Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*

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ABSTRACT

We investigated the hydraulic consequences of a major decrease in root-to-leaf area ratio (A_R:A_L) caused by nutrient amendments to 15-year-old *Pinus taeda* L. stands on sandy soil. In theory, such a reduction in A_R:A_L should compromise the trees' ability to extract water from drying sand. Under equally high soil moisture, canopy stomatal conductance (G_S) of fertilized trees (F) was 50% that of irrigated/fertilized trees (IF), irrigated trees (I), and untreated control trees (C). As predicted from theory, F trees also decreased their stomatal sensitivity to vapour pressure deficit by 50%. The lower G_S in F was associated with 50% reduction in leaf-specific hydraulic conductance (K_L) compared with other treatments. The lower K_L in F was in turn a result of a higher leaf area per sapwood area and a lower specific conductivity (conducting efficiency) of the plant and its root xylem. The root xylem of F trees was also 50% more resistant to cavitation than the other treatments. A transport model predicted that the lower A_R:A_L in IF trees resulted in a considerably restricted ability to extract water during drought. However, this deficiency was not exposed because irrigation minimized drought. In contrast, the lower A_R:A_L in F trees caused only a limited restriction in water extraction during drought owing to the more cavitation resistant root xylem in this treatment. In both fertilized treatments, approximate safety margins from predicted hydraulic failure were minimal suggesting increased vulnerability to drought-induced dieback compared with non-fertilized trees. However, IF trees are likely to be so affected even under a mild drought if irrigation is withheld.

Key-words: leaf-specific hydraulic conductivity; leaf water potential; soil moisture; vapour pressure deficit; vulnerability curve; water transport; xylem cavitation.

INTRODUCTION

Investigations ranging from plant physiology at the cellular level to mass and energy exchange at the regional scale rely on understanding the regulation of gas exchange (Jarvis 1995; Sellers *et al.* 1997). Over the short term, plants respond to soil and plant water deficits by reducing stomatal conductance and water loss. Over the longer term, adjustments in architecture and intrinsic physiology can occur. Leaf shedding and root growth triggered by water stress (Linder *et al.* 1987; Tyree *et al.* 1993) result in an increased root-to-leaf ratio (A_R:A_L) that favours a high water balance during drought. Osmotic adjustment and increased resistance to xylem cavitation (Alder, Sperry & Pockman 1996) can lower the range of water potential (Ψ) for gas exchange. *Pinus taeda* L. (loblolly pine) can serve as a model system for investigations of gas exchange regulation across a wide range of soils and environmental conditions because of its wide range in the southeast United States and its considerable plasticity (Teskey *et al.* 1987). A recent comparison across soil types indicated that trees in sandy soil produced deeper roots, more vulnerable xylem, and increased their A_R:A_L nearly sixfold compared with genetically similar trees in loam soil. The consequence of these adjustments was the maintenance of a similarly high proportion of extractable water from both soils (Hacke *et al.* 2000).

In this paper, we focus on the influence of nutrient versus water availability on water use traits and hydraulic architecture of *P. taeda* growing in sand. While the inherently low water availability in a drying sand versus less porous soil is associated with an increase in A_R:A_L with soil porosity (Sperry *et al.* 1998), nutrient amendments used to promote growth on sterile sand have the effect of reducing A_R:A_L (Keyes & Grier 1981; Linder & Axelsson 1982; Linder *et al.* 1987; Gower *et al.* 1994; Haynes & Gower 1995; Landsberg & Gower 1997). Balancing this antagonism may be critical for plants in sandy soil where a high A_R:A_L is required to offset the tendency for rhizosphere conductance in these soils to plummet even under modest water deficits (Sperry *et al.* 1998). It is possible that tree responses to nutrient and water amendments may significantly compromise drought tolerance in these soils.

At our study site (see below), water and nutrient treatments have been ongoing since 1993 and basic responses have been documented (Albaugh *et al.* 1998). For *P. taeda* in sandy soil, fertilization (F), or a combination of irrigation and fertilization (IF) increased projected leaf area index (*L*) twofold relative to the control (C), while irrigation (I) alone increased *L* by only 16% (Table 1, Albaugh *et al.*

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Table 1. Mean tree diameter at 1·4 m above-ground (*d*) height (*h*), sapwood area per ground area ($A_S:A_G$), projected leaf area index (*L*) both maximum value and during the time in which roots were sampled (at start of growing season), sapwood area-to-leaf area ratio at breast height ($A_S:A_L$), root area index (*R*), root-to-leaf area ratio (minimum value at start of growing season, $A_R:A_L$), canopy stomatal conductance (G_S) at vapour pressure deficit (*D*) = 1 kPa (G_{Sref}), sensitivity of G_S to *D* ($dG_S/dlnD$) under high native soil moisture ($0.08 > \theta_R > 0.065$ m³ m⁻³) and under continuous irrigation ($\theta_R > 0.08$ m³ m⁻³; asterisked values), whole tree hydraulic conductance averaged over days when Ψ_L was measured (K_L), apparent specific conductivity (Kh/A_S), maximum root specific hydraulic conductance (k_h/A_S), and sensitivity of k_s to water potential ($dk_s/dln\Psi$), of control, irrigated, fertilized, and irrigated, fertilized (C, I, F, and IF, respectively)

	C	I	F	IF
d (mm)	122 ± 11	121 ± 8	156 ± 12	180 ± 10
h (m)	8·8	8·8	11·9	12·5
$A_S:A_G$ (cm² m⁻²)	10·2	10·1	17·0	24·9
L (m² m⁻²)	1·4	1·6	2·7	2·9
Maximum *L* (m² m⁻²)	1·9	2·0	3·6	4·0
$A_S:A_L$ (cm² m⁻²)	5·3	4·8	4·5	6·3
R (m² m⁻²)	14·2 ± 2·1[a]	12·3 ± 1·8[a]	12·5 ± 1·7[a]	11·5 ± 1·0[a]
$A_R:A_L$ (m² m⁻²)	9·8	7·9	4·6	3·9
G_{Sref} (mmol m⁻² s⁻¹)	85 ± 9[a]	75 ± 8[a]	39 ± 4[b]	80 ± 7[a]
$dG_S/dlnD$ (mmol m⁻² s⁻¹ kPa⁻¹)	46 ± 5[a]	42 ± 4[a]	20 ± 3[b]	40 ± 5[a]
G_{Sref}* (mmol m⁻² s⁻¹)	123 ± 38[a]	117 ± 33[a]	52 ± 20[b]	177 ± 72[a]
$dG_S/dlnD$* (mmol m⁻² s⁻¹ kPa⁻¹)	94 ± 36[a]	94 ± 32[a]	41 ± 22[b]	75 ± 37[a]
K_L (mmol m⁻² s⁻¹ MPa⁻¹)	1·1 ± 0·3[a]	1·0 ± 0·2[a]	0·5 ± 0·1[b]	1·1 ± 0·3[a]
$K·h/A_S$ (mmol mm⁻¹ MPa⁻¹)	18·3	18·3	13·2	21·8
k_h/A_S (mmol m⁻¹ s⁻¹ MPa⁻¹)	0·11 ± 0·01[a]	0·12 ± 0·02[a]	0·06 ± 0·01[b]	0·11 ± 0·01[a]
$d(k_h/A_S)/dln\Psi$ (mmol m⁻¹ s⁻¹ MPa⁻²)	0·04 ± 0·005[a]	0·04 ± 0·005[a]	0·02 ± 0·005[b]	0·04 ± 0·005[a]

Values are means ± 1 SE, *n* = 3 for continuous irrigation and K_L, *n* = 4 for *R*, *n* = 8 for high native soil moisture and root measurements. Values of the same variable not accompanied with the same letter are significantly different (*P* < 0·05). Because K_L within each treatment did not vary among days (*P* > 0·3), Table 1 presents the average of the SE obtained for each of the 6 d.

1998). The rather subtle effect of irrigation alone is because control plants themselves were not substantially water limited as a result of their extensive and deep (> 2 m) root system (Hacke *et al*. 2000; B. E. Ewers *et al*. unpublished results). The dramatic increase in leaf area caused by nutrient addition suggests corresponding adjustments in water use – particularly in the F plot where leaf area was added but irrigation was not supplied. Accordingly, a previous study showed a large drop in transpiration per leaf area (E_L) in F, but not in IF trees relative to controls (Ewers *et al*. 1999). While the latter study could attribute the drop in E_L to a lower leaf-specific hydraulic conductance (K_L) in F versus IF trees, it could not determine why the doubling of leaf area should decrease K_L in F but not in IF trees. Nor were the consequences of shifts in allocation for water extraction explored.

In this study, we provide an empirical and theoretical analysis of the architectural and physiological parameters contributing to *P. taeda* water use across the four water versus nutrition treatments (C, I, F, IF).

Theoretical framework and hypotheses

Our analysis and hypotheses are based on established relationships for steady-state flow through the soil–plant continuum. A 'supply function' describing the availability of water flow to the leaves is derived from Darcy's law (modified from Whitehead & Jarvis 1981; Tyree & Ewers 1991; Whitehead 1998):

$$E_L = K_L \cdot (\Psi_S - \Psi_L - h\rho_w g), \tag{1}$$

where Ψ_S and Ψ_L are the bulk soil and leaf water potentials, and $h\rho_w g$ is the gravitational pull on water column of density ρ_w up a tree of height *h*. Importantly, the supply function has built-in limitations because K_L declines with Ψ owing to drying soil, cavitation in xylem, and other factors. The opposition between increasing driving force required to sustain increasing E_L and the decrease in K_L creates a minimum Ψ_L (Ψ_{Lcrit}) and associated maximum transpiration rate (E_{Lcrit}), which, when exceeded, causes hydraulic failure by driving K_L to zero (Tyree & Sperry 1988). The E_{Lcrit} as a function of Ψ_S defines the maximum water extraction capability of the plant, and is heavily influenced by $A_R:A_L$ and cavitation resistance (Sperry *et al*. 1998). We used a transport model previously applied to control trees (Hacke *et al*. 2000) to determine the effects of $A_R:A_L$ and cavitation resistance on E_{Lcrit} across the four treatments.

Differences in K_L between treatments in the absence of soil drying and cavitation can be attributed to architectural parameters like *h* and sapwood area per leaf area ($A_S:A_L$), and also to the hydraulic conductivity per cross-sectional

area of the flow path (specific conductivity). A simplified relationship that approximates these dependencies (Oren *et al*. 1999; Schäfer, Oren & Tenhunen 2000) is:

$$K_L = \frac{K \cdot h}{A_S} \cdot \frac{A_S}{A_L} \cdot \frac{1}{h} \qquad (2)$$

where K is hydraulic conductance of the whole plant supply line. The term (Kh/A_S) is K normalized for differences in plant length (assumed proportional to h) and expressed per sapwood area at a reference point in the flow path. It serves as an 'apparent specific conductivity' for the plant and was useful for comparison of size-independent conducting efficiency between treatments.

The stomatal response to changes in hydraulic architecture can be predicted from Eqn 1 by substituting canopy stomatal conductance (G_S) and vapour pressure deficit (D) for E_L:

$$G_S = K_L / D \cdot (\Psi_S - \Psi_L - h\rho_w g) \qquad (3)$$

This equation assumes steady-state conditions, a negligible influence of leaf boundary layer conductance, and that G_S is less than its maximum value set by maximum stomatal aperture and density (G_{Smax}). It predicts that for a given height and water potential difference, G_S is proportional to K_L and inversely proportional to D.

A consequence of G_S being inversely proportional to D (Jarvis 1976; McNaughton & Jarvis 1991) is that the sensitivity of G_S to increasing D in terms of $\Delta G_S / \Delta D$ will be proportional to G_{Smax} or its proxy (Oren *et al*. 1999). We tested this for each treatment using the empirical relationship between G_S and D:

$$G_S = G_{Sref} - (m) \cdot \ln D, \qquad (4)$$

where G_{Sref} (i.e. G_S at $D = 1$ kPa) is a surrogate for G_{Smax}, and the sensitivity of G_S to D is quantified by the slope m ($= dG_S/d\ln D$). The slope of the correlation between m and G_{Sref} in a variety of plants under light-saturated conditions has been shown empirically and theoretically to be near 0·6. The theoretical slope, derived from Eqn 3 assuming constant regulation of Ψ_L as D varies, shows a variation of $< \pm 0·05$ with a 10-fold change in the ratio of boundary layer-to-stomatal conductance, and $< \pm 0·1$ with changes in the ΔD range (Oren *et al*. 1999). This relationship means that G_{Sref} and D capture most of the variation in G_S. If this relationship holds for *P. taeda*, we can use G_{Sref} as a proxy for the response of G_S versus D in comparing stomatal behaviour across cultural treatments.

Based on the relationships above, we evaluated the following set of hypotheses concerning nutrient and water treatments at the *P. taeda* study site. (1) Building on previous results from the site (Ewers *et al*. 1999), we expect that under favourable soil moisture, G_{Sref} and K_L will be lower in F, than in C, I, and IF treatments. (2) The lower K_L in F than C, I, and IF trees will be associated with reduced $A_S:A_L$ and apparent specific conductivity (Kh/A_S; Eqn 2) whereas these components will remain constant across other treatments. (3) Lower G_{Sref} in F trees will be accompanied by

lower G_S sensitivity to D. (4) Lower $A_R:A_L$ in fertilized trees will reduce their ability to extract water from drying sand and render them more sensitive to drought stress.

MATERIALS AND METHODS

Setting

The Southeast Tree Research and Education Site (SETRES) was established in the Sandhills of North Carolina (34°48′ N 79°12′ W) on an infertile, well-drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series) in 1992. Annual precipitation averages 1210 mm with occasional growing season water deficits.

Sixteen 50×50 m treatment plots (including a 10 m wide buffer) separated by 10 m untreated buffers were established in a mixed families stand of North Carolina Piedmont *P. taeda* planted in 1984 in a 2×3 m spacing. Treatments were a 2×2 factorial combination of nutrition and water additions. Nutrient treatments have been maintained since March 1992 and water addition since April 1993. Nutrient treatment consists of optimal nutrition defined as maintaining nitrogen concentration of 1·3% in upper canopy foliage with phosphorus, potassium, calcium, and magnesium balanced with nitrogen levels. Boron is also added to maintain foliar concentrations above 12 p.p.m. Foliar nutrient status has been monitored monthly and applied annually to meet target values. Water addition has been made to keep available soil moisture between field capacity and 40% of available soil water in the upper 0·50 m of the soil profile corresponding to 30 mm soil water in that layer as measured with time domain reflectometry. For more details on nutrition and water treatments see Albaugh *et al*. (1998) and Murthy *et al*. (1996).

From July 25 to August 8, 1998 we continuously irrigated a portion of our measurement subplot in all four treatments to compare G_S at similar maximum water content. The continuous irrigation raised soil moisture to levels above the standard irrigation treatment, and above the highest that rains can naturally maintain, even temporarily, in this fast draining soil. A sprinkler was placed such that it could reach three trees on which sap flux and Ψ_L were measured (see below). In all treatments, the maximum flow of water permitted a minimum coverage of 2·5 m radius that included the neighbouring tree of each of the three individuals plus halfway to the next tree.

Plant biomass measurements

We calculated projected L using allometric relationships, adjusting for seasonal trends based on canopy surface analyser (LAI-2000, Li-Cor Co., Lincoln, Nebraska, USA; see Albaugh *et al*. 1998; Ewers *et al*. 1999). Whole tree $A_S:A_L$ was calculated from L and sapwood area determined from breast-height cores (Ewers *et al*. 1999). All sided root area index (R), required for calculating $A_R:A_L$, was from another study (B. E. Ewers *et al*. unpublished results). Roots

were excavated to 1·9 m in a 1 × 1 m pit incrementally to 0·15, 0·30, 0·50, 0·90, 1·1, 1·3, 1·5, 1·7, and 1·9 m. Roots from each depth interval were sorted into 0–1, 1–2, and 2–5 mm size classes and oven dried at 65 °C. Total R was determined from a length to mass relationship constructed from sub-samples of each size class. Summary results from that study (B. E. Ewers *et al*. unpublished results) that were necessary for analysis and interpretation of data in this study are provided in Table 1.

Sap flux measurements

We measured sap flux in stem xylem of eight trees per treatment, located in a subplot in the treated buffer of each treatment, all in one block, with Granier-type sensors (Granier 1987; Ewers *et al*. 1999; Ewers & Oren 2000) from August 1996 to January 1998. Measurements were made on the north side of stems (1·4 m above ground) at two depths: (1) the outer 20 mm of the xylem in eight trees, and (2) the next 20 mm of the xylem in a subset of five trees to account for radial patterns in sap flux (Phillips, Oren & Zimmermann 1996). We calculated the average sap flux (J_S), weighting the outer sap flux by the sapwood area represented in that xylem band and the inner sap flux by the sapwood area internal to the outer band (Oren *et al*. 1998; Ewers *et al*. 1999; Ewers & Oren 2000). This assumes that inner sap flux represents the flux in the xylem internal to 40 mm from the cambium. Xylem in this innermost radial position represents < 15% of the xylem in the IF stand (Ewers *et al*. 1999), the fastest growing among all treatments (Albaugh *et al*. 1998). There was no systematic circumferential variation in flux (Ewers & Oren 2000).

During the continuous irrigation experiment, sap flux in the three irrigated trees per plot was normalized by the difference between the average of the three trees and average of the other five trees, obtained from the entire data set except the irrigation week. This was carried out because the water supply was inadequate to allow irrigation to be continuously applied to all trees, and intertree variability would have obscured the population response to irrigation. Normalizing as above facilitates merging of data collected during the continuous irrigation experiment with the rest of the data.

Environmental measurements

A relative humidity and temperature probe (Vaisala HMP 35C, Campbell Scientific, Logan, UT, USA) was positioned at a height of 7 m in the centre of each subplot and provided data for calculating D (Goff & Gratch 1946). Photosynthetic photon flux density (Q_o) was measured above the canopy (Li-190 s, Li-Cor). Soil volumetric water content (θ) was measured using automated time domain reflectometry (TDR) probes with 6-cm-long steel rods (Theta Probe, Delta-T Devices, Cambridge, UK) at 0·05, 0·1, 0·25, 0·5, 1·0, and 2·0 m depth. The 2·0 m probe was only available from June to July 1998 and θ at 2 m averaged only 0·002 m³ m⁻³ higher than at 1·0 m, with very little variation. This

average difference was used to estimate θ at 2 m for the rest of the data set based on the continuous measurements made at 1·0 m. Soil water potential was calculated from Campbell (1974):

$$\Psi_S = \Psi_e \cdot (\theta/\theta_S)^{-b}, \tag{5}$$

where Ψ_e is the soil matric potential at air entry, θ_S is saturated volumetric water content and the exponent b is related to soil texture. We used $b = 2\cdot56$ (Abrahamson *et al*. 1998) and $\theta_S = 0\cdot46$ m³ m⁻³ (Hacke *et al*. 2000). A weighted θ (θ_R) and Ψ_S (Ψ_{SR}) were calculated using the root area profile to 1·9 m (B. E. Ewers *et al*. unpublished results).

Xylem flux and all environmental sensors were sampled every 30 s and 30 min average values were logged (DL2, Delta-T Devices).

Calculations of E_L and G_S

To calculate E_L, J_S is combined with sapwood-to-leaf area ratio ($A_S:A_L$; Oren *et al*. 1998; Ewers & Oren 2000). We calculated G_S from E_L and D using the simplification suggested by Monteith & Unsworth (1990) as shown in Phillips & Oren (1998). The simplified calculation was permitted because in all treatments in this stand: (1) D is close to the leaf-to-air vapour pressure deficit, i.e. boundary layer conductance is high, (2) D has no vertical gradient through the canopy, and (3) the amount of water stored in the trees above the probes is negligible (Ewers & Oren 2000). Relative errors in G_S, caused by instrument limitations, were kept to < 10%, by limiting G_S calculations to $D > 0\cdot6$ kPa (Ewers & Oren 2000)

Measurements of leaf water potential

Ψ_L was measured with a pressure chamber on single fascicles from the mid-canopy of three trees in C, I, F, and IF. One fascicle was taken from each tree and immediately placed in an airtight plastic bag with a wet towel. All Ψ_L measurements were taken within 10 min of removal from the tree. On July 14 and August 8, 1997, one branch from each treatment was placed in a plastic bag with a wet towel to stop transpiration and determine whether Ψ_L of transpiring needles was similar to that of non-transpiring needles. Non-transpiring branches were not different from transpiring branches ($P > 0\cdot3$).

Measurements of Ψ_L were made every 3 h for a 24 h period on July 15, and August 18, 1997, and May 19, July 8, 21, and 23, 1998. These days were sunny and dry.

Vulnerability curve and root anatomy measurements

We constructed vulnerability curves by applying known negative xylem pressures to excised stem and root segments using a centrifugal force method (Alder *et al*. 1997; Hacke *et al*. 2000). Eight root (1·6–4·1 mm in diameter) and four branch segments were collected as described in Hacke *et al*. (2000) from each treatment in each block in April 1998.

Roots were sampled in the top 0·2 m of soil. An additional sample of four roots was collected from 1·9 m depth in C. The loss of conductivity as a function of Ψ was described with the weibull function (Sperry *et al.* 1998), as

$$k_{\text{h}} = k_{\text{Max}} \cdot e^{-(\Psi/d)c}, \tag{6}$$

where k_{h} is hydraulic conductivity of the segment (flow rate per pressure gradient), k_{Max} is maximum hydraulic conductivity, Ψ is the applied water potential, and c and d are curve fitting parameters.

We measured tracheid diameters of the two outer growth rings in three roots of each treatment. Measurements were made in three radial sectors at 120° intervals on a free hand transverse section, using a light microscope interface with a bit pad (Donsanto Microplan II, Natick MA, USA) to trace lumen area and calculate the diameter of the equivalent circle. We calculated the hydraulic mean diameter from the diameter distribution weighted in proportion to its theoretical contribution to hydraulic conductivity according to the Hagen–Poiseuille law. Mathematically, the hydraulic mean tracheid diameter equals $\Sigma d^5/\Sigma d^4$ (Sperry & Ikeda 1997).

Statistical and data analyses

All statistical analyses were performed using SAS procedures GLM and MIXED (version 6·12, SAS institute, Cary, NC, USA). When data were collected repeatedly on the same tree (i.e. Ψ_{L}) repeated measures ANOVA was used. Non-linear curve fits were performed in SIGMAPLOT (version 4·5, SPSS, San Rafael, CA, USA). Curve fits were performed on individual experimental units and then ANOVA was used to test for difference among treatments in the fitting parameters. We analysed boundary lines, based on the methodology of Schäfer, Oren & Tenhunen (2000).

Model application

We used the model presented in detail in Sperry *et al.* (1998) and applied to the *P. taeda* C treatment in Hacke *et al.* (2000) to evaluated the effect of K_{L}, $A_{\text{R}}{:}A_{\text{L}}$ and vulnerability to cavitation on E_{Lcrit}, E_{L}, and the potential for water extraction. Below we provide a brief description of the model.

The model solves the steady state of Eqn 1 by incrementally increasing E_{L} at a temporally constant bulk Ψ_{S} (but spatially variable depending on moisture profile). The drop in Ψ in the continuum is used to calculate the reduction in K_{L} from rhizosphere drying and xylem cavitation. The model output is the predicted relationship between E_{L} and Ψ_{L} for any soil moisture profile together with the maximum E_{L} (E_{Lcrit}) above which hydraulic failure ensues. Integration of E_{Lcrit} versus Ψ_{S} provides an estimate of the maximum water extraction capability of the tree (as shown in Fig. 1, Hacke *et al.* 2000).

The model requires initialization at saturated conditions using the hydraulic conductance of the rhizosphere, root system, and shoot system. The initial, saturated K_{L} was
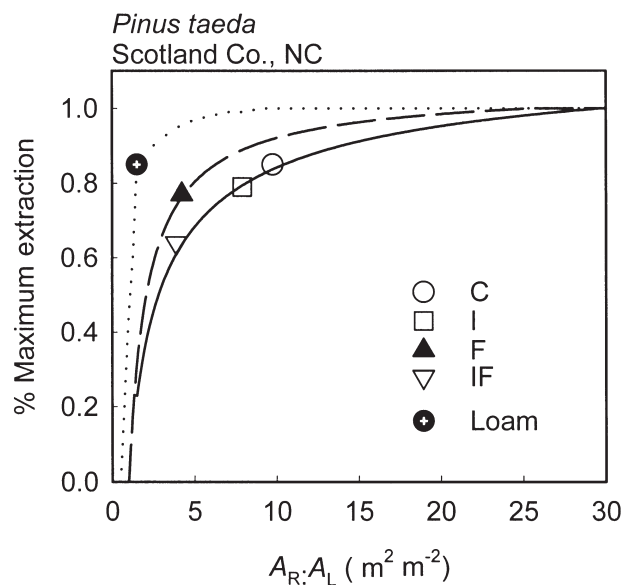

Figure 1. Extraction potential versus root-to-leaf area ratio ($A_{\text{R}}{:}A_{\text{L}}$) in control, irrigated, fertilized, and irrigated/fertilized (C, I, F, and IF, respectively). Extraction potential is defined as the area under the E_{Lcrit} versus Ψ_{S} curves for the field range of Ψ_{SR}. Extraction potential is expressed relative to the value at $A_{\text{R}}{:}A_{\text{L}} = 30$. This value was chosen as a liberal estimate of the maximum likely physiological value for a woody plant. Symbols correspond to measured values of $A_{\text{R}}{:}A_{\text{L}}$. The loam soil is from Hacke *et al.* (2000).

determined using the mean values calculated in May and June, prior to significant soil drying, and midday (12·0 –14·0 h) conditions of $D > 1{\cdot}5$ kPa. The root and shoot components were each assumed to constitute 50% of the plant hydraulic resistance under saturated conditions; however, sensitivity analyses of this setting indicate that it does not have a major influence E_{Lcrit} (Sperry *et al.* 1998). The root system was divided into lateral and axial root components. Lateral components withdrew water from six soil layers centred on θ measurement depths. Initial K_{L} values in the root system were determined using an iterative procedure that solved for the value of K_{L} in the root collar that was half way between the field values of Ψ_{S} and Ψ_{L}. Once the model was appropriately initialized, it was used to determine E_{Lcrit} as a function of root weighted Ψ_{S} (Ψ_{SR}). All other model parameters were as described in Hacke *et al.* (2000).

RESULTS

Canopy stomatal conductance and sensitivity to vapour pressure deficit

As hypothesized, the mean canopy stomatal conductance, G_{S} in F was lower than that of the other treatments even when soil moisture was the most favourable ($\theta_{\text{R}} > 0{\cdot}065$ m³ m⁻³, Fig. 2a). The mean values ($n = 8$ trees for each datum) represent boundary line conditions using 0·2 kPa D bins and 1 SD for data selection (see method in Schäfer, Oren
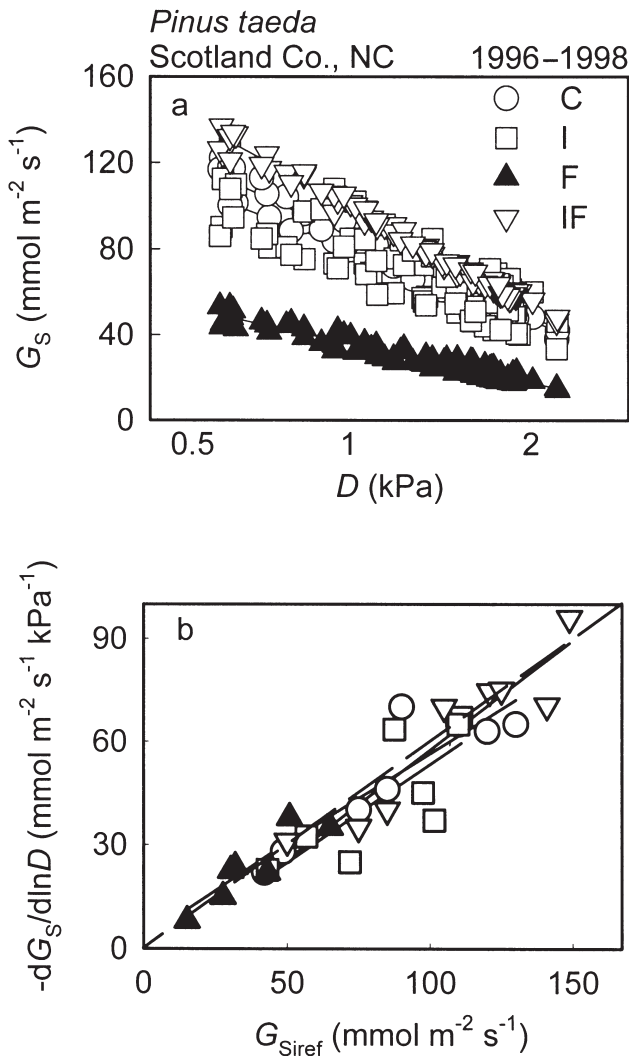
Figure 2. (a) Average stomatal conductance G_S of the control, irrigated, fertilized, and irrigated/fertilized (C, I, F, and IF, respectively) trees when soil volumetric water content normalized by root area index (θ_R) > 0·065 m³ m⁻³ versus the natural logarithm of vapour pressure deficit (D). (b) Slope of the response of G_S of individual trees ($n = 8$) to the natural logarithm of vapour pressure deficit ($dG_S/d\ln D$) versus G_S at vapour pressure deficit = 1 kPa (G_{Siref}).

& Tenhunen 2000). All regressions in Fig. 2a were highly significant ($P < 0·001$) and the r^2 was 0·75, 0·68, 0·80, and 0·87 for C, I, F, and IF, respectively. The value of G_S at $D = 1$ kPa (G_{Sref}) was significantly lower in F (Table 1, $P < 0·001$) compared with the other treatments which were not significantly different from each other ($P > 0·2$). Also as expected, the lower G_{Sref} in F trees was associated with a lower stomatal conductance sensitivity to D ($dG_S/d\ln D$, Eqn 4) in F trees versus other treatments (Table 1, $P < 0·001$).

The pattern in G_{Sref} and $dG_S/d\ln D$ across treatments held even when soil water content was raised to a similarly high value in all treatments by continuous irrigation. Although continuous irrigation increased G_{Sref} in all treat-

ments, the increase was smallest in F and it remained lower than other treatments (Table 1, G_{Sref} *, $P < 0·001$). The other treatments continued to be not significantly different from each other ($P > 0·2$). Stomatal conductance sensitivity to D increased proportionally to G_{Sref} in all treatments, but the increase was not significant (Table 1, $dG_S/d\ln D$*, $P > 0·05$) due to the low number of replicates ($n = 3$).

We evaluated whether any of the treatments resulted in a significant deviation from the theoretical relationship between the sensitivity of the stomata to D and G_{Sref} based on constant Ψ_L regulation in response to changes in D (Oren *et al.* 1999). The independent variable in Fig. 2b corresponds to the values of G_{Sref} from Fig. 2a, and the dependent variable corresponds to the slope of the regression lines in Fig. 2a (= $dG_S/d\ln D$). The data in Fig. 2b represent the eight trees per treatment contributing to the means in Fig. 2a. There was a significant, linear relationship ($P < 0·001$) between G_{Siref} and $dG_{Si}/d\ln D$ for all treatments (Fig. 2b) and the intercept was not significant ($P > 0·4$ for all treatments; i represents the individuals). The slope of the relationship between G_{Siref} and $dG_{Si}/d\ln D$ was 0·52, 0·57, 0·55, and 0·64 for C, I, F, and IF, respectively. Only C was significantly different ($P < 0·05$) from the theoretical value of 0·6 (Oren *et al.* 1999) indicating lower than expected sensitivity.

Leaf water potential and leaf specific conductance

There was no treatment effect on Ψ_L whether it was assessed at predawn throughout the 2 year study period ($P > 0·4$, Fig. 3b), or measured diurnally on sunny days (Fig. 3a). The lack of an irrigation effect on predawn Ψ_L reflects both the reliance of these trees on deep water (Ewers *et al.* 1999; Hacke *et al.* 2000) and the fast draining nature of the soil that minimizes the long-term increase in water content from irrigation. These factors may also explain why predawn Ψ_L was unrelated to Ψ_{SR} ($P > 0·3$). Only when irrigation was applied continuously (late July 1998) was there an increase in both predawn and mid-day Ψ_L (0·3–0·4 MPa, $P < 0·05$, Fig. 3b). Otherwise, the mean mid-day Ψ_L was 1·6 MPa and did not vary with time, θ, or treatment ($P > 0·2$) indicating an isohydric regulation of Ψ_L.

Using the complete diurnal Ψ_L data collected in each of the days shown in Fig. 3b, we related Ψ_L to E_L (Fig. 4). The relationship was highly significant in all treatments ($P < 0·001$), and θ did not explain the residual variation in Ψ_L ($P > 0·2$) despite some variation in soil moisture conditions (0·05 m³ m⁻³ < θ_R < 0·08 m³ m⁻³) in all treatments. The slopes of the relationship in Fig. 4 were used to calculate K_L (Eqn 1) using predawn Ψ_L as a proxy for Ψ_S. K_L was only calculated during times in which D was greater than 0·6 kPa to minimize the effect of water storage on estimates of E_L (Ewers & Oren 2000). As hypothesized, K_L in F was significantly lower (by ~ 50%) than the other treatments ($P < 0·001$; Table 1) which were not different from each other.

The 50% reduction in K_L in F trees versus non-fertilized trees (C and I) was contributed to by all factors in Eqn 2.
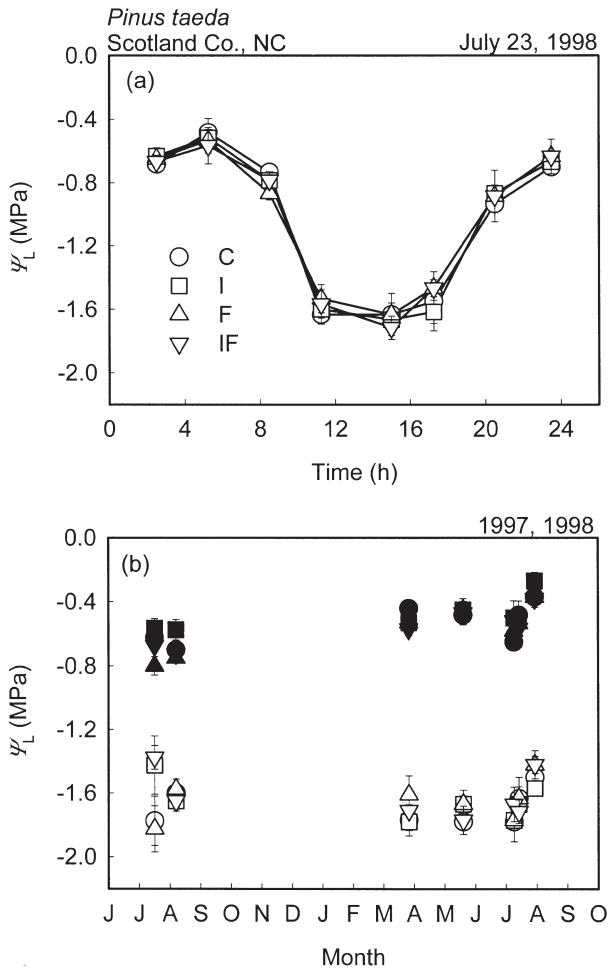
Figure 3. (a) Diurnal leaf water potential (Ψ_L) for control, irrigated, fertilized, and irrigated/fertilized (C, I, F, and IF, respectively) trees. Bars are 1 SE of the mean ($n = 3$). (b) Ψ_L versus month starting in June. Closed symbols are pre-dawn and open symbols are mid-day. Bars and symbols are the same as (a).

Compared with average values for C and I trees, the F trees showed a 35% increase in height (h), an 80% increase in maximum L, a 28% reduction in apparent specific conductivity (Kh/A_S), and an 11% reduction in $A_S{:}A_L$ (Table 1). In contrast, the 0% reduction in K_L in IF trees versus non-fertilized trees was a result of the negative effects of increases in h (42%) and L (93%) being offset by increases in apparent specific conductivity (19%) and $A_S{:}A_L$ (25%). These differences occurred despite any difference in pre-dawn or mid-day water potentials between treatments, and they persisted even when continuous irrigation was applied across all treatments to further minimize any variation in soil water content (Table 1, asterisked values). As hypothesized, the main factors contributing to the lower K_L in F versus IF trees were the lower apparent specific conductivity and lower $A_S{:}A_L$ in the former. Consistent with the lower $A_S{:}A_L$ in F trees was the reduced enhancement of sapwood growth in F versus IF trees (currently 17 versus 25 cm^2 sapwood area/m^{-2} ground area, respectively).

Vulnerability curves and tracheid anatomy

We used Eqn 5 to quantify the vulnerability of stem and root segments to cavitation (Fig. 5a). Vulnerability of branch xylem was similar in all treatments as reflected in the similarity of their fitting parameter in Eqn 5 ($P > 0.4$; average $c = 3.5$ and $d = 6.8$, and 50% loss of conductivity occurring at an average $\Psi = -3.5$ MPa). For roots collected in C, the vulnerability of fine roots collected at 1.9 m depth was similar to that of roots collected near the surface, as reflected in the similarity of their fitting parameters ($P > 0.4$). In roots collected near the soil surface, the parameter c was significantly higher in F than in the other treatments ($P < 0.001$; 1.8 and 1.2, respectively), reflecting a steeper slope to the vulnerability curve. The value of the parameter d was similar in all treatments ($P > 0.2$), averaging 1.8. The Ψ for 50% loss of conductivity was lower in F than the other treatments ($P < 0.01$; -1.25 and -1.0 MPa, respectively).

The hydraulic conductivity (k_h) of root xylem was highly variable within each treatment (0.2–1.7 mmol m s^{-1} MPa^{-1}). In order to test the hypothesis that vulnerability to cavitation is related to maximum hydraulic conductivity, we normalized k_h of each root by its cross-sectional area to estimate specific conductivity (k_h/A_S, Tyree & Ewers 1991). We then related maximum k_h/A_S, obtained at $\Psi = 0$ (k_{smax}), to the root's vulnerability of k_h/A_S to decreasing Ψ in the range of 0.5–3.0 MPa. The slope of the relationship between k_h/A_S and Ψ in the selected range was linearized by natural logarithm transformation of Ψ and resulted in a good fit (r^2 ranging from 0.89 to 0.99). We tested the hypothesis by regressing the vulnerability to cavitation of roots (dk_s/dlnΨ) against their k_{smax}. All treatments showed the same relationship between dk_s/dlnΨ and k_{smax} ($P > 0.7$), with F showing lower k_{smax} and a proportionally lower dk_s/dlnΨ ($P < 0.01$; Fig. 5b & Table 1).
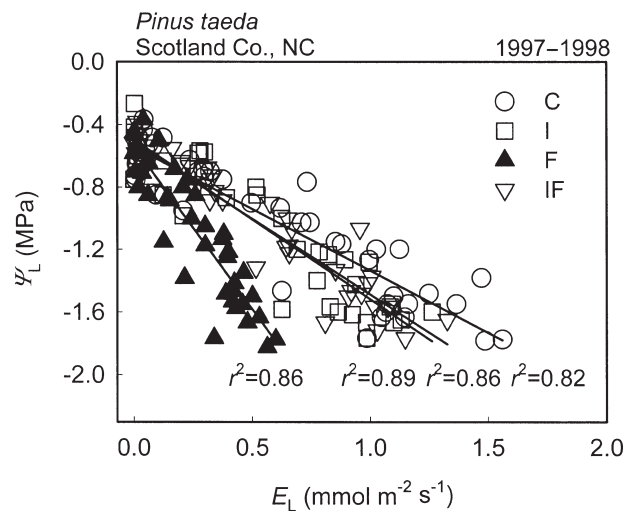

Figure 4. Leaf water potential (Ψ_L) versus transpiration per unit leaf area (E_L) for control, irrigated, fertilized, and irrigated/fertilized (C, I, F, and IF, respectively).

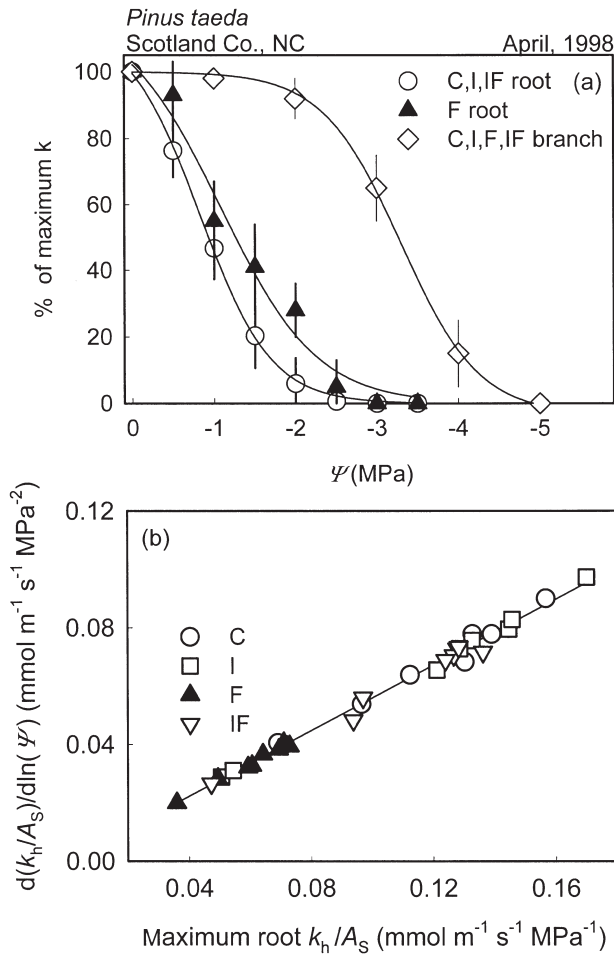**Figure 5.** (a) Vulnerability curves showing the percentage loss of hydraulic conductivity in the xylem (k) versus xylem water potential (Ψ) in the control, irrigated, fertilized, and irrigated/fertilized (C, I, F, and IF, respectively) roots and branches. Bars are 1 SE of the mean ($n = 8$ for roots, $n = 4$ for branches). (b) The slope of the relationship between root specific conductivity (k_h/A_S) and the natural logarithm of Ψ relationship from the vulnerability curves of individual roots versus the maximum k_h/A_S. Roots of F (closed symbols) were significantly different from roots of other treatments ($P < 0.01$).

Both tracheid diameter distribution, and mean hydraulic tracheid diameters in root xylem were similar in all treatments ($P > 0.2$ and 0.4, respectively). The hydraulic mean diameter was 62.8 ± 4.5 μm.

Root-to-leaf area ratio and root distribution

Both water and nutrient addition caused $A_R:A_L$ to decrease from its value of 9.8 in control trees (Table 1). Nutrient addition had the most significant effect, causing an over 50% reduction in $A_R:A_L$ relative to controls. The lowest $A_R:A_L$ was 3.9 in IF trees. Reduction in $A_R:A_L$ was primarily accounted for by the large increase in A_L with improved nutrition, accompanied with a small reduction in A_R in shallow soil layers (< 0.4 m) rather than a reduction

in root density at depth (B. E. Ewers *et al.* unpublished results).

Model analysis of water extraction potential

We used the model (Sperry *et al.* 1998) to compare the water extraction potential across treatments based on $A_R:A_L$ data and vulnerability curves. We plotted E_{Lcrit} as a function of Ψ_{SR} for each treatment (Fig. 6, dashed lines). In these simulations, bulk Ψ_S was assumed uniform throughout the soil profile to facilitate comparison between treatments. The dashed lines in Fig. 6 define the maximum extraction of water the trees can achieve from a uniformly drying soil. The y intercept of the line is proportional to the maximum K_L and is thus similar in all but the F treatment where it is lower. The reduction in E_{Lcrit} with Ψ_{SR} is greater for lower $A_R:A_L$ and more vulnerable xylem. As hypothesized, the E_{Lcrit} 'envelope' was widest in C and I (with higher $A_R:A_L$), but more restricted in F and especially IF (with lower $A_R:A_L$).

The E_L data for days with $D > 1.5$ kPa (to show maximum E_L) are also shown in Fig. 6 (symbols) to allow comparison of approximate safety margins from hydraulic failure across treatments. Safety margins are approximate because the data were obtained for generally non-uniform Ψ_S profiles whereas E_{Lcrit} was estimated for uniform Ψ_S. The comparison suggests that all treatments approached hydraulic failure as Ψ_{SR} dropped. The smallest safety margins occurred in the fertilized treatments that also had the most restrictive E_{Lcrit} limits. The rather modest influence of irrigation treatments on Ψ_{SR} is evident. The largest irrigation effect was within the fertilized treatments where irrigation kept minimum Ψ_{SR} above -0.3 MPa in IF versus -0.5 MPa in F trees. The combination of low $A_R:A_L$ and low Ψ_{SR} in the F treatment resulted in E_L of these trees converging on E_{Lcrit} under water stressed conditions (Fig. 6c).

The influence of $A_R:A_L$ on water extraction potential is summarized in Fig. 1 where the area under the E_{Lcrit} versus Ψ_{SR} envelope (extraction potential) is shown versus $A_R:A_L$. As $A_R:A_L$ increases, so does extraction, approaching a maximum value at high $A_R:A_L$. The shape of the extraction curve depends on soil type and cavitation resistance. Because all treatments were in the same soil, only two curves were needed to represent the treatments because only the F trees had distinctive (more resistant) cavitation resistance. The greater cavitation resistance in F trees (Fig. 5) enhanced extraction at a given $A_R:A_L$ (Fig. 1, compare dashed versus solid curve).

The extraction at the treatment $A_R:A_L$ is indicated by symbols on the curves. Interestingly, despite the more than 50% reduction in $A_R:A_L$ in F versus C trees (Table 1), extraction decreased only to 0.77 from 0.86 of maximum, respectively. This relatively slight decrease in extraction was because the increase in cavitation resistance offset the effect of lower $A_R:A_L$. In comparison, IF trees had the lowest $A_R:A_L$ of all treatments (Table 1) and showed no increase in cavitation resistance (Fig. 5). As a result, relative extraction was only 0.64 compared with 0.77 in IF
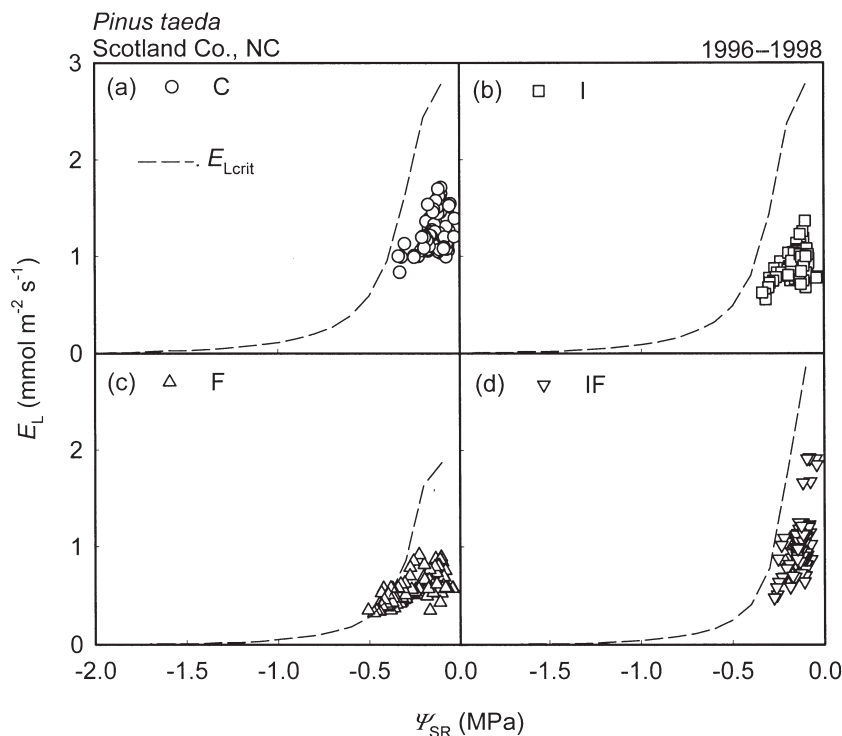
Figure 6. Transpiration per unit leaf area (E_L) versus soil water potential weighted by root area (Ψ_{SR}) in trees of control, irrigated, fertilized, and irrigated/fertilized (C, I, F, and IF, respectively). The dashed line is the predicted critical value of E_L (E_{Lcrit}) before catastrophic hydraulic failure.

versus F, respectively (Fig. 1). Low extraction potential from drying soil was not as consequential for IF trees where irrigation kept Ψ_{SR} higher than in F (Fig. 6).

DISCUSSION

Our results add to a growing body of work emphasizing the need to study whole-plant gas exchange in the context of the underlying hydraulic architecture (Tyree & Ewers 1991). Responses of gas exchange to light environment (Whitehead *et al.* 1996; Maherali, DeLucia & Sipe 1997), developmental changes (Meinzer & Grantz 1990; Mencuccini & Grace 1996), drought (Cochard, Breda & Granier 1995), defoliation (Pataki, Oren & Philips 1998), root–shoot ratio (Teskey, Hinckley & Grier 1983; Meinzer & Grantz 1990), and D (Meinzer *et al.* 1997) are influenced to a large extent by adjustments in the water supply to the canopy. The novelty in our study is its analysis of the interaction between nutrient versus water supply on architectural and stomatal parameters. Our results indicated that changes in G_S, stomatal sensitivity to D, and water extraction in response to nutrient and water amendments are underlain by changes in A_R:A_L, cavitation resistance, and specific conductivity.

The 50% reduction in G_{Sref} in F compared with the other treatments was a result of architectural changes (a 50% decrease in K_L) rather than a direct response to soil or plant water potential. This confirms our first hypothesis, and it substantiates the conjecture originating during an earlier study at this site, namely that E_L was lower in F because treatment effects reduced G_S and K_L (Ewers *et al.* 1999).

However, the explanation for lower G_S and K_L in F hypothesized in Ewers *et al.* (1999), that nutrient amendment without water irrigation reduced fine root area and depth, is incorrect because F and IF treatments had similar A_R:A_L (Table 1) and root distributions (B. E. Ewers *et al.* unpublished results). Instead, as proposed in our second hypothesis, the lower K_L was attributable to a lower specific hydraulic conductance and A_S:A_L in F versus IF trees. In contrast, IF trees maintained K_L despite increases in height and leaf area by increases in A_S:A_L and apparent specific conductivity relative to unfertilized trees.

The reduction in apparent specific conductivity in F versus other treatments was reflected in the much lower specific conductivity of the root xylem in this treatment (k_h/A_S, Table 1). This was not associated with any difference in tracheid diameter. It may have resulted from different pit membrane structure, shorter tracheid length, or a greater amount of irreversible embolism in F roots. Although all roots were flushed to reverse embolism prior to the k_h/A_S measurement, some tracheids may be sealed off permanently and resist refilling (Sperry & Tyree 1990). In contrast to the F trees, the greater apparent specific conductivity in IF trees was not associated with a higher specific conductivity of the root xylem.

Interestingly, increased resistance to xylem cavitation in F roots versus other treatments also accompanied their lower k_h/A_S (Fig. 5). The phenomenon of a decrease in k_h/A_S accompanying the decrease in vulnerability to cavitation was general across treatments, but the mean and variation in k_h/A_S were lower in fine roots in F (Fig. 5 & Table 1). However, given the distributions in k_h/A_S and vul-

nerability found in the four treatments, it is unclear whether we observe in F a population of roots born with low vulnerability, or the portion of a population, one with originally a wide range in vulnerability, that survived periods of water stress. A comparison between *P. taeda* on sand versus loam soils showed large differences in cavitation resistance, but no difference in specific conductivity (Hacke *et al.* 2000). Comparisons across conifer species can also show no correspondence between cavitation resistance and specific conductivity (Cochard 1992). A study with hybrid poplar showed an increase in cavitation resistance with P fertilization, but a decrease with N (Harvey & van den Driessche 1997). In contrast, we only saw an effect of fertilization (N and P) in combination with drought.

Consistent with our third hypothesis, stomatal sensitivity to D was proportional to maximum stomatal conductance and was less for F versus other trees. There was no difference between the theoretical proportionality of G_{Sref} and $dG_S/dlnD$ expected for constant Ψ_L regulation in response to D (~ 0·6, Oren *et al.* 1999) and the proportionality found in I, F, and IF. The lower than expected sensitivity of C trees (Fig. 2b) may reflect less tight Ψ_L regulation with D, but we have no evidence to bear on this. Interestingly, Meinzer *et al.* (1997) found that variation in stomatal response to D between species of tropical trees was eliminated when results were normalized for $A_S:A_L$, suggesting a similar dependence of stomatal sensitivity to D on underlying hydraulic architecture.

The approximate halving of $A_R:A_L$ in response to fertilization (Table 1) had the result of reducing the potential for water uptake during soil drought as expected from our fourth and final hypothesis (Figs 1 & 6). The model predicted that if irrigation were to be withheld from IF trees, a drop in Ψ_{SR} by 0·1 MPa or more would require extreme stomatal closure to avoid hydraulic failure. Although the F trees had similarly low $A_R:A_L$ as IF trees, they were not as restricted in their water uptake under drought because of their more cavitation-resistant root xylem (Fig. 6, compare dashed lines in c versus d). The relatively low Ψ_{SR} experienced by F trees resulted in the lowest E_L measured in any treatment, and the convergence of E_L on E_{Lcrit} during drought (Fig. 6c).

Water uptake in all four treatments was restricted to relatively high Ψ_{SR} (Fig. 6) because of the sharp decline in sand conductivity with matric potential. This constraint imposed by sand is presumably an important reason for the very deep root systems seen in all treatments. Deep roots insure that at least a portion of the root system will remain in soil with water potential above – 0·4 MPa, thus allowing significant water uptake. *P. taeda* of similar genotype and age growing on loam soil exhibited a much broader range of Ψ_S for water uptake and much shallower root systems (Hacke *et al.* 2000). In this finer soil, a much lower $A_R:A_L$ is required to maximize extraction potential as shown in Fig. 1 (dotted line). The $A_R:A_L$ at this site was 1·68, or less than half that of the lowest $A_R:A_L$ of the fertilized sand trees.

Although we do not know the cause and effect leading to the observed architectural and water use adjustments in F versus IF trees, we offer the following sequence of events as a working hypothesis that is consistent with the results. Application of nutrients bolstered shoot growth at the expense of root growth leading to a drop in $A_R:A_L$. However, the decrease in $A_R:A_L$ combined with the sand soil required a more abrupt reduction in G_S during even moderate drought to avoid hydraulic failure and to maintain the isohydric Ψ_L regulation characteristic of the species. As a result of irrigation, the IF trees escaped the Ψ_S minima that induced major stomatal closure and/or loss of hydraulic conductance in F trees. The chronic stress in F trees resulted in lower hydraulic conductance not only because of partial cavitation, but also because of the production of more cavitation-resistant xylem with lower conducting efficiency. Up to a point, the more cavitation-resistant xylem provides the same benefit for improved extraction as an increase in $A_R:A_L$, and allows F trees to extract moisture to a lower Ψ_S.

Even with the production of more cavitation-resistant xylem, the reduction in $A_R:A_L$ induced in both fertilized treatments increases the probability of hydraulic failure as soil dries. This may cause a catastrophic cavitation event followed by a loss of fine roots and perhaps branches, and ultimately a lower carbon uptake. Indeed, during a severe drought, trees in fertilized stands of *Pinus radiata* lost leaf area, and even died, while adjacent unfertilized stands escaped with little effect (Linder *et al.* 1987). It is likely that if irrigation water is withheld, IF trees would suffer leaf and root dieback, with surviving plants producing less vulnerable roots as in the F treatment. We conclude that the tendency for nutrient addition to reduce $A_R:A_L$ in nutrient poor sand soils makes these trees more vulnerable to dieback during a drought episode.

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