al. (1999), Kolari et al. (2004) and Altimir et al. (2006).

Sap flow was measured with Granier-type sensors (diameter 2 mm, length 50 mm; Granier 1987) installed at breast height on two trees. Two 3-mm-wide holes were drilled 100 mm apart into a stem into which were inserted brass tubes filled with thermally conducting silicone compound. The sensors were inserted in the brass tubes and positioned well within the sapwood. Sap flow was calculated according to the original calibration of Granier (1987) (Clearwater et al. 1999). Data were logged every minute, and 10-min means were stored by the data logger. The baseline maximum temperature difference between the heated and unheated sensor was determined each night. Although we measured only two trees, the relative decline in sap flow during the drought was similar in both trees (not shown).

Daily E_{max} between day of year (DOY) 182 and 242 was estimated with the 95% percentile (because it is robust to potential outliers) for each of the three gas exchange shoots and the two trees with sap flow measurements. Relative maximum transpiration rate was expressed as $E_{\text{max}}/E_{\text{max}}|_{\Psi_s=0}$. We estimated $E_{\text{max}}|_{\Psi_s=0}$ based on the mean E_{max} for DOY 182–200 when mean daily VPD was above 1.5 kPa (to exclude cloudy days). During this period, there was no significant effect of (mean or maximum) VPD, (mean or maximum) photosynthetic photon flux (PPF), or θ on E_{max} (all $P > 0.2$), and we therefore assumed Ψ_{min} was closely approached. Leaf area was stable during this period because leaf expansion was already complete. Relative E_{max} for each day was averaged across the three shoots, and across the two sap flow trees.

Leaf-specific hydraulic conductance was estimated from concurrent measurements of E_L (from the automated chambers) and Ψ_L during July and early August 2002. Soil water potential was above –0.1 MPa during this period, as estimated from measurements of θ and the soil water retention curve. Based on Equation 4, k_p was estimated as $0.78 \pm 0.15 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ ($n = 18$).

Relative daily maximum transpiration rate was predicted by the model (Equation 11) for each soil horizon separately based on the parameters described above. To assess which soil horizon had most influenced the drought response of E_L , we used the model as if water uptake were from one layer only.

Maritime pine stand

Sap flow measurements were available from the Le Bray field site (44°42′ N, 0°46′ W), located 20 km southwest of Bordeaux, France. Mean annual temperature is 12.5 °C, and mean annual rainfall about 930 mm. The site supports a 32-year-old maritime pine (*Pinus pinaster*) plantation, with an understory of *Molinia coerulea* (L.) Moench.

The soil water retention curve was reconstructed assuming that θ reached the so-called permanent wilting point during the summers of 1997 through 2002. In these years, multiple dry summers occurred, and the water balance model (GRAECO)

was calibrated to measurements of θ over this period (Porté 1999, Alexander Bosc, personal communication, INRA Bordeaux, France). During each drought, θ converged to values close to $0.04 \text{ m}^3 \text{ m}^{-3}$. Based on the assumptions of the water balance model GRAECO, we tentatively used this point as an estimate of θ at $\Psi_s = -1.5$, and from this, estimated the parameters of the soil water retention curve (Table 2). Soil hydraulic conductivity at saturation was derived from measurements made by Brejon de Lavergnée (1988) (Table 2).

The soil depth is 80 cm, at greater depth a toxic hardpan excludes root penetration (Ogée and Brunet 2002). Measurements of θ_{sat} were available from Ogée et al. (2001), who found much larger θ_{sat} in the top 20 cm of soil than in the remaining 60 cm. We averaged θ_{sat} by weighting with root surface area over the soil profile.

Sap flow measurements were obtained from Delzon et al. (2004a, 2004b). Sap flow was measured with Granier-type sensors (Granier 1987) at the base of the crown of eight maritime pine trees throughout 2001 and 2002. The measurements were corrected for the radial pattern in sap flow with separate measurements on two trees (Delzon et al. 2004b) and averaged across the eight trees.

Soil volumetric water content was measured weekly with several TDRs distributed over the 80-cm-deep soil profile and averaged. Plant hydraulic conductance and Ψ_{min} were measured by Delzon et al. (2004a). Fine root biomass (< 2 mm diameter) was sampled over the soil depth range (Pierre Trichet, INRA Bordeaux, France, unpublished data). Assuming a constant specific root density of 400 kg m^{-3} and a root diameter of 0.7 mm (assumed to be equal to fine root diameter of the boreal Scots pine stand), root biomass was converted to total root length.

As in the boreal Scots pine stand, we normalized E_{max} by $E_{\text{max}}|_{\Psi_s=0}$. Because there were insufficient summer days with high θ (where it could be assumed that Ψ_{min} was reached), we fit a simple empirical regression model to the daily E_{max} (which was estimated with the 95% percentile) for all wet days of both years. We used linear regression with daily total PPF, mean daily VPD, minimum temperature (T_{min}) and their squared terms, for all data with $\theta > 0.14$ (above which there was no effect of θ on E_L). This linear model was then used to

predict $E_{\text{max}}|_{\Psi_s=0}$ for the whole dataset. The measured relative maximum transpiration rate was then expressed as the ratio of E_{max} to $E_{\text{max}}|_{\Psi_s=0}$. We then used Equation 11 to estimate the decline in relative E_{max} with declining θ , based on the soil and plant parameters of the stand (Table 2).

Sensitivity analysis

We focused on the sensitivity of model predictions of relative transpiration rate to changes in Ψ_{min} , because this is a difficult parameter to measure. The value for Ψ_{min} was varied between -0.5 and -10 MPa (the lower limit found in plants, Kolb and Davis 1994). A more thorough sensitivity analysis to soil type and other model parameters is given by Sinclair (2005) for a similar model (see Discussion), which agreed with additional analyses made with our model (data not shown).

Results

The soil water flow model was tested in the boreal Scots pine stand against shoot gas exchange and sap flow data for the summer drought of 2006. During the drought, Ψ_s in the top 5 cm declined below -2 MPa, and in the deeper layers reached almost -1 MPa (Figure 2). There was a close correspondence between the decline in E_L of single shoots at the top of the canopy and total tree transpiration rate as estimated by sap flow (Figure 3). We used soil parameters and measurements of θ in each soil layer separately, acting as if all uptake were from only the one layer. All parameters were measured (Table 2), and no parameters were fine-tuned. For the top layer (0–5 cm) only, the model predicted zero transpiration when E_L was almost unaffected by soil water (Figure 4). In the deeper layers, and especially below 25-cm depth, the model produced a good fit between measured and modeled daily E_{max} (Figure 4). At this site, about 35% of the total root biomass is in the topmost 5 cm of soil (Ilvesniemi and Liu 2001), and rooting density is several times higher in this layer than deeper in the soil profile (Table 2). However, Ψ_s in deeper soil layers remained much higher than in the top soil layer (Figure 2), partly because θ was higher, and partly because the soil texture was finer (Table 2). Relative E_{max} was frequently above unity when there

Table 2. Soil and plant parameters for the boreal Scots pine stand (Hyytiälä) and for the maritime pine stand (Le Bray). Measurements on three different soil horizons were available for the Hyytiälä stand, but on only one soil horizon for the Le Bray stand. See Table 1 for symbol definitions and units. For the Hyytiälä stand, estimates of $\log(-\Psi_e)$, b and their standard errors (in parenthesis) were obtained with a mixed-effects model, and Ψ_e was found by back-transformation¹. The number of measured retention curves was 44 for layer A, 47 for layer B and 37 for layer C. Original data were from Mecke et al. (2002), which we reanalyzed.

Stand	L	$10^{-3} \text{ k}_{\text{PL}}$	Ψ_{min}	Horizon	Depth	$\log(-\Psi_e)$	b	Ψ_e	K_{sat}	L_v	θ_{sat}
Hyytiälä	8	0.78	-2	A	0 – 5	-0.48 (0.08)	4.14 (0.11)	-0.68	24.5	36210	0.62
				B	5 – 25	-0.34 (0.08)	4.46 (0.13)	-0.81	5.7	15160	0.52
				C	25 – 80	-0.56 (0.15)	6.40 (0.35)	-0.74	11.4	1490	0.38
Le Bray	3.9	0.5	-1.7	All	0 – 80	-	3.0	-0.91	85.0	3210	0.55

¹ $\hat{\sigma}^2$ is the mean squared error of the fitted model (the residual term of the innermost random effect), which is used to estimate bias corrected Ψ_e as $\Psi_e = -e^{\frac{1}{2}\hat{\sigma}^2} e^{\log(-\Psi_e)}$.

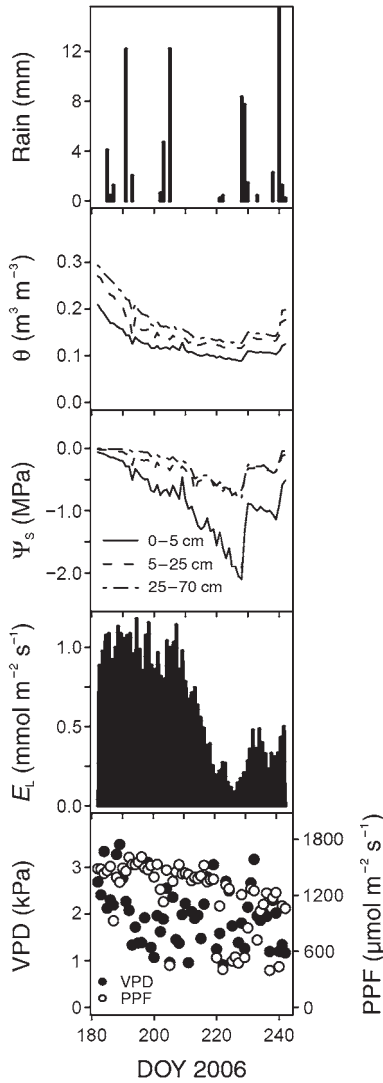


Figure 2. Daily rain, measured soil water content (θ), estimated soil water potential (Ψ_s), leaf transpiration rate (E_L) as measured by one of the three automated gas exchange chambers during the summer of 2006 in the boreal Scots pine stand, and daily maximum vapor pressure deficit (VPD) and daily maximum photosynthetic photon flux (PPF).

was ample soil water, because $E_{\max}|_{\Psi_s=0}$ was estimated as the mean of E_{\max} of the period preceding the drought, so E_{\max} was higher than average on some days and lower than average on others.

For the maritime pine site, daily E_{\max} was predicted by linear regression for periods of ample soil water. The fit was good ($r^2 = 0.96$; see Table 3), most of the variation being explained by daily total irradiance. Next, we predicted how well the soil water flow model predicted the relative decline in E_{\max} with declining θ . Figure 5 shows that the model predicts the decline well, although there is substantial variation around the mean. At low θ (0.05 – 0.07 $\text{m}^3 \text{m}^{-3}$), E_{\max} declined almost to zero, and the point at which this occurred corresponded well with the model predictions. Again, E_{\max} in wet soil can be larger than unity, because it was derived from a regression model, so

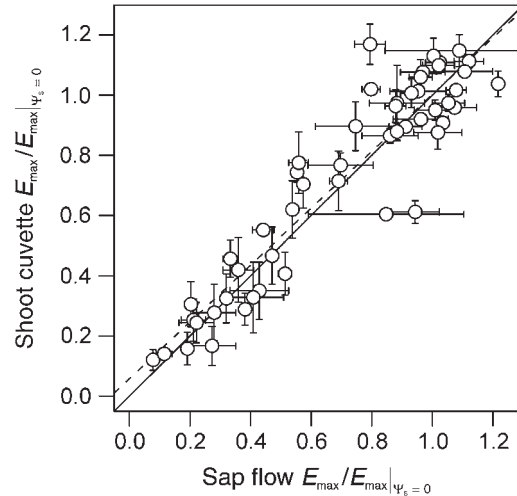


Figure 3. Comparison between daily relative maximum transpiration rate ($E_{\max}/E_{\max}|_{\Psi_s=0}$) for the boreal Scots pine stand estimated with sap flow and with automated gas exchange chambers. Data are means for two trees (sap flow) and three shoots at the top of the canopy (automated chamber system); error bars equal 1 standard error. Solid line shows a 1:1 relationship; dashed line is a least-squares regression line ($y = 0.057 + 0.944x$, $r_{\text{adj}}^2 = 0.864$, $P < 0.0001$). The intercept was not significantly different from zero ($P = 0.167$), and the slope not different from unity ($P = 0.299$).

that some days are below and some days above the fitted values of E_{\max} . After the dry period in 2002 (around DOY 250), θ increased almost to pre-drought values, but tree transpiration did not recover completely, which was not predicted by the model. An earlier drought episode in 2002 was also not correctly predicted by the model.

We tested the sensitivity of the $E_{\max}/E_{\max}|_{\Psi_s=0}$ curves (Equation 11) to Ψ_{\min} , both as a function of θ and of Ψ_s . Gradually changing Ψ_{\min} from -0.5 to -10 MPa initially affected the decline in E_{\max} , but at more negative Ψ_{\min} (< -2 MPa) the effect was small (Figure 6). If k_s were large compared with k_p , a graph of $E_{\max}/E_{\max}|_{\Psi_s=0}$ versus Ψ_s would yield straight lines with a slope of $-1/\Psi_{\min}$. Instead, with these plant and soil parameters, k_s becomes nearly 10^4 times smaller than k_p at $\Psi_s = -1.5$ MPa. With k_s decreasing to such low values, it is not surprising that Ψ_{\min} has little influence on water uptake in dry soil.

Discussion

We studied how θ influenced E_L if daily Ψ_{\min} is constant and loss of hydraulic conductance due to xylem embolism is avoided, as occurs in many woody species. The model successfully predicted how declining θ affected daily E_{\max} in a maritime pine and a Scots pine stand (Figures 4 and 5). However, in the maritime pine stand, there were differences before and after the severe drought in 2002: E_L did not recover to pre-drought values, contrary to expectations given the increase in θ (around DOY 250; Figure 5), indicating some carry-over effect of the drought that the model did not consider. Ewers et al. (2001) reported a similar result for *Pinus taeda* L. It is pos-

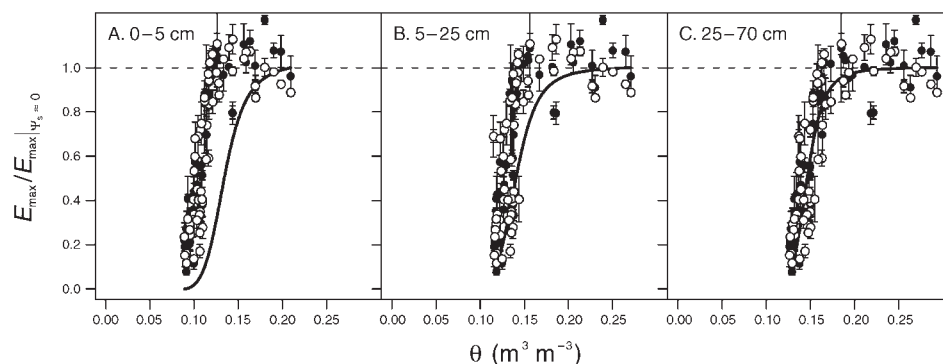


Figure 4. Measured and simulated decline in relative daily maximum transpiration rate ($E_{\max}/E_{\max}|_{\psi_s=0}$) as a function of soil water content (θ) at three depths in the boreal Scots pine stand. Measured daily maximum transpiration (estimated with the 95% percentile) averaged for three automated chambers is denoted by \circ , and bars equal 1 standard error (SE) across these three chambers for each day; and daily maximum transpiration determined from sap flow measurements is denoted by \bullet , and bars equal 1 SE based on the two trees. Lines are predictions with the steady-state model (Equation 11) and parameters for each layer (Table 2), assuming each time that all water uptake is from only that layer.

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sible that Ψ_{\min} was not constant during the drought, because regulation of Ψ_L may not be precise (Sperry and Pockman 1993) and water loss continues through the cuticle (Kerstiens 1996), resulting in xylem embolism (Sperry and Tyree 1988), lowering k_p after the drought and explaining why E_L did not return to pre-drought values. If this is the case, embolization

characteristics of the plant are necessary in the model to explain the decline in E_L in response to severe drought, because the central assumption of constant k_p is violated (Sperry et al. 1998, Hacke et al. 2000). However, other mechanisms may be responsible for the carry-over effect of drought, such as increased root mortality (Deans 1979, Marshall 1986), increased leaf mortality (Vilagrosa et al. 2003), hysteresis in K_S (Hillel 1980) and increased xylem susceptibility to embolism after multiple cycles of embolization and refilling (Hacke et al. 2001).

The correspondence between shoot-level E_{\max} and that measured by sap flow was remarkably good for the boreal Scots pine trees, given that the shoots were measured only at the top of the canopy (Figure 3). This suggests that, during drought, there is no significant change in the distribution of stomatal conductance within the crown of Scots pine. If, for example, shade foliage were more sensitive to drought, sap flow (total canopy transpiration) would decline more sharply with decreasing θ than E_L measured in sun foliage. Differences in drought response within the canopy could be expected when there are differences in k_L or Ψ_{\min} between sun and shade canopy foliage. For example, Lemoine et al. (2002) found higher drought sensitivity of shade foliage than sun foliage within a *Fagus sylvatica* L. crown, and Dang et al. (1997) reported higher sensitivity to VPD in sun leaves than in shade leaves in *Pinus banksiana* Lamb. and *Populus tremuloides* Michx.,

Table 3. Parameters and diagnostics of the linear model predicting daily maximum tree transpiration (E_{\max} ; $\text{mmol m}^{-2} \text{s}^{-1}$) for the maritime pine stand based on sap flow measurements when $\theta > 0.15 \text{ m}^3 \text{ m}^{-3}$. The model was $E_{\max} = \beta_0 + \beta_1(\text{PPF}) + \beta_2(\text{PPF})^2 + \beta_3(\text{VPD}) + \beta_4(\text{VPD})^2 + \beta_5 T_{\min}$ (daily total PPF in $\text{mol m}^{-2} \text{ day}^{-1}$, mean daily VPD in kPa and T_{\min} in $^{\circ}\text{C}$). The successive r^2 is that of the regression model with only those terms included; for example r^2 increased from 0.87 (with only PPF) to 0.91 when including the squared term of PPF. Final r^2_{adj} was 0.96, residual SE = 0.167 and $n = 98$. For all parameters, $P < 0.0001$.

Parameter	Estimate (SE)	Successive r^2
β_0	-0.49 (0.058)	–
β_1	0.072 (0.0057)	0.87
β_2	-0.00076 (0.00009)	0.91
β_3	1.3 (0.16)	0.94
β_4	-0.35 (0.064)	0.95
β_5	0.019 (0.0053)	0.96

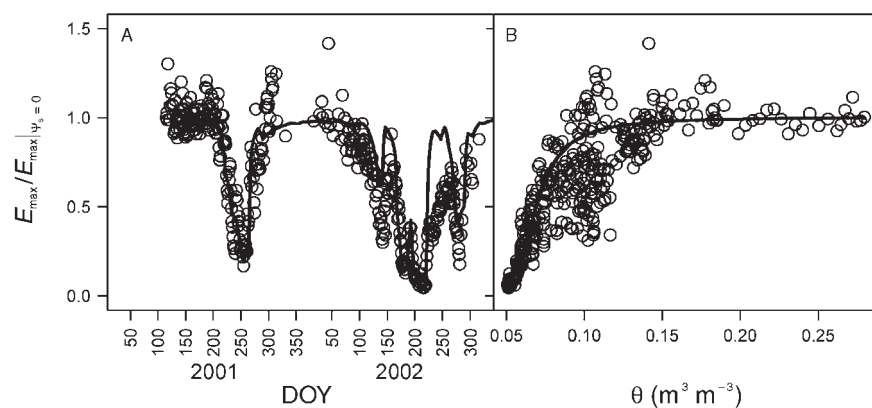


Figure 5. Measurements of daily maximum transpiration rate in the maritime pine stand relative to that predicted by a linear regression (that does not include θ) ($E_{\max}/E_{\max}|_{\psi_s=0}$) versus (A) day of year (DOY) and (B) soil water content (θ). Only data obtained when daily total photosynthetic photon flux exceeded $15 \text{ mol m}^{-2} \text{ s}^{-1}$ are shown, which excludes some wintertime data with high variance. The solid line is the relative decline in transpiration rate predicted with the steady-state flow model (Equation 11).

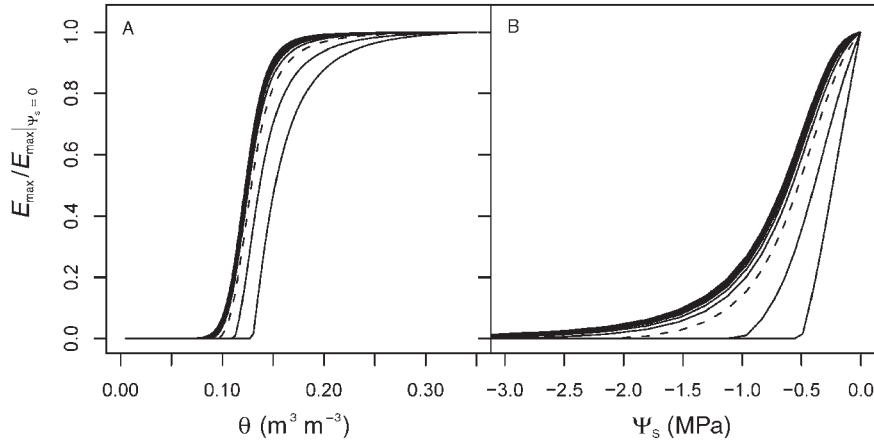


Figure 6. Sensitivity of relative maximum transpiration rate ($E_{\max}/E_{\max}|_{\Psi_s=0}$) to minimum leaf water potential (Ψ_{\min}) as a function of (A) soil volumetric water content (θ) and bulk soil water potential (Ψ_s). Relative E_{\max} was determined by dividing E_{\max} by its value obtained in wet soil (Equation 11). Curves from right to left correspond to Ψ_{\min} values of -0.5 and -1 MPa, and values from -2 (dashed line) to -10 MPa in steps of 1 MPa. All other parameters were taken from the boreal Scots pine stand (Table 2).

whereas Sellin and Kupper (2004) as well as Zweifel et al. (2002) reported the opposite for *Picea abies*, and L. Ewers et al. (2007) found that the response of stomatal conductance to VPD was consistent with isohydric behavior in both upper and lower branches of *Pinus taeda*. Within-canopy differences in drought response were small in our Scots pine trees, allowing us to make inferences on whole-tree response based on measurements by the automated shoot chamber system.

We implemented only one soil layer in the model, because we aimed to test if a simple model could explain the general trends in the data, and if not, what kind of additional detail would be required. The model for the boreal Scots pine stand predicted the decline in E_{\max} for three soil layers assuming water uptake was from one layer at a time. The results showed that predictions based on the water content of only the top layer resulted in a severely biased prediction of the onset of drought, likely because water uptake gradually shifted to lower wetter layers (Figure 4). Rambal (1984) demonstrated in a *Quercus coccifera* L. stand that water uptake shifts to deeper soil layers as drought progresses. The limitation to a shift to deeper layers is that the bulk of the root surface area is usually in the top layer. Presumably for this reason, Oren et al. (1998) found that the top layer was most important for predicting the drought response of *Pinus taeda*. Similarly, for *Pseudotsuga menziesii* (Mirb.) Franco and *Pinus ponderosa* growing on deep soil (> 2 m), although only 4–20% of water uptake was from the upper 20 cm, θ of the top layer affected the rate of water uptake during drought much more than θ of deeper soil layers (Warren et al. 2005). The response in that study was also steep (Figure 7). Further analysis of these data with models that include the interaction between vertical variations in root surface area and θ is needed (cf. Gardner 1964, Federer 1979, Sperry et al. 1998, Lai and Katul 2000, Feddes et al. 2001).

We successfully tested the model on two sites, but more data are needed at other sites to illustrate the effect of soil type on E_{\max} (Sperry et al. 2002). For a qualitative comparison, we reviewed the literature and extracted relative E_{\max} curves for forest stands where E_L or CO_2 uptake was measured (see Appendix for details). These published relationships showed remarkably similar shapes and slopes (Figure 7). We then used the

model (Equation 11) to predict relative E_{\max} as a function of θ for the generalized soil types from Cosby et al. (1984; Table 4), based on plant parameters from the boreal Scots pine stand. A more direct quantitative comparison was not possible, because plant parameters were unavailable and soil water retention curves were uncertain in most published reports. Nonetheless, the relationships predicted by the model were similar in shape and slope to published relationships determined from measurements, and the range of θ at which E_{\max} starts to decline was similar for the model and the measurements. For example, data from Kelliher et al. (1998) are for a coarse sandy soil and are similar to predictions with the model based on Cosby's sandy soil. Ewers et al. (2001) and Oren et

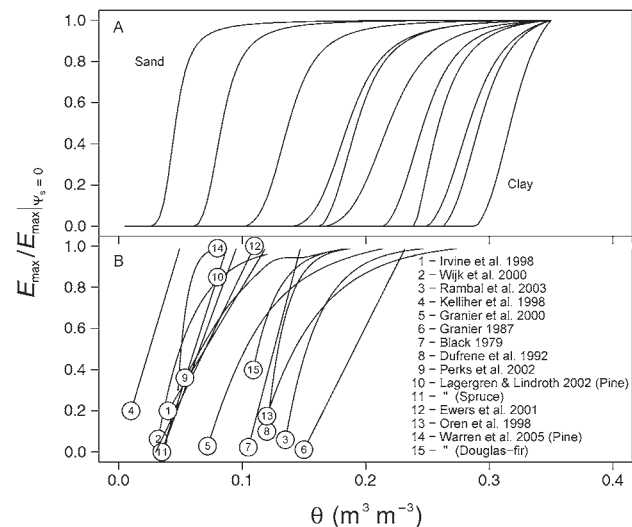


Figure 7. (A) Model (Equation 11) predictions of the decline in relative maximum transpiration rate ($E_{\max}/E_{\max}|_{\Psi_s=0}$) with declining soil water content (θ) for the generalized soil types shown in Table 3. Plant parameters were taken from the boreal Scots pine stand. (B) Relative decline in transpiration rate, stomatal conductance or assimilation rate as a function of θ as measured in the given studies (see Appendix). Curve 4 (Kelliher et al. 1998) was measured on a coarse sandy soil, and Curve 6 (Granier 1987) on a loamy soil. Other studies were carried out on intermediate soil types in terms of texture.

Table 4. General soil type classes from Cosby et al. (1984) and the parameters for the soil water retention (except θ_{sat} , for which soil type dependence is uncertain) and hydraulic conductivity curves. Abbreviations: b , soil texture parameter; Ψ_e , soil water potential at saturation (kPa); and K_{sat} , saturated hydraulic conductivity ($\text{mol m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$).

Soil type	b	Ψ_e	K_{sat}
Sand	2.79	-0.68	264.3
Loamy sand	4.26	-0.36	79.8
Sandy loam	4.74	-1.38	29.7
Loam	5.25	-3.48	19.1
Silty loam	5.33	-7.43	15.9
Sandy clay loam	6.77	-1.32	25.2
Clay loam	8.17	-2.58	13.9
Silty clay loam	8.72	-6.04	11.5
Silty clay	10.39	-3.17	7.6
Sandy clay	10.73	-0.96	40.9
Light clay	11.55	-4.58	5.5

al. (1998) reported data for *Pinus taeda* on a fairly sandy and a loamy soil, respectively, and their data agree with the model based on generalized soil types. Therefore, although widely different species in different climates were compared, the response to decreasing θ was strongly controlled by soil type. This is not surprising given the link between soil type and the soil water retention curve (Equation 10) and soil hydraulic conductivity function (Equation 9), but it illustrates that variation among plant types is of lesser importance than variation among soil types (Hacke et al. 2000).

The relative decline in E_{max} was highly insensitive to Ψ_{min} (Figure 6). This result agrees with the simulations by Sinclair (2005), who used a similar model and found that Ψ_{L} had minor effects on relative transpiration rate. Oren et al. (1999) found that response of stomatal conductance to VPD was similar across plants when response was normalized to stomatal conductance at a reference VPD. The insensitivity of E_{max} to Ψ_{min} when E_{max} was normalized at Ψ_{S} near 0 is consistent with their finding and is a direct consequence of near-constant Ψ_{L} in response to both VPD and Ψ_{S} (Oren et al. 1999). Nevertheless, our results are subject to the simplifications in the model, and a more thorough analysis of plant versus soil controls on water use has been carried out by Hacke et al. (2000) and Sperry et al. (2002), using a model that separates plant components differing in conductivity and embolization characteristics (Sperry et al. 1998). Hacke et al. (2000) showed that plant properties of *Pinus taeda* (root:shoot ratio, hydraulic conductance, etc.) strongly acclimate to soil type, further complicating the study of the interaction between effects of soil and plant properties on water uptake during drought. Nonetheless, the insensitivity of the simple isohydric model to variation in Ψ_{min} allows application of this model when estimates of Ψ_{min} are uncertain (cf. Sinclair 2005).

Although Ψ_{min} has minor effects on the relative transpiration rate when k_{pl} is constant, it directly affects the absolute values of E_{max} when ample water is available (Jones and Sutherland 1991), all else being equal. In simple steady-state flow, the

maximum flow rate increases proportionally with a decrease in Ψ_{min} or an increase in k_{p} . Decreases in Ψ_{min} beyond about -2 MPa had little effect, whereas the decrease from -0.5 to -2 MPa had a large effect on water uptake from dry soil (Figure 6). The ability to maintain even lower Ψ_{L} would be useful only if soil water flow remains possible at such low Ψ_{S} values. Hacke et al. (2000) found that *Pinus taeda* was more resistant to embolism in a finer textured soil. Further, the ability to maintain lower Ψ_{L} may be more closely related to survival than to the ability to take up water. During prolonged drought, Ψ_{L} still decreases, although stomata are closed, because of cuticular transpiration, and because the ability to maintain low Ψ_{L} without critical collapse of the hydraulic transport system is advantageous. In agreement with this idea, Cochard (1992) found that Ψ_{min} was related to drought tolerance in several coniferous species, and Maherali et al. (2004) found correlations between cavitation resistance and annual precipitation.

The classic approach to studying plant-soil water relations involves use of predawn Ψ_{L} measurements, which are assumed to reflect Ψ_{S} around the roots, thus obviating the need for soil water measurements (Reich and Hinckley 1989). However, predawn Ψ_{L} measurements do not include the soil resistance component, which becomes obvious during the day when transpiration occurs (Gardner 1960, Tuzet et al. 2003). Williams et al. (2001) found that increasing soil resistance with drought was the most important factor underlying the decline in tree transpiration in *Pinus ponderosa*, and Fisher et al. (2006) came to the same conclusion for a tropical rain forest. Besides, evidence is accumulating that predawn Ψ_{L} does not equilibrate with Ψ_{S} (Donovan et al. 2001), at least partly because nighttime transpiration is common (Iritz and Lindroth 1994, Snyder et al. 2003, Daley and Phillips 2006, Dawson et al. 2007). Further, Schmidhalter (1997) found that predawn Ψ_{L} may reflect the wetter parts of the soil, not an average. Including the k_{S} component in a steady-state model of water flow requires additional parameters, but because the behavior is more realistic, this component is vital in models of plant water uptake.

The two central assumptions of our model were a constant daily Ψ_{min} and a constant k_{p} . Neither assumption is entirely consistent with empirical evidence. For example, Hölttä et al. (2005) demonstrated some daily embolization in Scots pine (in the stand we studied) when θ was high. For the same species, Irvine et al. (1998) showed that Ψ_{min} was not constant during a drought. We used these simplifying assumptions because they led to a model that is easier to parameterize than a model allowing both parameters to vary. Because we calculated the relative E_{max} , estimates were highly insensitive to Ψ_{min} (Figure 6), implying that even if Ψ_{min} varies during drought, it has little effect on model predictions of relative E_{max} . In contrast, a decrease in k_{p} during drought is typical in isohydric plants (Sperry et al. 1998, Delzon et al. 2004a). In our case, k_{S} was virtually zero at a Ψ_{S} of about -1.5 MPa, well above Ψ_{min} (see Figure 6), so that if changes in k_{p} occurred near these water potentials, they would not affect E_{max} . In fine-textured soils that maintain conductivity at much lower water potentials, or for plants with low resistance to xylem

embolism, plant embolization characteristics become important (Hacke et al. 2000, Sperry et al. 2002).

We conclude that the assumption of a constant Ψ_{\min} during drought, combined with a constant k_p , leads to a practical model for predicting the decline in relative daily E_{\max} during drought. Model predictions agreed well with measurements, except for a brief period after a severe drought. For the two pine species studied, including further detail about plant or soil compartments appears to be unnecessary to explain the decline in daily E_{\max} during drought.

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Appendix

Literature review

We reviewed the literature for relationships in tree species between transpiration, stomatal conductance or CO₂ assimilation measurements and soil water content (θ). Ideally, we sought paired experiments with an irrigated control and a drying plot (Irvine et al. 1998, Perks et al. 2002). In most cases, however, we had to extract from the study the “baseline” gas exchange rate when soil water was in ample supply, and divide the rate as a function of θ by this baseline rate. This way, the various studies were normalized to be equivalent in meaning to Equation 11, i.e., the relative rate of transpiration (or CO₂ assimilation) with decreasing θ . In some cases, empirical models were fit in-

cluding a term for θ , which we were able to extract from the results. Soil water content was usually measured by time-domain reflectometry in the uppermost soil layer, but sometimes it was reported for a deeper layer, or averaged across the profile (e.g., Rambal et al. 2003). In some cases, water potential or some relative measure was reported and we used the reported soil water retention curve to convert to θ . Granier (1987) reported only relative extractable water, and we used the soil water retention curve for a loam soil (loam was reported as the soil type, and the estimate of the permanent wilting point matched that in the original study) to convert to θ (Table 4).