

Hydraulic responses to height growth in maritime pine trees

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ABSTRACT

As trees grow taller, decreased xylem path conductance imposes a major constraint on plant water and carbon balance, and is thus a key factor underlying forest productivity decline with age. The responses of stomatal conductance, leaf area: sapwood area ratio ($A_L : A_S$) and soil–leaf water potential gradient ($\Delta\Psi_{S-L}$) to height growth were investigated in maritime pine trees. Extensive measurements of *in situ* sap flow, stomatal conductance and (non-gravitational) needle water potential ($\tilde{\Psi}_L = \Psi_L - \rho_w gh$) were made during 2 years in a chronosequence of four even-aged stands, under both wet and dry soil conditions. Under wet soil conditions, $\tilde{\Psi}_L$ was systematically lower in taller trees on account of differences in gravitational potential. In contrast, under dry soil conditions, our measurements clearly showed that $\tilde{\Psi}_L$ was maintained above a minimum threshold value of -2.0 MPa independently of tree height, thus limiting the range of compensatory change in $\Delta\Psi_{S-L}$. Although a decrease in the $A_L : A_S$ ratio occurred with tree height, this compensation was not sufficient to prevent a decline in leaf-specific hydraulic conductance, K_L (50% lower in 30 m trees than in 10 m trees). An associated decline in stomatal conductance with tree height thus occurred to maintain a balance between water supply and demand. Both the increased investment in non-productive versus productive tissues ($A_S : A_L$) and stomatal closure may have contributed to the observed decrease in tree growth efficiency with increasing tree height (by a factor of three from smallest to tallest trees), although other growth-limiting responses (e.g. soil nutrient sequestration, increased respiratory costs) cannot be excluded.

Key-words: *Pinus pinaster*; hydraulic conductance; stomatal regulation; tree height; water potential.

INTRODUCTION

In their review of various hypotheses to explain the decline in above-ground forest productivity with height growth, Ryan & Yoder (1997) concluded that the reduced ability of tall trees to transport water to their crowns plays a key role. As xylem path conductance decreases with tree height, the requirement that trees maintain a balance

between water supply and demand may lead to a reduction in stomatal conductance (g_s), resulting in reduced CO_2 uptake and photosynthesis.

For tree species that are susceptible to catastrophic xylem cavitation, or some other dysfunction, if their foliage water potential falls below a critical threshold, height-related stomatal closure may be crucial to plant survival. Several gas exchange studies have found reductions in stomatal or crown conductance with increasing tree size and age (Saliendra, Sperry & Comstock 1995; Bond & Kavanagh 1999; Hubbard, Bond & Ryan 1999; Salleo *et al.* 2000), in association with decreasing hydraulic conductance (Yoder *et al.* 1994; Hubbard *et al.* 1999; Ryan *et al.* 2000; Schafer, Oren & Tenhunen 2000).

However, adaptations other than stomatal closure may also contribute to maintaining plant water balance under height growth. These include: (a) the production of xylem vessels with increased permeability (Pothier, Margolis & Waring 1989); (b) a decrease in transpiring leaf area relative to xylem conductive area (Vanninen *et al.* 1996; McDowell *et al.* 2002a); (c) an increase in the fine root-leaf ratio (Sperry *et al.* 1998; Magnani, Mencuccini & Grace 2000); (d) an increase in the maximum water potential gradient between soil and leaf (Hacke *et al.* 2000); and (e) increased water storage in the stem (Phillips *et al.* 2003b). For many species these mechanisms are insufficient to offset the direct reduction in xylem hydraulic conductance due to height growth (Mencuccini & Grace 1996a, b; Mencuccini & Magnani 2000; McDowell *et al.* 2002b).

Therefore, quantifying these hydraulic responses to height growth is a prerequisite to understanding and predicting water balance and growth throughout the life cycle of trees. The objective of this study was to quantify changes in stomatal conductance (g_s), leaf area: sapwood area ratio ($A_L : A_S$) and soil-to-leaf water potential gradient ($\Delta\Psi_{S-L}$) under height growth, for maritime pine trees growing in south-west France. We aimed to overcome some of the limitations of previous experimental studies, by combining independent measurements of gas exchange (sap flow, porometer, ^{13}C discrimination), of needle water potential, and of foliage and sapwood areas performed *in situ* on individual trees within a chronosequence of four 'ideal' forest stands (monospecific, even-aged, uniform soil characteristics, flat topography) over two contrasting growing seasons (wet and dry).

A simple hydraulic model provides a useful framework for studying combined changes in g_s , $A_L : A_S$ and $\Delta\Psi_{S-L}$

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under height growth. When needle temperature is equal to air temperature (a good approximation for many conifers), and water storage is ignored, the balance between water demand and supply can be expressed by:

$$E_L = g_s D = K_L \Delta \Psi_{S-L} \quad (1)$$

where E_L is tree transpiration rate per unit leaf area, g_s is stomatal conductance per unit leaf area, D is the air water vapour saturation deficit, K_L is the leaf-specific hydraulic conductance between the soil and leaves, and $\Delta \Psi_{S-L}$ is the soil-to-leaf total water potential gradient. K_L may be expressed in terms of physical properties of the conducting system (Whitehead, Edwards & Jarvis 1984; Whitehead 1998):

$$K_L = k_s \frac{A_S}{A_L} \frac{1}{h} \quad (2)$$

where k_s is sapwood-specific hydraulic conductivity, h is tree height (strictly speaking, soil-to-leaf transport path length), and A_S and A_L are sapwood area and leaf area, respectively. Combining Eqns 1 and 2 then gives:

$$g_s \frac{A_L}{A_S} \frac{1}{\Delta \Psi_{S-L}} = \frac{k_s}{D} \frac{1}{h} \quad (3)$$

where our three factors of interest appear on the left-hand side. We see that, for given values of D and k_s the possible combined responses of g_s , $A_L : A_S$ and $\Delta \Psi_{S-L}$ to height growth fall between two extremes. With no change in either $A_L : A_S$ or $\Delta \Psi_{S-L}$, g_s must decline in inverse proportion to height. In contrast, with no change in g_s , an increase in $A_S : A_L$ and/or $\Delta \Psi_{S-L}$ must occur, whose multiplicative effect is proportional to height.

Our specific objectives were:

- 1 to determine whether hydraulic homeostasis occurs in maritime pine trees, such that needle water potential is maintained above a critical threshold.
- 2 to quantify the role of variations in g_s , $A_L : A_S$ and $\Delta \Psi_{S-L}$ in maintaining water balance under height growth (Eqn 3).

MATERIALS AND METHODS

Site description

We studied a chronosequence of maritime pine stands (*Pinus pinaster* Ait.) in the Landes de Gascogne Forest, south-west France. The regional climate is maritime (mean annual temperature of 13 °C, mean annual precipitation of 977 mm) with marked drought in late summer (August–September). Four study sites (Hermitage L, Bray, Hermitage M, Baudes) were selected within even-aged, monospecific stands of maritime pine with an understorey consisting mainly of *Molinia coerulea* (L.) Moench. Tree age in 2002 was 10, 32, 54 and 91 year, respectively. The stands were selected to minimize genetic variability (Landes provenance) and management differences. Each site had a podzolic sandy humic soil with a cemented B_n horizon limiting

the root depth to –0.8 m. The sites had extremely low soil phosphorus and nitrogen levels, and an average pH-H₂O of 4.0. Scaffolding was erected at the centre of each site for canopy measurements (height range 12–30 m).

Precipitation, air temperature, humidity and radiation were similar among stands (data not shown). In all stands, significant water stress occurred at the end of summer 2001 and throughout summer 2002. In the Results below, wet and dry soil conditions are defined as soil water deficit <0.50 and >0.65, respectively. Outlier data for the 32-year-old stand in spring–summer 2002, reflecting atypically severe soil water stress induced by adjacent agricultural groundwater extraction, were excluded from statistical analyses.

Sapwood area, leaf area and biomass of trees

The stand characteristics of the chronosequence in 2001, summarized in Table 1, were obtained as follows. Estimates of diameter at 1.3 m (d) in 2001 for each tree in the chronosequence were obtained from circumference measurements. For each stand, top height (h) was measured on ~100 trees stratified according to tree basal area, and diameter under the live crown (d_{LC}) was obtained from circumference measurements on 30 trees chosen randomly. For each of the latter, sapwood area at 1.3 m (A_S) and under the live crown ($A_{S,LC}$) were estimated as follows. First, the ratio of heartwood radius to total stem radius was measured on fresh wood cores extracted in three azimuth directions at 1.3 m and one azimuth direction under the living crown. The hydroactive part of the xylem was distinguished by transparency under diffuse light. A_S and $A_{S,LC}$ were then calculated as total wood area under bark minus heartwood area, at 1.3 m and under the live crown, respectively. The two youngest stands had negligible heartwood area under the live crown. In the two oldest sites, the heartwood radius ranged from 20 to 120 mm according tree size. These measurements served to establish, for each stand, statistical relationships between d_{LC} and d ($r^2 = 0.95–0.98$), between A_S and d ($r^2 = 0.84–0.94$), and between $A_{S,LC}$ and d_{LC} for the entire chronosequence ($r^2 = 0.97$, Delzon *et al.* 2004). These relationships were then used to derive A_S and $A_{S,LC}$ in all trees for which d was measured.

Tree leaf area (A_L) was estimated from an allometric relationship with d_{LC} and specific leaf area (σ), as described in Table 2. We also estimated above-ground annual tree biomass increment per unit leaf area (i.e. tree growth efficiency, ΔW_a) from an allometric relationship between W_a , d and tree age (Table 2). These relationships were established from previous data (Porté *et al.* 2000, 2002) complemented by more recent data from two other stands aged 10 and 50 year (Trichet and Bert, unpublished).

Xylem sap flow measurements

Sap flow in six representative trees in the youngest stand, and in seven trees in each of the older stands, was measured

Table 1. Stand characteristics of the maritime pine chronosequence in 2001

	10 year	n	32 year	n	54 year	n	91 year	n
Top height, h (m)	8.46 ± 0.08	126	20.21 ± 0.11	118	26.65 ± 0.11	129	28.36 ± 0.26	70
Diameter at 1.3 m, d (mm)	142.5 ± 0.1	637	298.8 ± 0.1	1921	436.7 ± 0.3	485	513.2 ± 0.4	463
Basal area, g (m ² tree ⁻¹)	0.016 ± 0.0002	637	0.072 ± 0.0005	1921	0.153 ± 0.002	485	0.213 ± 0.003	463
Sapwood area at 1.3 m, A_s (m ² tree ⁻¹)	0.013 ± 0.0001	637	0.042 ± 0.0003	1921	0.082 ± 0.001	485	0.130 ± 0.002	463
Sapwood area under the living crown, $A_{s,LC}$ (m ² tree ⁻¹)	0.011 ± 0.0001	637	0.017 ± 0.0001	1921	0.025 ± 0.0003	485	0.036 ± 0.0006	463
Tree leaf area, A_L (m ² tree ⁻¹)	48.54 ± 0.47	637	90.26 ± 0.66	1921	142.73 ± 2.11	485	226.61 ± 4.69	463
Stand density (tree ha ⁻¹)	1180		500		250		155	
Stand basal area, G (m ² ha ⁻¹)	19.23 ± 0.21		36.00 ± 0.26		38.22 ± 0.50		32.96 ± 0.52	
Stand sapwood area (m ² ha ⁻¹)	15.54 ± 0.17		20.84 ± 0.17		20.39 ± 0.32		20.21 ± 0.33	
Plant area index, PAI (m ² m ⁻²)	3.41		3.04		2.51		1.85	
Leaf area index, LAI (m ² m ⁻²)	2.86		2.26		1.78		1.76	

Values are mean ± standard error. PAI (m²_{plant} m⁻²_{ground}) was estimated from measurements of total light interception using an optical method (DEMON). LAI (m²_{leaf} m⁻²_{ground}) = $A_L \times \text{stand density (tree m}^{-2}\text{ground)}/2$.

using a constant heating radial flowmeter (Granier 1985, 1987) during the period April 2001 to January 2003 in the three youngest stands, and during the period March 2002 to January 2003 in the 91-year-old stand. Sensors were installed on the east side of the stems 1 m below the live crown, because at this height azimuthal variation in the sap flux density of maritime pine is small (Loustau, Domec & Bosc 1998). Data were recorded every 10 s and averaged every 30 min with dataloggers (Model 21X; Campbell Scientific Ltd, Shepshed, UK) and multiplexers (model AM416; Campbell Scientific Ltd). The calibration coefficient of (Granier 1985) was used to calculate the sap flux density, J_s (kg m⁻² h⁻¹).

Where possible, the two probes within each sensor were inserted in the same horizontal plane, the temperature difference between the probes with heating turned off then being negligible (< 0.01 mV). When tree stems were too small or branch insertions were present, the probes were inserted one above the other. In this configuration, a vertical temperature gradient correction must be applied (Do & Rocheteau 2002a, b; Lundblad, Lagergren & Lindroth 2001). Several times during the experiment, we measured

the temperature gradient (dT) between such probes with heating turned off for 3–4 d. Among the variables tested (radiation, air humidity, wind speed and temperature), the most satisfactory statistical correlation for dT was found with temperature alone. Such a relationship was established for each tree, allowing continuous correction of dT without which the mean daily sap flux densities in the 10-, 32-, 54- and 91-year-old trees would have been over-estimated by 3, 6, 6 and 5%, respectively.

In two or three trees in each stand, additional mobile sensors were inserted deeper into the sapwood to measure the radial profile of sap flux density. In all trees, sap flux density declined with increasing depth within the sapwood, the relative decline being greater in larger diameter trees and zero within the heartwood (Delzon *et al.* 2004), as found in previous studies (Čermák *et al.* 1990; Granier *et al.* 1994; Phillips, Oren & Zimmermann 1996; Čermák & Nadezhdina 1998; Schafer *et al.* 2000). These results enabled sap flux density measurements made in the outer 20 mm to be scaled to the entire sapwood using a correction factor (C) that depended on d_{LC} ($C = -1.17643 d_{LC} + 1.1936$ with $r^2 = 0.90$, Delzon *et al.* 2004).

Table 2. Allometric models derived from data of Porté *et al.* (2000, 2002) complemented by data from two other stands aged 10 and 52 year (Trichet and Bert, unpublished).

Variables estimated	Model	Parameters values		
		Mean	Asymptotic standard error	Degrees of freedom
A_L	$a_1 \cdot d_{LC}^{a_2} \cdot \sigma$	$a_1 = 0.0433$ $a_2 = 2.043$	0.008 0.059	102
W_a	$b_1 \cdot d^{b_2} \cdot y^{b_3}$	$b_1 = 0.076$ $b_2 = 2.031$ $b_3 = 0.347$	0.0216 0.0716 0.0389	86

A_L (m² tree⁻¹) = tree leaf area, d_{LC} (cm) = diameter under the live crown, σ (m² kg⁻¹) = specific leaf area (Table 3), W_a (kg tree⁻¹) = above-ground tree biomass, d (m) = diameter at 1.3 m, y (year) = tree age.

Leaf-level measurements

The non-gravitational component of needle water potential ($\tilde{\Psi}_L = \Psi_L - \rho_w g h$) and stomatal conductance (g_s) were measured in each stand during six clear days spanning both growing seasons (June, July and September 2001; June, August and September 2002). Measurements were made on several whorls of three trees in each stand. Only the 10- and 54-year-old (adjacent) stands could be measured on the same day; the other two stands were measured one or two days later. The value of $\tilde{\Psi}_L$ was estimated as the negative of the balance pressure applied using pressure chambers on fully expanded needles in the upper crown, every 10 min from predawn ($\tilde{\Psi}_P$) until sunset (a total of 2006 such measurements during the experiment).

Stomatal conductance (g_s) was measured every 10 min with null-balance porometers (Li-1600; Li-Cor Inc., Lincoln, NE, USA) equipped with a cylindrical chamber, from morning (as soon as foliage was completely dry) until 1700 h. One-year-old needles were removed and gas exchange measurements were completed within 3 min. Previous work on maritime pine in our laboratory has shown that the gas exchange of detached needles is the same as that of attached needles for at least 5 min following detachment. Immediately following the porometer measurements, the length (l_n) and diameter (d_n) of the chamber needles were measured with an electronic calliper, and the total surface area of each needle was estimated as $(1 + \pi/2)l_n d_n$.

$^{13}\text{C} : ^{12}\text{C}$

Carbon discrimination from annual ring cellulose provided an independent measure of height-related changes in g_s per unit of photosynthesis. From the base of each tree on which sap flow measurements were conducted, cores were taken at the end of the study period and the ratio $^{13}\text{C} : ^{12}\text{C}$ determined. For each tree, sampling consisted of four cores taken from four azimuthal directions, from which the annual rings for 2001 and 2002 were extracted and pooled by year. Cellulose was extracted by the method described by Lambrot & Porté (2000). Cellulose $\delta^{13}\text{C}$ was analysed with an isotope ratio mass spectrometer (FISONS Isochrom, Manchester, UK) at INRA, Laon (France).

Needle nitrogen content

In January 2001 and 2002, 100 needles in the upper crown of 10 trees per stand were harvested and kept cool during transfer to the laboratory. One needle from each tree was frozen at -20°C and chlorophyll *a* and *b* content were analysed colorimetrically using a spectrophotometer (Jenway 6405UV/Vis; Jenway, Felsted, Dunmow Essex, UK) (Inskip & Bloom 1985). The remaining needles were dried at 70°C for 72 h, mineralized with hot sulphuric acid and assayed colorimetrically for concentrations of N and P using a Technicon auto-analyser (O'Neill & Webb 1970). Specific needle area (σ) was calculated as the ratio of needle area (estimated as above) to dry weight.

Meteorological measurements

In each stand, micrometeorological data were collected every 10 s at 2 m above the canopy and averaged every 30 min. These data included wind speed (u , m s^{-1}), air temperature (T_a , $^\circ\text{C}$), air humidity (H , Pa), net radiation (R_n , W m^{-2}), global radiation (R , W m^{-2}), photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$), atmospheric pressure (P , atm), and precipitation (P_i , mm). All sensors were cross-calibrated before installation.

Soil volumetric water content was measured using two techniques, an FDR water content reflectometer system (CS615 water content reflectometer; Campbell Scientific Ltd), and a TDR-TRASE system (TRASE 6050 \times 1: Soil Moisture, Santa Barbara, CA, USA). In each of the two older sites (54- and 91-year-old trees), four soil moisture depth profiles were monitored using stainless steel CS615 probes inserted horizontally at depths of 0.15, 0.3, 0.6, 0.9 and 1.3 m. At each of the two younger sites, four profiles were monitored using TRASE probes installed vertically and horizontally at depths of 0.1, 0.15, 0.3, 0.5, 0.7, 0.8 m. Data were collected every 4 h, except at the site of the 32-year-old trees where they were collected on a weekly basis. A cross-comparison of the two techniques was carried out at one site and showed close agreement. The soil water deficit (δ_M) was calculated as:

$$\delta_M = \frac{M_{\max} - M}{M_{\max} - M_{\min}} \quad (4)$$

where M_{\max} , M_{\min} and M are the maximal, minimal and actual soil water contents (0–0.8 m depth), respectively.

Data analysis

Transpiration and canopy conductance

Tree transpiration rate per unit leaf area (E_L) was calculated from the measured sap flux density in the outer 20 mm (J_s) as:

$$E_L = J_s \cdot \frac{A_{\text{S,LC}}}{A_L} \cdot C \quad (5)$$

where $A_{\text{S,LC}}$ is the sapwood cross-sectional area under the live crown, A_L is the tree leaf area and C is the correction factor for the radial profile of sap flux density. Because sap flux density was measured under the live crown, we assumed that the lag between measured sap flux density and transpiration was negligible during the experiment. Indeed, the correlation between E_L and current values of D and potential evapotranspiration (PET) was consistently greater than that between E_L and previous values of D and PET, regardless of the lag time (30–180 min), suggesting that crown capacitance did not strongly affect E_L (Schulze *et al.* 1985; Phillips *et al.* 1997; Phillips & Oren 1998). Stand transpiration (E) was calculated from the mean sap flux density (\bar{J}_s) of six or seven trees per stand, multiplied by a weighted sapwood area for each stand (calculated as the sum over all trees of $A_{\text{S,LC}} \cdot C$ for each tree).

As the needle temperature was not measured, canopy conductance for water vapour, g_c ($\text{mmol m}^{-2} \text{s}^{-1}$), was estimated by inversion of the Penman–Monteith equation using transpiration and microclimate measurements, as follows:

$$g_c = \frac{g_a \cdot E \cdot \gamma}{s \cdot Rn_a + \rho \cdot c_p \cdot D \cdot g_a - E \cdot (s + \gamma)} \quad (6)$$

where E (W m^{-2}) is the stand transpiration, γ (J kg^{-1}) is the psychrometric constant, s (Pa K^{-1}) is the slope of the saturation vapour pressure–temperature curve, Rn_a (W m^{-2}) is the net radiation absorbed by the canopy, ρ (kg m^{-3}) is the density of dry air, c_p ($\text{J K}^{-1} \text{kg}^{-1}$) is the specific heat of air, D (Pa) is the vapour pressure deficit, and g_a (m s^{-1}) is the aerodynamic conductance. The latter was estimated from wind speed as:

$$g_a = \frac{k^2 \cdot u}{\ln[(z - d_0) / z_0]} \quad (7)$$

where z_0 is the surface roughness (approximately $0.1h$), h is the mean tree height, d_0 is the zero plane displacement (approximately $0.75h$), k is the von Karman constant, and u (m s^{-1}) is the wind speed at height z_0 . In this study, g_c was calculated after excluding data from periods of rainfall or $D < 100$ Pa.

Leaf-specific hydraulic conductance

Whole-tree leaf-specific hydraulic conductance, K_L ($\text{mmol H}_2\text{O m}^{-2} \text{leaf s}^{-1} \text{MPa}^{-1}$) was calculated for three trees per stand from linear regressions between tree transpiration rate per unit leaf area (E_L) and the non-gravitational component of needle water potential ($\tilde{\Psi}_L = \Psi_L - \rho_w gh$) on the same tree, according to:

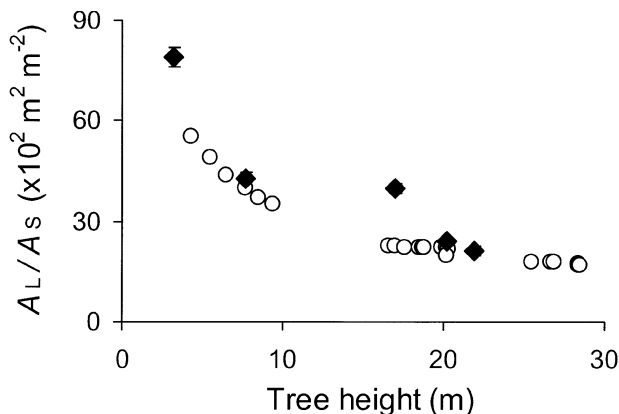


Figure 1. Height-related changes in leaf area: sapwood area ratio ($A_L : A_S$). \blacklozenge , mean values of $A_L : A_S$ measured directly in biomass campaigns (Porté *et al.* 2000, 2002; complemented with data from two other stands aged 10 and 50 years); bars indicate standard errors. \circ , mean values of $A_L : A_S$ estimated from allometric relationships using diameter measurements on all trees since 1996 in our chronosequence of four maritime pine stands.

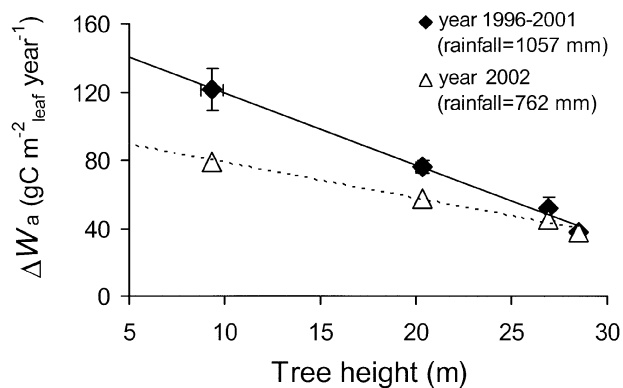


Figure 2. Variation of mean above-ground annual tree biomass increment per unit leaf area (tree growth efficiency, ΔW_a , $\text{gC m}^{-2} \text{year}^{-1}$) with tree height for the four stands of our chronosequence. \blacklozenge , average over all trees in each stand for wet years (1996–2001); \triangle , values for the dry year 2002 only.

$$K_L = \frac{E_L}{\Delta \tilde{\Psi}_{P-L}} \quad (8)$$

Here $\Delta \tilde{\Psi}_{P-L} = \tilde{\Psi}_P - \tilde{\Psi}_L$ (MPa) is the difference between the measured pre-dawn and current water potentials. No gravitational correction term $\rho_w gh$ is required in Eqn 8. From Eqn 1 the pre-dawn zero-flow condition ($E_L = 0$) is $\Psi_S = \Psi_P$ which implies $\Delta \Psi_{S-L} = \Delta \Psi_{P-L}$; then, because $\Delta \Psi_{P-L} = \Delta \tilde{\Psi}_{P-L}$ at a given height, Eqn 1 implies Eqn 8.

We used an analysis of variance (ANOVA) to test for a stand effect on water potential and needle mineral content, and a repeated-measures ANOVA to test for a height effect on leaf-specific hydraulic conductance (SAS procedure GLM, Version 8.1; SAS Institute, Cary, NC, USA). Non-linear curve fits were performed with SAS procedure NLIN.

RESULTS

Tree above ground increment

The leaf area : sapwood area ratio was significantly lower in tall trees (Fig. 1), being on average 7900, 3500 and 1700 $\text{m}^2 \text{m}^{-2}$ for heights of 3, 10 and 28 m, respectively. Although tree leaf area (A_L) increased markedly with tree height (Table 1), the increase in sapwood area at stem base (A_S) was proportionately greater (despite an associated large increase in heartwood area), resulting in a large decrease in $A_L : A_S$. In contrast, the ratio $A_L : A_{S,LC}$ varied little with tree age or height (data not shown).

Above-ground annual tree biomass increment per unit leaf area (i.e. tree growth efficiency) decreased by a factor of three between the smallest and tallest trees (Fig. 2). The height-related decline in tree growth efficiency was less rapid in 2002, when a prolonged period of water stress occurred. Figure 2 suggests a larger growth response to changes in soil water content for small trees than for tall trees.

Needle water potential

Figure 3 shows the diurnal course of the non-gravitational component of needle water potential ($\tilde{\Psi}_L = \Psi_L - \rho_w gh$) in the chronosequence stands under wet (Fig. 3a; $\delta_M < 0.5$) and dry (Fig. 3b; $\delta_M > 0.65$) soil conditions. In all stands, on wet soil $\tilde{\Psi}_L$ decreased to a minimum value ($\tilde{\Psi}_m$) around 13–14 h then increased until the end of measurement period (approximately 22 h). The value of $\tilde{\Psi}_L$ was systematically lower in taller trees by an amount equal to the corresponding gravitational potential difference (Fig. 3a). Pre-dawn water potential ($\tilde{\Psi}_p$) varied by 0.36 MPa between the tallest and smallest trees, whereas the corresponding variation in $\tilde{\Psi}_m$ was less significant (0.28 MPa) (Table 3). The maximum soil-to-leaf total water potential gradient, $\Delta\Psi_{S-L,max}$ ($= \tilde{\Psi}_p - \tilde{\Psi}_m$), was therefore smaller for tall trees.

In contrast, our data obtained on dry soil indicate the existence of a common minimum threshold value for $\tilde{\Psi}_L$ of approximately -2.0 MPa, independent of tree height

(Fig. 3b). On the driest day in the 32-year-old stand ($\delta_M > 0.85$), $\tilde{\Psi}_p$ was equal to the threshold value and remained there throughout the day as transpiration had ceased. Our results also indicate that, on dry soil, $\tilde{\Psi}_p$ was lower and the diurnal minimum $\tilde{\Psi}_L$ was reached sooner than on wet soil. In summary, $\Delta\Psi_{S-L}$ varied less with tree height under dry soil conditions due to the threshold constraint.

Leaf-specific hydraulic conductance

Whole-tree leaf-specific hydraulic conductance, K_L , was measured concurrently only under wet soil conditions. The value of K_L decreased linearly with increasing tree height, being 50% lower in tall trees (28 m) than in small trees (8 m) (Fig. 4). Height, rather than age, affected hydraulic conductance, as evidenced by the two oldest stands (54 and 91 year) with similar heights (27 and 28 m) and K_L values.

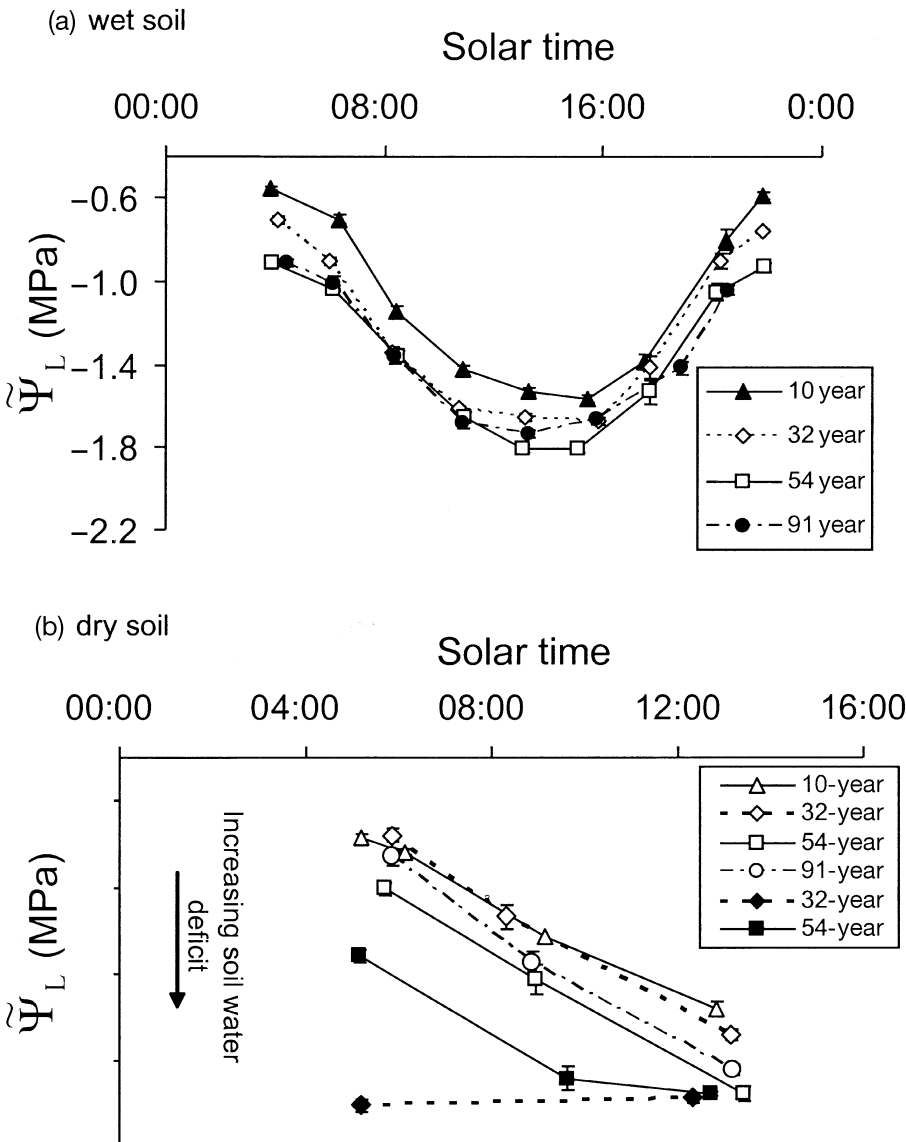


Figure 3. Diurnal course of the mean non-gravitational component of needle water potential ($\tilde{\Psi}_L = \Psi_L - \rho_w gh$) during clear days on (a) wet soil ($\delta_M < 0.5$) and (b) dry soil ($\delta_M > 0.65$) in 2001 and 2002, for each stand in the maritime pine chronosequence. Data obtained on the day of highest measured soil water deficit ($\delta_M > 0.85$) at the 32- and 54-year-old stands are presented by filled symbols.

Table 3. Mean values of predawn and diurnal minimum non-gravitational needle water potential ($\tilde{\Psi}_P$ and $\tilde{\Psi}_m$; MPa), diurnal maximum soil-to-leaf water potential difference ($\Delta\Psi_{S-L,max} = \tilde{\Psi}_P - \tilde{\Psi}_m$), tree transpiration per unit leaf area at $D = 1500$ Pa on wet soil (E_L), specific leaf area (σ , $m^2 kg^{-1}$), nitrogen and phosphorus concentration (N and P, % of dry mass), and total chlorophyll concentration (Chl, $\mu g g^{-1}$ of fresh mass), obtained from measurements across the chronosequence in 2001 and 2002

Age	h (m)	$\tilde{\Psi}_P$ (MPa)	$\tilde{\Psi}_m$ (MPa)	$\Delta\Psi_{S-L,max}$ (MPa)	E_L ($kg m^{-2} h^{-1}$)	σ ($m^2 kg^{-1}$)	N (%)	P (%)	Chl ($\mu g g^{-1}$)
10 year	8.46	-0.55 a	-1.50 a	0.96 a	0.037	6.80 a	1.29 a	0.068 b	612.44 a
32 year	20.21	-0.70 b	-1.66 b	0.95 a	0.021	6.11 b	1.20 a	0.080 a	734.97 a
54 year	26.65	-0.89 c	-1.79 c	0.90 b	0.012	5.88 bc	1.32 a	0.057 c	755.30 a
91 year	28.36	-0.91 c	-1.78 c	0.86 b	0.011	5.67 c	1.29 a	0.055 c	676.36 a

Significant differences between stands (5% level, Student–Newman–Keuls-test) are indicated by different letters.

Crown and stomatal conductance

We compared the stomatal conductance between stands in terms of its response to vapour pressure deficit (D), and found a consistent pattern with height and D , independent of the measurement method. Mean values of crown conductance per unit of leaf area (g_c) for all days from April 2001 until December 2002 are presented in Fig. 5a and b) for wet and dry soil, respectively. The value of g_c was systematically lower for taller trees over a wide range of D (maximum g_c at $D = 1000$ Pa, 10 year: $160 mmol m^{-2} s^{-1}$; 32 year: $110 mmol m^{-2} s^{-1}$; 54 year: $65 mmol m^{-2} s^{-1}$; 91 year: $60 mmol m^{-2} s^{-1}$). In each stand, g_c was lower on dry soil than on wet soil, and the variation in g_c between stands was less marked on dry soil. Transpiration per unit of leaf area decreased with tree height (Table 3, mean values of E_L for six to seven trees per stand at PAR > 800 and $D = 1500$ Pa for clear days on wet soil). The value of E_L for 8 m trees was three times that of 28 m trees, the latter being similar to 27 m trees.

These data were consistent with porometer measurements of stomatal conductance (Fig. 5c). For sunlit needles in the upper crown under saturating irradiance, and $D = 1000$ Pa, g_s for 8 m trees was approximately 40%

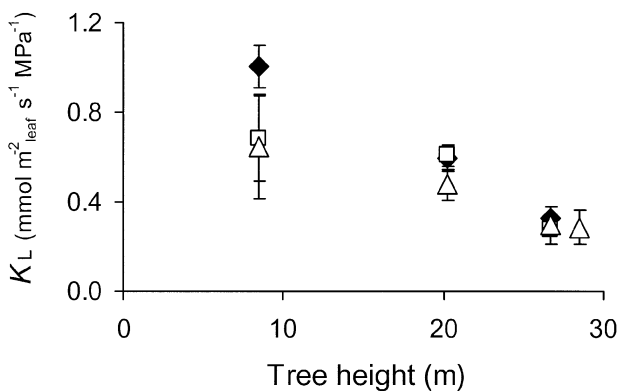


Figure 4. Variation of leaf-specific hydraulic conductance (K_L) with tree height, determined during 3 d on wet soil for each stand in 2001 and 2002. Each point is the average of three trees per stand; \blacklozenge , June 2001; \square , July 2001; \triangle , June 2002; bars indicate standard errors. Repeated-measures ANOVA showed a significant effect of height ($F = 11.87$, $P < 0.0108$).

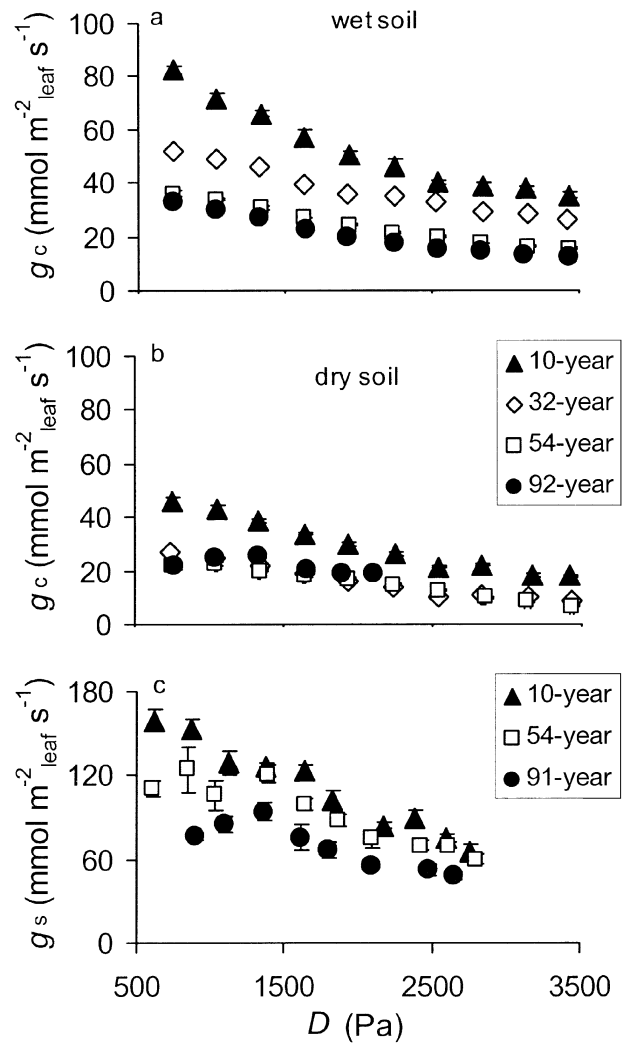


Figure 5. Mean values of canopy conductance (g_c), determined from sap flow measured on six to seven trees per site, versus air saturation deficit (D), on (a) wet and (b) dry soil. Data measured between April 2001 and December 2002. (c) Mean values of light-saturated stomatal conductance (g_s) versus air saturation deficit (D) for 1-year-old needles for three stand ages. All g_s measurements were made *in situ* on three trees per stand on wet soil (2002), using a steady-state null balance porometer.

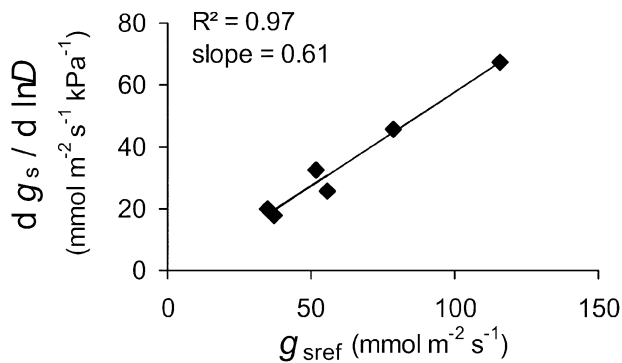


Figure 6. Sensitivity of mean stomatal conductance to air pressure deficit (D) as a function of canopy stomatal conductance at $D = 1000$ Pa (g_{sref}), for each stand in each of 2001 and 2002. Data not shown for the 32-year-old stand in 2002 (outlier due to extreme soil water stress) or the 91-year-old stand in 2001 (no measurement).

higher than for 28 m trees. Stomatal conductance sensitivity to vapour pressure deficit [$m = dg_s/d(\ln D)$] was higher in smaller trees, increasing linearly with g_{sref} (g_s at $D = 1000$ Pa) under saturating light conditions (Fig. 6). The slope m/g_{sref} (approximately 0.6) is similar to that reported for mesic-adapted species (Oren *et al.* 1999).

$\delta^{13}C$

The $\delta^{13}C$ of annual ring cellulose increased similarly with tree height in each year (Fig. 7). The outlier datum reflects the severe and prolonged soil water deficit at the 32-year-old stand in 2002.

DISCUSSION

Hydraulic homeostasis occurs in maritime pine trees

Our results indicate that hydraulic homeostasis occurs, such that the non-gravitational component of needle water potential ($\tilde{\Psi}_L$) is maintained above a common minimum threshold (-2.0 MPa) independently of tree age and height. This was especially evident under dry soil conditions. At similar values of D , $\tilde{\Psi}_L$ varied between stands within the bounds defined by $\tilde{\Psi}_p = \Psi_s - \rho_w gh$ and the threshold value (-2.0 MPa). The latter is close to the cavitation threshold of -2.2 MPa (Cochard, unpublished results) previously observed in even-aged stands of maritime pine growing in Portugal (Loustau, Granier & El-Hadj Moussa 1990; Loustau *et al.* 1996). Similar homeostatic behaviour has been reported for Ponderosa pine ($\Psi_{min} = -2.0$ MPa) (Yoder *et al.* 1994; Hubbard *et al.* 1999; Ryan *et al.* 2000), Red alder ($\Psi_{min} = -1.1$ MPa) and Western hemlock ($\Psi_{min} = -2.1$ MPa) (Bond & Kavanagh 1999), European oaks (Cochard, Breda & Granier 1996) and Water birch (Saliendra *et al.* 1995), but not for Lodgepole pine (Yoder *et al.* 1994), Douglas-fir (McDowell *et al.* 2002b; Phillips *et al.* 2002) or Saligna eucalyptus (Barnard & Ryan 2003). As our study underlines,

homeostatic behaviour (if it exists) will not be observed unless air and soil humidities are sufficiently low.

Maritime pine shows a considerable degree of stomatal control, maintaining trees above the threshold $\tilde{\Psi}_L$ and thus following a conservative strategy (Jones & Sutherland 1991). This strategy may be especially beneficial for evergreen species with their considerable investment in long-lived foliage, for which water-stress-related foliage loss would represent an important cost to the tree. Sperry *et al.* (2002) suggested that trees growing in sand (as in this study) have a much narrower margin of safety than those in finer loam soil, because of the more sensitive $K(\Psi)$ water characteristic for sand.

Multiple hydraulic responses to height growth

The decrease in leaf-specific hydraulic conductance (K_L) with increasing tree height is a commonly observed phenomenon (Mencuccini & Grace 1996b; Hubbard *et al.* 1999; Ryan *et al.* 2000; Phillips, Bond & Ryan 2001; McDowell *et al.* 2002b), although it may not be universal (Phillips *et al.* 2002). In our study, the 50% lower value of K_L in 28 m trees compared with 8 m trees may reflect numerous underlying factors, including increased water path length (Mencuccini & Grace 1996a, b), changes in root : shoot ratio and architecture, and decreased sapwood permeability of stem, petiole or root with age. Tree age itself had little effect on K_L , as shown in Fig. 4 by the data for 27 m (54-year-old) and 28 m (91-year-old) trees.

The decrease in K_L with height implies that adjustments in $A_L : A_S$ (decrease) and $\Delta\Psi_{s-L}$ (increase) were insufficient to offset the increased path length and gravitational potential of tall trees. A decrease in $A_L : A_S$ with tree height appears to be a response common to many species (Mencuccini & Grace 1996b; Bond & Ryan 2000; Mencuccini & Magnani 2000; Ryan *et al.* 2000; Schafer *et al.* 2000; McDowell *et al.* 2002a). In contrast, hydraulic

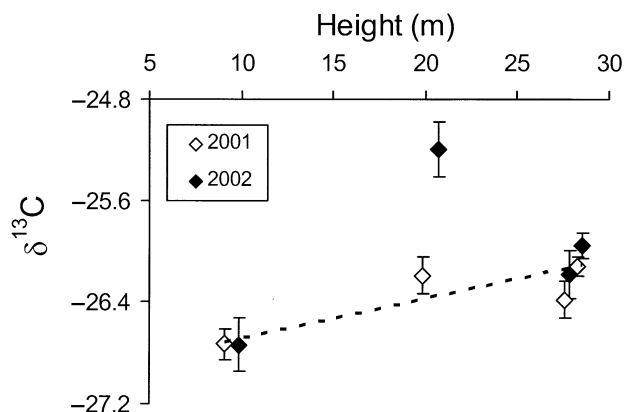


Figure 7. Mean values of $\delta^{13}C$ in annual ring cellulose as a function of tree height. Each point is the average of six to seven trees per stand for which water flux measurements were made in 2001 (\diamond) and 2002 (\blacklozenge); bars indicate standard errors. Dotted line: linear regression for all data excluding the datum of the 32-year-old stand in 2002 (outlier due to extreme drought stress).

homeostasis limits the degree to which $\Delta\Psi_{s-L}$ can increase.

From studies of Douglas-fir (McDowell *et al.* 2002b; Phillips *et al.* 2002) and *Saligna eucalyptus* (Barnard & Ryan 2003), it has been suggested that decreases in both $A_L : A_S$ and the threshold foliage potential can completely compensate for increased tree height. In these studies, the authors put forward the hypothesis of a decrease in minimum water potential as trees grow taller. However, because needle water potential in these studies was measured in unstressed conditions, the diurnal minimum water potential may not have attained its threshold value. Under such conditions, full adjustment of $\Delta\Psi_{s-L}$ can occur.

In our study, adjustment of $\Delta\Psi_{s-L}$ was limited by the threshold value of Ψ_L , and the decrease in $A_L : A_S$ was insufficient to offset the decline in K_L with increasing tree height. Consequently, an associated decline in stomatal conductance with tree height occurred to maintain a balance between water supply and demand. Both canopy (sap flow) and stomatal (porometer) conductance decreased dramatically with height, results corroborated by carbon discrimination measurements which integrate stomatal behaviour over time (Farquhar, Ehleringer & Hubick 1989). A similar decrease in stomatal conductance has been observed in various tree species, including European beech (Schafer *et al.* 2000), *Ponderosa pine* (Yoder *et al.* 1994; Hubbard *et al.* 1999; Ryan *et al.* 2000; Irvine *et al.* 2002) or lodgepole pine (Yoder *et al.* 1994) but not, for example, in Douglas-fir (McDowell *et al.* 2002b) or *Saligna eucalyptus* (Barnard & Ryan 2003).

In some studies sap flow measurements were used to estimate the crown conductance of individual trees ($g_c = E_L/D$), in contrast with other studies (Yoder *et al.* 1994; Hubbard *et al.* 1999; McDowell *et al.* 2002b) in which leaf gas exchange measurements were made on 1-year-old needles. McDowell *et al.* (2002b) failed to find a consistent pattern for height-related changes in stomatal conductance and foliar $\delta^{13}C$, suggesting that selective cuvette measurements of g_s are inadequate for revealing trends with height.

Our study supports this suggestion; we found that crown conductance estimated from whole stands was a more robust method for this purpose than leaf-level measurements made on selected days. Our data are also self-consistent in highlighting the relatively limited response of taller trees to air and soil drying, in terms of either growth efficiency (Fig. 2), crown conductance (Fig. 5a & b) or stomatal conductance (Figs 5c & 6).

To quantify the relative role of compensations via leaf area: sapwood area ratio and stomatal conductance, measured values of canopy conductance (g_c) were compared with various theoretical estimates of g_s (Fig. 8). First, g_s was predicted from Eqn 3 as a function of mid-crown height using measured values of $A_L : A_S$ (Fig. 1) and maximum $\Delta\Psi_{s-L}$ (Table 3) for each stand, and the values so obtained were normalized to that for the smallest stand (Fig. 8, solid line). This prediction was in reasonably good agreement with g_c measured on wet soil at $800 < D < 1200$ kPa and $PAR > 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 8, symbols), suggesting that sapwood-specific hydraulic conductivity (k_s) did not change significantly with tree height, in contrast to Pothier *et al.* (1989). These results fall between the two theoretical extremes (fixed g_s , or fixed $A_L : A_S$ and $\Delta\Psi_{s-L}$) evoked in the Introduction (Fig. 8, dashed lines). Our measurements indicate that g_s and $A_L : A_S$ decreased by 38 and 55%, respectively, over the range 8 to 28 m in tree height. Similar results have been shown for *Fagus sylvatica* L. by Schafer *et al.* (2000), where a height-related decrease in stomatal conductance was accompanied by a decrease in $A_L : A_S$. Indeed this pattern occurs in tree species generally, although in one recent study of *Quercus garryana* $A_L : A_S$ increased with tree height (Phillips *et al.* 2003a).

Potential causes of growth decline with age

We have demonstrated a marked decline in tree growth efficiency with height in maritime pine, as observed elsewhere (McDowell *et al.* 2002b; Ryan *et al.* 2004), although our conclusions as to the underlying causes must remain

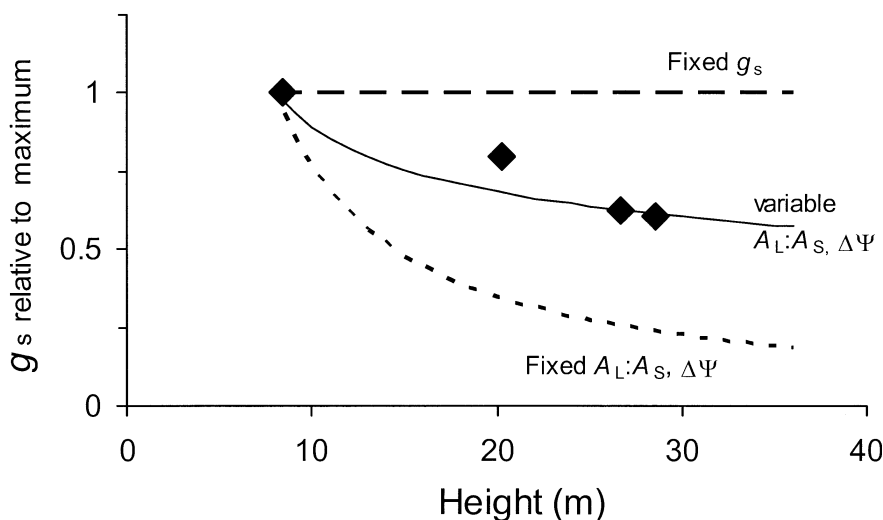


Figure 8. Diamonds: mean canopy conductance per unit leaf area (g_c) measured at reference vapour pressure deficit ($800 < D < 1200$ kPa), radiation ($PAR > 1200$) and on wet soil, as a function of tree height (h). Solid line: g_c predicted from Eqn 3 using measured values of leaf area: sapwood area ratio ($A_L : A_S$) and maximum soil-to-leaf water potential gradient ($\Delta\Psi_{s-L,max}$) in each stand. Lower dashed line: g_c predicted from Eqn 3 assuming fixed $A_L : A_S$ and $\Delta\Psi_{s-L}$, implying $g_c \propto 1/h$. Upper dashed line: hypothetical limit of fixed g_s , implying from Eqn 3 a decline in $A_L : A_S$ and/or an increase in $\Delta\Psi_{s-L}$.

tentative. Our study suggests that at least part of this decline may be attributed to a decrease in stomatal conductance, implying a reduction in CO₂ diffusion into the leaf (Wong, Cowan & Farquhar 1985). The observed decrease in leaf area : sapwood area ratio, implying an increased investment in non-productive versus productive tissues, may also have contributed to the growth decline. A stomatal effect is consistent with the observed increase in $\delta^{13}\text{C}$ with height. Although the $\delta^{13}\text{C}$ increase could also have occurred through an increase in photosynthetic capacity, we observed no differences in either needle nitrogen content or photosynthetic capacity between trees in our chronosequence (*A-C_i* and *A-PAR* curves measured on detached branches in the laboratory; Delzon, unpublished results). However, from this we cannot exclude the possibility that part of the decline in growth efficiency reflected lower soil nutrient availability caused by nutrient sequestration in the biomass and detritus of older stands, which may induce a reduction in total tree needle area even if needle nutrient content remains unaffected.

CONCLUSION

Our extensive chronosequence data clearly demonstrate that for maritime pine both the leaf area : sapwood area ratio and stomatal conductance decrease with height growth, whereas compensatory adjustment in soil-to-leaf water potential gradient is limited by the phenomenon of hydraulic homeostasis, especially evident in dry soil conditions. These data significantly reinforce previous observations of combined stomatal and structural compensations to height growth in other tree species. Further modelling and experimental studies are required to ascertain whether, for maritime pine, the observed height-related decline in tree growth efficiency can be attributed to stomatal closure and greater investment in non-productive tissues alone, or whether other growth-limiting responses (e.g. soil nutrient sequestration, increased respiratory costs) are also involved.

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