Adjustment of tree structure in response to the environment under hydraulic constraints

F. MAGNANI*†, J. GRACE‡ and M. BORGHETTI§

CNR-IMGPF, via A. Vannucci 13, I-50134 Firenze, Italy, ‡IERM, University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh EH9 3JU, UK, and §DPV, Università della Basilicata, Contrada Macchia Romana, I-85100 Potenza, Italy

Summary

1. The hypothesis is tested that functional limitations, possibly related to the risk of disruptive xylem embolism, maintain the leaf water potential of trees within a safety range. This strategy would particularly apply to conifers.

2. It is also hypothesized that homeostasis in water transport is achieved by a combination of short-term stomatal regulation and the optimal allocation of resources between transpiring foliage, conductive sapwood and absorbing roots.

3. The implications of this hypothesis for responses of plant structure to the environment are explored from a theoretical viewpoint, focusing in particular on the effects of temperature, vapour pressure deficit and soil water availability and texture.

4. A comparison with published data sets confirms model predictions of greater allocation to transpiring foliage with increasing temperature, and lower allocation with increasing vapour pressure deficit and soil drought. Allocation to fine roots would respond more strongly to drought, and the effect would be magnified by coarse soil textures.

5. The applicability of the model to other taxa remains to be determined, and the extent to which the observed structural adjustment is the result of phenotypic plasticity or long-term adaptation is still unclear.

Key-words: climate, homeostasis, hydraulic architecture, *Pinus*, water potential

Functional Ecology (2002) **16**, 385–393

Introduction

Significant progress has been made in understanding how gas exchange and gross primary production of trees are affected by a variety of factors. In comparison, the allocation of growth among tree organs is poorly understood; a general lack of basic knowledge on complex topics such as phloem loading, transport and unloading (Patrick 1997; Van Bel 1993) prevents the translation of knowledge into simple operational models.

Many studies on the environmental control of allocation in trees have focused on the final effect of the process – the resulting changes in allometric balance among tree parts (Cannell & Dewar 1994; Gower, Isebrands & Sheriff 1995). Plant structure is affected by a variety of environmental factors. Temperature, for example, alters the balance between foliage and fine roots (Wilson 1988); fine root production is also enhanced by high light and nutrient deprivation, such that the functional balance between carbon and nutrient acquisition is maintained and tissue nutrient concentration is kept near constant (Dewar, Ludlow & Dougherty 1994; Santantonio 1990). The same homeostatic principle could drive the response of root–shoot ratios to soil drought (Cannell & Dewar 1994), which often increases resource allocation to absorbing roots (Gower *et al*. 1995). A homeostasis in water transport underlies the models of Whitehead *et al*. (1984) and Givnish (1986). Whitehead *et al*. (1984) argued that a balance exists between the area of transpiring foliage, sapwood conducting area, tree height and humidity of soil and in the air. Givnish (1986) also predicted that growth will be maximized when the balance between foliage and conducting roots is tuned to the atmospheric environment, because of the detrimental effects of extreme water potentials on leaf gas exchange. However, both hypotheses focused on only one component of the plant hydraulic continuum, the sapwood or fine roots.

Recently we have combined these two approaches in a mathematical model of resource allocation and growth in coniferous trees (Magnani, Mencuccini & Grace 2000). The analysis is based on the hypothesis of optimal growth and homeostasis in water transport:

†Author to whom correspondence should be addressed. E-mail: federico@imgpf.fi.cnr.it

Table 1. Variables, parameters and units used in the model

Variable	Definition	Units
A_s	Sapwood area (on a ground area basis)	$m^2\ m^{-2}$
D	Vapour pressure deficit	Pa
D_0	Empirical coefficient for response to D	Pa
E_f	Transpiration per unit foliage area	$m^3\ m^{-2}\ s^{-1}$
f	Reduction factor (subscript: D, for vapour pressure deficit; Ψ, for soil water potential)	–
g_s	Stomatal conductance (superscript: max, maximum)	$m\ s^{-1}$
h	Tree height	m
l	Tissue longevity (subscript: r, fine root; s, sapwood)	year
L	Fine root density	$m\ m^{-3}$
r	Fine root radius	m
r_r	Root resistivity per unit fine root biomass	$MPa\ s\ kg\ m^{-3}$
r_s	Sapwood resistivity	$MPa\ s\ m^{-2}$
r_{soil}	Soil resistivity (superscript: sat, saturated)	$MPa\ s\ m^{-2}$
r_{soil}	Soil resistivity per unit fine root biomass	$MPa\ s\ kg\ m^{-3}$
R	Hydraulic resistance (superscript: f, per unit projected leaf area; g, per unit ground area; subscript: root, shoot, soil, total)	$MPa\ s\ m^{-1}$
T	Temperature	°C
W	Stand biomass (subscript: f, foliage; r, fine roots; s, sapwood)	$kg\ m^{-2}$
z	Rooting depth	m
η	Viscosity of water	MPa s
ρ	Density (subscript: s, sapwood; r, root)	$kg\ m^{-3}$
σ	Specific leaf area	$m^2\ kg^{-1}$
Ψ	Water potential (subscript: e, entry, leaf, foliage, soil)	MPa
Ψ_0	Ψ at complete stomatal closure	MPa
$\overline{\Psi}$	Critical leaf water potential	MPa

the assumption is made that minimum water potentials are constrained, possibly by the risk of destructive xylem embolism (Tyree & Sperry 1988), and that foliage production and tree growth are maximized within the limits imposed by this constraint. Using this approach, model predictions of plant structure and its changes over the lifetime of the tree have been compared with available experimental evidence for *Pinus sylvestris* in natural conditions (Magnani *et al.* 2000). The present paper explores the implications of this hypothesis for the response of tree structure and growth to the environment.

Theory and methods

OPTIMAL TREE STRUCTURE UNDER HYDRAULIC CONSTRAINTS

The link between plant design and tissue water relations can be explored by means of a simple model. All parameters and variables are defined in Table 1. Let E_f be the transpiration rate of a unit of leaf surface in the stand. If Ψ_{leaf} is the resulting leaf water potential, and (for simplicity) neglecting the effects of tree height on gravitational potential, we can then define the hydraulic resistance per unit foliage area across the soil–plant continuum (R_{tot}^f) as:

$$R_{tot}^f = \frac{\Psi_{soil} - \Psi_{leaf}}{E_f} \qquad \text{eqn 1a}$$

where Ψ_{soil} is soil water potential. Leaf-specific resistance can be scaled to the stand level as:

$$R_{tot}^f = W_f \cdot \sigma \cdot R_{tot}^g \qquad \text{eqn 1b}$$

where W_f is stand foliage biomass, σ is specific leaf area and R_{tot}^g is stand hydraulic resistance on a ground area basis, which can be viewed as the sum in a series of three distinct components located in the shoot, fine roots and soil, respectively.

Shoot hydraulic resistance (R_{shoot}^g) is affected by the length of the hydraulic pathway, related to tree height h, and by the cross-sectional area A_s of conducting sapwood, again expressed on a ground area basis (Whitehead *et al.* 1984):

$$R_{shoot}^g = \frac{r_s \cdot h}{A_s} = \frac{r_s \cdot h^2 \cdot \rho_s}{W_s} \qquad \text{eqn 2}$$

where r_s is sapwood resistivity and W_s and ρ_s are sapwood biomass and density, respectively. According to the pipe model theory (Shinozaki *et al.* 1964), a constant sapwood cross-sectional area has been assumed in equation 2 throughout the plant, once axes of the same branching order are summed together.

Root hydraulic resistance (R_{root}^g) is mainly associated with the movement of water from the epidermis to the stele (Passioura 1988); it is therefore inversely related to the surface of fine roots and, approximately, to fine root biomass W_r:

$$R_{root}^g = \frac{r_r}{W_r} \qquad \text{eqn 3}$$

where r_r is resistivity per unit root biomass.

Soil hydraulic resistance (R_{soil}^g) is also influenced by the biomass of fine roots exploring the soil. From

single root theory, R_{soil}^g can be approximated as (Passioura & Cowan 1968):

$$R_{soil}^g = \frac{-\ln(\pi \cdot r^2 \cdot L)}{4 \cdot \pi \cdot L \cdot z} \cdot r_{soil} = \frac{r_{soil}^r}{W_r} \qquad \text{eqn 4}$$

where r is root radius, L is fine root density in the soil, z is rooting depth and r_{soil} is soil hydraulic resistivity. Rooting depth is assumed to increase with fine root biomass, implying a constant fine root density throughout the soil. Soil resistivity per unit root biomass (r_{soil}^r) is therefore defined as:

$$r_{soil}^r = -\frac{1}{4} \cdot \ln(\pi \cdot r^2 \cdot L) \cdot r^2 \cdot \rho_r \cdot r_{soil} \qquad \text{eqn 5}$$

where ρ_r is the basal density of fine roots and is assumed to be equal to sapwood density.

Soil hydraulic resistivity is a direct function of soil water potential and can be expressed as (Campbell 1985):

$$r_{soil} = r_{soil}^{sat} \cdot \left(\frac{\Psi_{soil}}{\Psi_e} \right)^{2+3/b} \qquad \text{eqn 6}$$

where the resistivity of saturated soil (r_{soil}^{sat}), soil entry potential (Ψ_e) and the empirical coefficient b are all functions of soil texture. Tabulated values of soil hydraulic parameters for key textural types, computed according to Campbell (1985) can be found in Sperry *et al.* (1998). Soil saturated resistivity is lower in coarse soils. At the same time, the coarser the soil, the steeper the increase in soil resistivity with decreasing water potentials.

Experimental evidence (reviewed for *P. sylvestris* in the Results section) suggests that under natural conditions, leaf water potential does not usually exceed a critical value $\overline{\psi}$, which could be dictated in coniferous species by the risk of diffuse xylem embolism and tissue dieback (Tyree & Sperry 1988). The maintenance of such a functional homeostasis imposes a tight constraint on plant structure, as it requires from equations 1–4 that hydraulic resistances conform to:

$$R_{tot}^f = W_f \cdot \sigma \cdot \left(\frac{r_r + r_{soil}^r}{W_r} + \frac{h^2 \cdot \rho_s \cdot r_s}{W_s} \right) \leq \frac{\Psi_{soil} - \overline{\psi}}{E_f} \qquad \text{eqn 7}$$

Equation 7 is fully equivalent to the model of Whitehead *et al.* (1984) when the role of roots is disregarded (when $r^r = r_{soil}^r = 0$) and to the model presented by Givnish (1986) when, in contrast, stem hydraulic resistance is neglected (when $r_s = 0$).

The functional requirements of equation 7 could not be met unless new foliage growth was always supported by an adequate quantity of sapwood and fine roots. Moreover, the reduction in hydraulic resistance needed to sustain new foliage will be achieved at minimum cost, in order to reserve as many resources as possible for foliage growth and so maximize plant height increments and, ultimately, tree survival and fitness. In particular, optimal growth under hydraulic

constraints requires that the ratio of marginal hydraulic returns to marginal annual cost for carbon investment in either roots or sapwood, once discounted for tissue turnover, should be the same (Case & Fair 1989):

$$\frac{\partial R_{tot}^g}{\partial W_r} \bigg/ \frac{1}{l_r} = \frac{\partial R_{tot}^g}{\partial W_s} \bigg/ \frac{1}{l_s} \qquad \text{eqn 8}$$

where l_r and l_s are fine root and sapwood longevity, respectively. From equations 2 and 3, this corresponds to (Magnani *et al.* 2000):

$$\frac{r_r + r_{soil}^r}{W_r^2} \cdot \frac{W_s^2}{h^2 \cdot \rho_s \cdot r_s} = \frac{l_s}{l_r} \qquad \text{eqn 9}$$

After rearranging, the balance between sapwood area and fine root biomass is predicted to be:

$$\frac{A_s}{W_r} = \frac{c}{\rho_s} \qquad \text{eqn 10}$$

where the coefficient c is a function of tissue characteristics and soil hydraulic resistivity:

$$c = \sqrt{\frac{r_s}{r_r + r_{soil}^r} \cdot \frac{l_s}{l_r} \cdot \rho_s} \qquad \text{eqn 11}$$

The balance between sapwood area and fine root biomass will therefore depend on soil textural characteristics, and will in general shift towards larger root biomass under dry conditions.

When combined with the general requirement of functional homeostasis of equation 7, equation 10 translates into hydraulic constraints, representing the optimal balance between transpiring foliage and conductive tissues under given environmental conditions:

$$\frac{W_f}{W_r} = \frac{R_{tot}^f}{\sigma \cdot (r_r + r_{soil}^r)} \cdot \left(1 + h \cdot c \cdot \frac{l_r}{l_s} \right)^{-1} \qquad \text{eqn 12}$$

$$\frac{W_f}{A_s} = \frac{R_{tot}^f}{\sigma \cdot r_s} \cdot \left(h + \frac{l_s}{c \cdot l_r} \right)^{-1} \qquad \text{eqn 13}$$

The allometric balance between W_f and A_s, W_r can be seen to depend on tree height, less carbon being allocated to foliage as the stand ages, as discussed in detail by Magnani *et al.* (2000) who give a more detailed description of the mathematical development of equations 9–13.

The basic constraints captured by equations 10–13 are not altered qualitatively by including the effects of height and gravitational potential, which are equivalent to a change in critical water potential, $\overline{\psi}$ in equation 7.

FUNCTIONAL AND STRUCTURAL RESPONSE TO KEY ENVIRONMENTAL PARAMETERS

The effects of temperature, air humidity and soil water potential on plant function and structural design are considered here. Low temperatures dramatically increase the hydraulic resistance of the soil–plant continuum (Cochard *et al.* 2000). In the case of sapwood resistance the effect is purely physical, and is
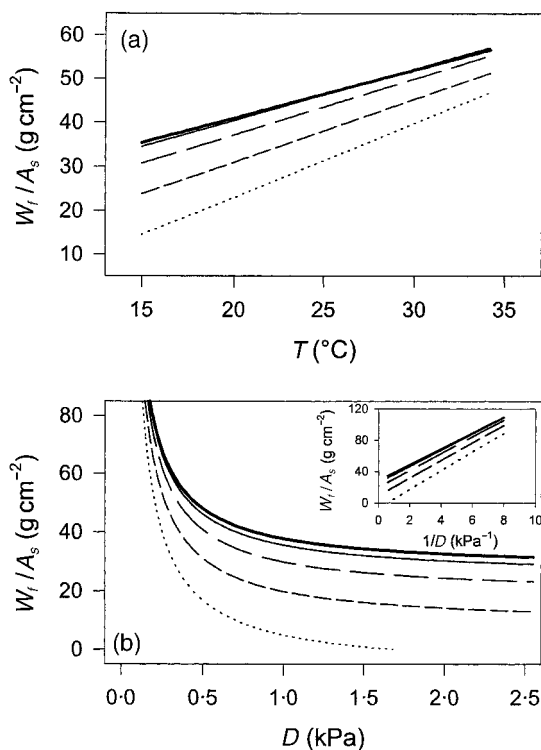
Fig. 1. Response of plant structure to temperature and humidity. Simulated response to (a) temperature (T) and (b) air vapour pressure deficit (D) of foliage biomass : sapwood area ratio (W_f/A_s), as affected by soil water potential (thick line, -0.1; thin line, -0.2; long dashes, -0.3; short dashes, -0.4; dotted line, -0.5 MPa). The curvilinear response to vapour pressure deficit is equivalent to a linear response to $1/D$ (inset). Sensitivity to both environmental factors increases under conditions of low water availability. A vapour pressure deficit of 1.5 kPa and a temperature of $15\,°C$ were assumed, respectively, in the two simulations. Sand and clay fractions were 0.4 and 0.1, respectively.

determined by the response to temperature of water viscosity, η. The relationship can be represented as:

$$r_s \propto \eta = \frac{1}{a_1 + a_2 \cdot T} \qquad \text{eqn 14}$$

where T is temperature and a_1 and a_2 are empirical parameters (with $R^2 = 0.998$ in the range 0–40 °C; Douglas, Gasiorek & Swaffield 1985). From equation 13, foliage biomass per unit sapwood area should increase linearly with temperature (Fig. 1a):

$$\frac{W_f}{A_s} \propto \frac{1}{\eta} = a_1 + a_2 \cdot T \qquad \text{eqn 15}$$

Root resistance responds even more dramatically to low temperatures, as a result of the reduced fluidity of plasma membranes that water has to cross at the level of the endodermis. This is demonstrated by a re-analysis of root hydraulic conductance (= $1/R_{root}$) data for a coniferous, two dicot and two monocot species (BassiriRad, Radin & Matsuda 1991; Fennell & Markhart 1998; Markhart *et al.* 1979; Smit-Spinks, Swanson & Markhart 1984; Fig. 2). The foliage : fine root biomass ratio is expected in the model to follow
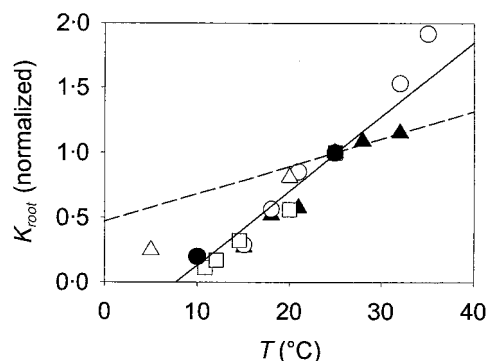
Fig. 2. Response of root hydraulic conductance ($K_{root} = 1/R_{root}$) to temperature. Data for *Hordeum vulgare* (▲) and *Sorghum bicolor* (○, BassiriRad *et al.* 1991); *Glycine max* (□, Markhart *et al.* 1979); *Spinacia oleracea* (△, Fennell & Markhart 1998); *Pinus sylvestris* (●, Smit-Spinks *et al.* 1984), once normalized to 25 °C, fall onto a single line (solid line, $R^2 = 0.89$). The response that would be expected from changes in water viscosity alone is also drawn for a comparison (dotted line).

the same relationship. Moreover, in order to compensate their greater sensitivity to cold conditions, fine roots are expected to be favoured against sapwood area at low temperatures (equation 10).

The expected impact on plant structure of air humidity and soil water depends upon the response of transpiration to the plant's environment. Leaf transpiration can be approximated in conifers by imposed transpiration, the product of stomatal conductance (g_s) by air vapour pressure deficit (Whitehead *et al.* 1984). Air and soil humidity limitations reduce stomatal conductance below its maximum value g_s^{max}:

$$g_s = g_s^{max} \cdot f_D \cdot f_\psi \qquad \text{eqn 16}$$

where the modifiers f_D and f_ψ range in value between 0 and 1, and represent the effects of air vapour pressure deficit and soil water potential, respectively. According to Lohammar *et al.* (1980), the reduction induced by air vapour pressure deficit can be expressed as:

$$f_D = \frac{D_0}{D + D_0} \qquad \text{eqn 17}$$

where D is air vapour pressure deficit and D_0 is the value inducing a 50% stomatal closure. The response to soil water potential can be approximated by a simple linear function (Jones 1992):

$$f_\psi = 1 - \frac{\Psi_{soil}}{\Psi_0} \qquad \text{eqn 18}$$

where Ψ_0 represents the soil water potential corresponding to complete stomatal closure. Therefore, leaf transpiration can be represented as:

$$E_f \approx g_s \cdot D = g_s^{max} \cdot \frac{\Psi_0 - \Psi_{soil}}{\Psi_0} \cdot \frac{D_0 \cdot D}{D_0 + D} \qquad \text{eqn 19}$$

From equation 7, the hydraulic resistance per unit foliage area that can be safely maintained will decrease

asymptotically as D increases, mirroring the response of transpiration captured by equation 19. This constraint will cause a parallel decline in the biomass of foliage supported by unit sapwood area (Fig. 1b):

$$\frac{W_f}{A_s} \propto R_{tot}^f \propto \frac{D_0 + D}{D_0 \cdot D} = \frac{1}{D} + \frac{1}{D_0} \qquad \text{eqn 20}$$

From equation 10, the balance between foliage and absorbing roots is expected to respond in a similar way to T and D.

In response to soil drought, stomatal closure effectively prevents the onset of extreme leaf water potentials, despite the marked increase in soil–plant hydraulic resistance that is often reported (Breda *et al*. 1993; Irvine *et al*. 1998). From equations 7 and 19, the maximum resistance that can be withstood by the plant under hydraulic constraints can be expressed as:

$$R_{tot}^f = \frac{\Psi_{soil} - \overline{\Psi}}{E_f} \propto \frac{\Psi_{soil} - \overline{\Psi}}{\Psi_{soil} - \Psi_0} = 1 + \frac{\Psi_0 - \overline{\Psi}}{\Psi_{soil} - \Psi_0} \quad \text{eqn 21}$$

If $\overline{\Psi}$ is more negative than Ψ_0, stomata will shut completely and R_{tot}^f will therefore increase in dry soil without triggering substantial xylem cavitation (Fig. 3a), in good agreement with experimental evidence (Irvine *et al*. 1998). However, because of the parallel increase in soil hydraulic resistivity (equation 6; Fig. 3a), plant resistance per unit foliage area must be reduced if the hydraulic constraints are to be met. This will shift resources from foliage to conductive tissues under dry conditions, which will be more marked in coarse soils (Fig. 3b,c). Because of the parallel changes in the balance between sapwood and fine roots (equation 10), drought will increase allocation to fine roots (Fig. 3b), as often reported under field conditions.

TEST OF THE MODEL

The relationship between plant structure and environmental factors has been tested by comparison with published data sets. The effects of air vapour pressure deficit have been analysed in detail by DeLucia *et al*. (2000), and their results have been complemented by the meta-analysis of available information for *P. sylvestris* by Mencuccini & Bonosi (2001). The effects of temperature on the structure of pine species have been analysed by Palmroth *et al*. (1999), Cregg (1994) and Bongarten & Teskey (1987). The model has been fitted by nonlinear regression techniques (NLIN procedure, SAS 8·2, SAS Institute Inc., Cary, NC) on each data set, focusing on individual parameters in isolation.

Results and discussion

### THE HYPOTHESIS OF HOMEOSTASIS IN PLANT WATER RELATIONS

A review of 11 published data sets for *P. sylvestris* (Magnani 2000), encompassing a large range of conditions and including both seedlings and mature trees, confirms that minimum leaf water potential is maintained largely constant despite large ontogenetic and environmental differences ($\overline{\Psi} = -1\cdot4 \pm 0\cdot2$ MPa, $n = 16$), as assumed in equation 7. This contrasts with the more than threefold variation observed in R_{tot}^f in the same data set, between $1\cdot6$ and $4\cdot9 \times 10^7$ MPa s m^{-1}.

Tyree & Sperry (1988) suggested that minimum leaf water potentials under field conditions closely match the critical threshold for xylem cavitation. A meta-analysis of six data sets of xylem vulnerability in *P. sylvestris* is consistent with this view (Magnani 2000), suggesting a mean water potential threshold of $-1\cdot54$ MPa, although the scatter in the results is large (SD = $0\cdot3$ MPa).

Extensive xylem embolism is uncommon in *P. sylvestris* (Irvine *et al*. 1998; Waring, Whitehead & Jarvis 1979) and other coniferous species under natural conditions, in contrast with co-occurring broadleaf species (Cinnirella *et al*. 2002; Panek & Waring 1995; Sperry & Sullivan 1992; Sperry *et al*. 1994). However, reports are inconsistent. Waring & Running (1978), for example, reported xylem water content in old-growth *Pseudotsuga menziesii* down to about 50%, and highly variable over the year. Substantial embolism has also been observed in droughted *Pinus halepensis* trees (Borghetti *et al*. 1998).
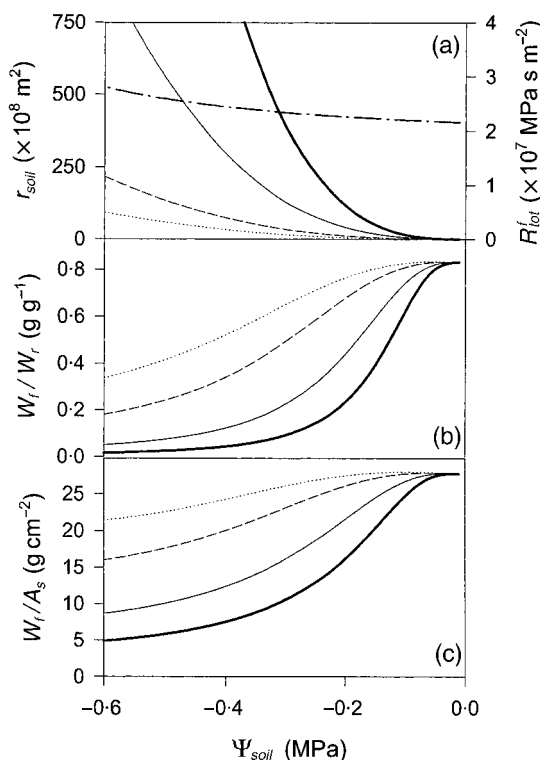
Fig. 3. Response of plant structure to soil water potential. (a) Simulated response to soil water potential Ψ_{soil} of total resistance per unit foliage area (R_{tot}^f; dot-dashed line) and soil resistivity (r_{soil}) at a temperature of 20 °C for a sand fraction ranging from 0·9 (solid line) to 0·4 (dotted line), assuming a constant clay fraction of 0·1. Predicted response to Ψ_{soil} of (b) foliage : fine root biomass ratio (W_f/W_r) and (c) foliage biomass : sapwood area ratio (W_f/A_s) for the same range of soil textures, assuming a vapour pressure deficit of 1·5 kPa.
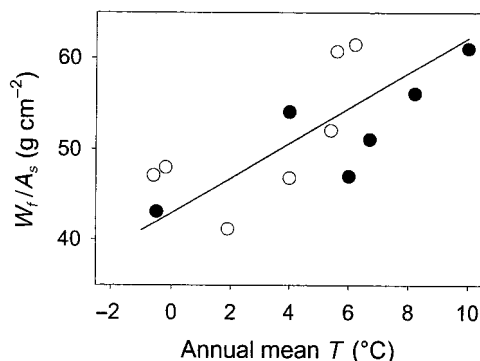
Fig. 4. Temperature effects on the ratio of foliage biomass to sapwood area (W_f/A_s) in *Pinus sylvestris* mature trees (Palmroth *et al*. 1999). Observed temperature effects along a European latitudinal transect (●) correspond to results from a provenance trial (○), referred to annual mean temperature at the site of origin. The variation in both data sets is well explained by the response of water fluidity (= $1/\eta$) to temperature (solid line; $R^2 = 0.52$, $P < 0.001$), as predicted by the model (equation 15; Fig. 1a).

Fig. 5. Temperature effects on the ratio of foliage to fine root biomass (W_f/W_r) in *Pinus ponderosa* (●; Cregg 1994) and *Pinus taeda* (○; Bongarten & Teskey 1987) seedlings from diverse geographic origins growing under constant conditions. Allometric data are referred to the mean temperature over the vegetation period at the site of origin. In both species, the response to temperature closely matches that reported for root hydraulic conductance in Fig. 2 (solid line; $R^2 = 0.62$, $P < 0.001$), as predicted by the model. The response of water fluidity (= $1/\eta$) to temperature is also shown for comparison (dotted line).
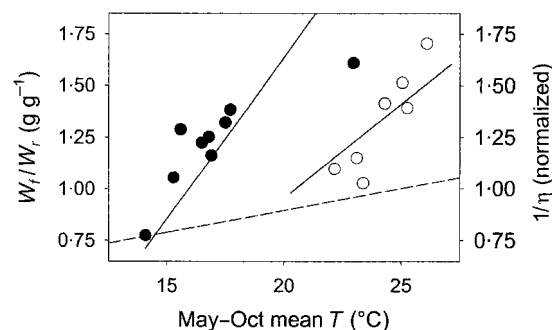
Cavitation avoidance is associated with a general lack of drought-induced leaf shedding in conifers. In the artificial drought experiment described by Irvine *et al*. (1998), needle loss was almost identical in droughted and control trees (unpublished results), as also reported for *P. halepensis* by Borghetti *et al*. (1998).

With the caveats discussed, the hypothesis that *P. sylvestris* (and possibly other coniferous species) has evolved a strategy of functional homeostasis and cavitation avoidance is supported by the experimental evidence.

RESPONSE OF PLANT STRUCTURE TO TEMPERATURE

The amount of foliage that can be supported by unit sapwood area (W_f/A_s) is predicted to increase in warm climates (Fig. 1a). Model predictions agree with the results of Palmroth *et al*. (1999), who analysed changes in the structure of *P. sylvestris* across Europe (Fig. 4; $R^2 = 0.52$, $P < 0.001$). The effects of temperature on the ratio between foliage and fine roots in *Pinus ponderosa* (Cregg 1994) and *Pinus taeda* seedlings (Bongarten & Teskey 1987) were also found to mirror closely reported changes in root hydraulic conductance (Fig. 5; $R^2 = 0.62$, $P < 0.001$), as predicted by the model. Observed differences within species seem to originate from long-term adaptation to local conditions, as average temperatures at the site of origin were considered. The same is true for the balance between foliage and sapwood area, as demonstrated by a comparison with results from a common garden experiment (Palmroth *et al*. 1999; Fig. 4).

Experimental studies on herbaceous species have consistently reported higher foliage : fine root ratios under warm conditions (Markhart *et al*. 1980; Wilson 1988). This has been suggested to result from a func-tional balance between foliage assimilation and root nutrient uptake (Cannell & Dewar 1994), assuming a higher sensitivity of root processes to temperature. However, the effect is also observed when only shoot temperature is increased (Wilson 1988). This result is at odds with the hypothesis of root–shoot functional balance, as such a treatment would enhance leaf photosynthesis but not root function, but is well explained by our model of optimal growth under hydraulic constraints. Warmer temperatures applied either to roots or shoot will reduce their hydraulic resistance. The effect will extend beyond the compartment being manipulated because of the effects on parameter *c* (equation 11), in agreement with experimental results.

RESPONSE OF PLANT STRUCTURE TO AIR HUMIDITY

Foliage : sapwood area ratios are predicted to decline in dry air (equation 20; Fig. 1b). Parallel changes are predicted for the ratio between foliage and fine roots. This agrees with the experimental results for three pine species presented in Fig. 6 ($R^2 = 0.87$, $P < 0.001$). In all three species, leaf area : sapwood area ratios decline asymptotically with increasing *D*, although *P. sylvestris* shows a much more gentle response. Data for conifers other than pines show no clear evidence of an adjustment to air humidity (DeLucia *et al*. 2000). The response of pines could explain their abundance in warmer, drier habitats (Richardson 1998).

According to DeLucia *et al*. (2000), common garden experiments with *P. ponderosa* seedlings point to a purely phenotypic rather than a genotypic effect in the structural adjustment to air humidity and transpiration rates, confirming previous findings by Mencuccini & Grace (1995). Strong phenotypic plasticity is assumed
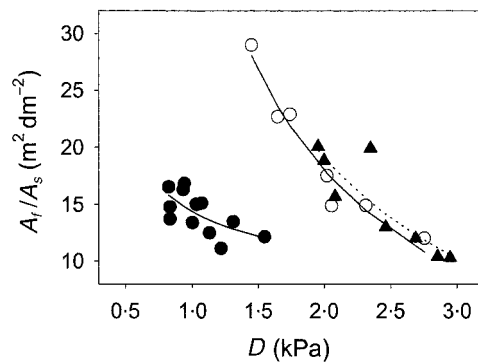
Fig. 6. Effects of air vapour pressure deficit (*D*) on the leaf-to-sapwood area ratio (A_f/A_s) of mature stands of *Pinus sylvestris* (●; Mencuccini & Bonosi 2001), *Pinus contorta* and *Pinus ponderosa* (○ and ▲, respectively; DeLucia *et al.* 2000). In each species the response to *D* is well explained by parallel changes in stomatal conductance and transpiration (solid line and dotted line; $R^2 = 0.87$, $P < 0.001$), as predicted by the model (equation 20; Fig. 1b).

to be typical of colonizing species such as pines (Sultan 2000).

Few other experimental studies have explicitly considered the effects of air humidity on plant structure. Smaller leaf specific conductances were observed by Bunce & Ziska (1998) in *Glycine max* and *Medicago sativa* plants grown under high vapour pressure deficits. As predicted by our model, this structural change was enough to offset the effects of humidity on transpiration rates, so that leaf water potential was not affected by the treatment. Darlington *et al.* (1997) observed a lower allocation to roots in *Picea mariana* and *Pinus banksiana* seedlings grown under high vapour pressure deficit.

RESPONSE OF PLANT STRUCTURE TO SOIL WATER AVAILABILITY

According to model predictions, water availability would change the ratio between foliage and conductive sapwood, with a shift away from foliage production under dry conditions (Fig. 3c). Even more important would be the effect on the functional balance between transpiring foliage and absorbing roots, which is predicted to decline in a sandy loam by as much as 75% as soil water potential decreases from saturation to –0·5 MPa (Fig. 3b). According to the model, however, the effects of water availability on tree structure would largely depend on soil texture, with stronger reductions in sandy soils (Fig. 3b,c).

Predicted changes in plant structure with changing soil water availability agree with recent evidence from experiments in which mature coniferous trees were droughted (Cinnirella *et al.* 2002; Irvine *et al.* 1998) or irrigated (Axelsson & Axelsson 1986; Ewers, Oren & Sperry 2000; Gower, Vogt, & Grier 1992). Model predictions of the effect of soil texture on plant hydraulic architecture have also been confirmed by the recent study of Hacke *et al.* (2000).

Conclusions

The proposed hypothesis of homeostasis for water transport in conifers appears to be supported by a large body of experimental evidence. Constancy in minimum leaf water potential is confirmed by experimental results under a wide range of conditions. The implications of the hypothesis also help to explain commonly observed changes in tree structure as a function of the environment. Although homeostasis in the face of sudden perturbations can be achieved only through stomatal regulation, structural changes appear to play a central role in the adjustment to prevailing environmental conditions over periods of months to years.

Our model is based on the simple and widely known observation of a regularity in plant function. Once implemented into a mathematical model, however, its heuristic value becomes apparent, as it could provide a physiologically based representation of resource allocation and plant structure in response to the environment and climate change (Friedlingstein *et al.* 1999).

Two questions remain unanswered. First, the limits of applicability of the model need to be determined. While some of the predictions of the model have general validity from herbs to trees, others would apply only to conifers, or are even limited to the genus *Pinus*. Second, it remains to be seen if, and to what extent, structural adjustments result from phenotypic plasticity or genetic adaptation under the long-term pressure of natural selection. The plant's potential to acclimate is an important evolutionary feature, enabling long-lived, sessile trees to tolerate the vagaries of the environment, but plasticity comes at a cost and could be limited despite its clear benefits (DeWitt, Sih & Wilson 1998). Whether or not individual trees have the potential to acclimate over a single generation to a variable environment has implications for the future response of forest ecosystems to climate change.

References

Axelsson, E. & Axelsson, B. (1986) Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Physiology* **2**, 189–204.

BassiriRad, H., Radin, J.W. & Matsuda, K. (1991) Temperature-dependent water and ion transport properties of barley and sorghum roots. *Plant Physiology* **97**, 426–432.

Bongarten, B.C. & Teskey, R.O. (1987) Dry weight partitioning and its relationship to productivity in loblolly pine seedlings from seven sources. *Forest Science* **33**, 255–267.

Borghetti, M., Cinnirella, S., Magnani, F. & Saracino, A. (1998) Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. *Trees* **12**, 187–195.

Breda, N., Cochard, H., Dreyer, E. & Granier, A. (1993) Water transfer in a mature oak stand (*Quercus petraea*). Seasonal evolution and effects of a severe drought. *Canadian Journal of Forest Research* **23**, 1136–1143.

Bunce, J.A. & Ziska, L.H. (1998) Decreased hydraulic conductance in plants at elevated carbon dioxide. *Plant Cell and Environment* **21**, 121–126.

Campbell, G.S. (1985) *Soil Physics with basic. Transport Models for Soil–Plant Systems.* Elsevier, Amsterdam.

Cannell, M.G.R. & Dewar, R.C. (1994) Carbon allocation in trees: a review of concepts for modelling. *Advances in Ecological Research* **25**, 50–104.

Case, K.E. & Fair, R.C. (1989) *Principles of Economics.* Prentice Hall, London.

Cinnirella, S., Magnani, F., Saracino, A. & Borghetti, M. (2002) The response of a mature *Pinus laricio* plantation to a three-year restriction of water supply: structural and functional acclimation to drought. *Tree Physiology* **22**, 21–30.

Cochard, H., Martin, R., Gross, P. & Bogeat-Triboulot, M.B. (2000) Temperature effects on hydraulic conductance and water relations of *Quercus robur* L. *Journal of Experimental Botany* **51**, 1255–1259.

Cregg, B.M. (1994) Carbon allocation, gas exchange, and needle morphology of *Pinus ponderosa* genotypes known to differ in growth and survival under imposed drought. *Tree Physiology* **14**, 883–898.

Darlington, A.B., Halinska, A., Dat, J.F. & Blake, T.J. (1997) Effects of increasing saturation vapour pressure deficit on growth and ABA levels in black spruce and jack pine. *Trees* **11**, 223–228.

DeLucia, E.H., Maherali, H. & Carey, E.V. (2000) Climate-driven changes in biomass allocation in pines. *Global Change Biology* **6**, 587–593.

Dewar, R.C., Ludlow, A.R. & Dougherty, P.M. (1994) Environmental influences on carbon allocation in pines. *Environmental Constraints on the Structure and Productivity of Pine Forest Ecosystems: A Comparative Analysis* (eds H.L. Gholz, S. Linder & R.E. McMurtrie), pp. 92–101. Ecological Bulletins, Copenhagen.

DeWitt, T.J., Sih, A. & Wilson, D.S. (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* **13**, 77–81.

Douglas, J.F., Gasiorek, J.M. & Swaffield, J.A. (1985) *Fluid Mechanics.* Longman Scientific, Harlow, UK.

Ewers, B.E., Oren, R. & Sperry, J.S. (2000) Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell and Environment* **23**, 1055–1066.

Fennell, A. & Markhart, A.H. (1998) Rapid acclimation of root hydraulic conductivity to low temperature. *Journal of Experimental Botany* **49**, 879–884.

Friedlingstein, P., Joel, G., Field, C.B. & Fungs, I.Y. (1999) Toward an allocation scheme for global terrestrial carbon models. *Global Change Biology* **5**, 755–770.

Givnish, T.J. (1986) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. *On the Economy of Plant Form and Function* (ed. T.J. Givnish), pp. 171–213. Cambridge University Press, Cambridge, UK.

Gower, S.T., Vogt, K.A. & Grier, C.C. (1992) Carbon dynamics of Rocky Mountain Douglas fir: influence of water and nutrient availability. *Ecological Monographs* **62**, 43–65.

Gower, S.T., Isebrands, J.G. & Sheriff, D.W. (1995) Carbon allocation and accumulation in conifers. *Resource Physiology of Conifers* (eds W.K. Smith & T.M. Hinckley), pp. 217–254. Academic Press, San Diego, CA.

Hacke, U.G., Sperry, J.S., Ewers, B.E., Ellsworth, D.S., Schäfer, K.V.R. & Oren, R. (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* **124**, 495–505.

Irvine, J., Perks, M.P., Magnani, F. & Grace, J. (1998) The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. *Tree Physiology* **18**, 393–402.

Jones, H.G. (1992) *Plants and Microclimate.* Cambridge University Press, Cambridge, UK.

Lohammar, T., Larsson, S., Linder, S. & Falk, S.O. (1980) FAST – Simulation models of gaseous exchange in Scots pine. *Structure and Function of Northern Coniferous Forests. An Ecosystem Study* (ed. T. Persson), pp. 505–523. Ecological Bulletins, Stockholm.

Magnani, F. (2000) Carbon allocation and tree growth under hydraulic constraints in Scots pine (*Pinus sylvestris* L.). PhD Thesis, University of Edinburgh, Edinburgh, UK.

Magnani, F., Mencuccini, M. & Grace, J. (2000) Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant Cell and Environment* **23**, 251–263.

Markhart, A.H., Fiscus, E.L., Naylor, A.W. & Kramer, P.J. (1979) Effect of temperature on water and ion transport in soybean and broccoli systems. *Plant Physiology* **64**, 83–87.

Markhart, A.H., Peet, M.M., Sionit, N. & Kramer, P.J. (1980) Low temperature acclimation of root fatty acid composition, leaf water potential, gas exchange and growth of soybean seedlings. *Plant Cell and Environment* **3**, 435–441.

Mencuccini, M. & Bonosi, L. (2001) Leaf–sapwood area ratios in Scots pine show acclimation across Europe. *Canadian Journal of Forest Research* **31**, 442–456.

Mencuccini, M. & Grace, J. (1995) Climate influences the leaf area–sapwood area ratio in Scots pine. *Tree Physiology* **15**, 1–10.

Palmroth, S., Berninger, F., Nikinmaa, E., Lloyd, J., Pulkkinen, P. & Hari, P. (1999) Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecologia* **121**, 302–309.

Panek, J.A. & Waring, R.H. (1995) Carbon isotope variation in Douglas-fir foliage: improving the $\delta^{13}C$-climate relationship. *Tree Physiology* **15**, 657–663.

Passioura, J.B. (1988) Water transport in and to roots. *Annual Review of Plant Physiology and Plant Molecular Biology* **39**, 245–265.

Passioura, J.B. & Cowan, I.R. (1968) On solving the non-linear diffusion equation for the radial flow of water to roots. *Agricultural Meteorology* **5**, 129–134.

Patrick, J.W. (1997) Phloem unloading. Sieve element unloading and post-sieve element transport. *Annual Review of Plant Physiology and Plant Molecular Biology* **48**, 191–222.

Richardson, D.M. (1998) *Ecology and Biogeography of Pinus.* Cambridge University Press, Cambridge, UK.

Santantonio, D. (1990) Modeling growth and production of tree roots. *Process Modelling of Forest Growth Responses to Environmental Stress* (eds R.K. Dixon, R.S. Meldahl, G.A. Ruark & W.G. Warren), pp. 124–141. Timber Press, Portland, OR.

Shinozaki, K. *et al.* (1964) A quantitative analysis of plant form – the pipe model theory. I. Basic analyses. *Japanese Journal of Ecology* **14**, 97–105.

Smit-Spinks, B., Swanson, B.T. & Markhart, A.H. (1984) Changes in water relations, water flux, and root exudate abscisic acid content with cold acclimation of *Pinus sylvestris* L. *Australian Journal of Plant Physiology* **11**, 431–441.

Sperry, J.S. & Sullivan, J.E.M. (1992) Xylem embolism in response to freeze–thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology* **100**, 605–613.

Sperry, J.S., Nichols, K.L., Sullivan, J.E.M. & Eastlack, S.E. (1994) Xylem embolism in ring-porous, diffuse porous, and coniferous trees of Northern Utah and interior Alaska. *Ecology* **75**, 1736–1752.

Sperry, J.S., Adler, F.R., Campbell, G.S. & Comstock, J.P. (1998) Limitation of plant water use by rhizosphere and xylem conductance. Results from a model. *Plant Cell and Environment* **21**, 347–359.

Sultan, S.E. (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* **5**, 537–542.

Tyree, M.T. & Sperry, J.S. (1988) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiology* **88**, 574–580.

Van Bel, A.J.E. (1993) Strategies of phloem loading. *Annual Review of Plant Physiology and Plant Molecular Biology* **44**, 253–281.

Waring, R.H. & Running, S.W. (1978) Sapwood water storage: its contribution to transpiration and effect upon water and conductance through the stems of old growth Douglas fir. *Plant Cell and Environment* **1**, 131–140.

Waring, R.H., Whitehead, D. & Jarvis, P.G. (1979) The contribution of stored water to transpiration in Scots pine. *Plant Cell and Environment* **2**, 309–317.

Whitehead, D., Edwards, W.R.N. & Jarvis, P.G. (1984) Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Canadian Journal of Forest Research* **14**, 940–947.

Wilson, J.B. (1988) A review of evidence on the control of shoot : root ratio, in relation to models. *Annals of Botany* **61**, 433–449.