The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance

J. IRVINE, M. P. PERKS, F. MAGNANI and J. GRACE

Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh EH9 3JU, U.K.

Summary We investigated the impact of drought on the physiology of 41-year-old Scots pine (*Pinus sylvestris* L.) in central Scotland. Measurements were made of the seasonal course of transpiration, canopy stomatal conductance, needle water potential, xylem water content, soil-to-needle hydraulic resistance, and growth. Comparison was made between drought-treated plots and those receiving average precipitation. In response to drought, transpiration rate declined once volumetric water content (VWC) over the top 20 cm of soil reached a threshold value of 12%. Thereafter, transpiration was a near linear function of soil water content. As the soil water deficit developed, the hydraulic resistance between soil and needles increased by a factor of three as predawn needle water potential declined from −0.54 to −0.71 MPa. A small but significant increase in xylem embolism was detected in 1-year-old shoots. Stomatal control of transpiration prevented needle water potential from declining below −1.5 MPa. Basal area, and shoot and needle growth were significantly reduced in the drought treatment. In the year following the drought, canopy stomatal conductance and soil-to-needle hydraulic resistance recovered. Current-year needle extension recovered, but a significant reduction in basal area increment was evident one year after the drought. The results suggest that, in response to soil water deficit, mature Scots pine closes its stomata sufficiently to prevent the development of substantial xylem embolism. Reduced growth in the year after a severe soil water deficit is most likely to be the result of reduced assimilation in the year of the drought, rather than to any residual embolism carried over from one year to the next.

Keywords: growth, sap flow, Scots pine, soil water deficit, stomatal conductance, xylem embolism.

Introduction

The increasing incidence of summer droughts in northern Europe may be causing a decline in the health of trees, and it has been hypothesized that severe soil water deficits in one summer may cause hydraulic and physiological responses that are carried over into subsequent years (Innes 1993). Yet there have been few experimental studies in which the relevant processes have been demonstrated in controlled field experiments, and the mechanism involved in such carry-over responses remains a matter of speculation.

One hypothesis is that soil water deficit can induce cavitation of the water columns in the xylem if they reach a critical tension during periods of high transpiration. Although early experiments involving saw-cuts in the trunks of trees provide evidence for "spare capacity" in the transport system (Greenidge 1955, Kozlowski 1964), it seems likely that the hydraulic resistance of the tree or its branches increases during drought as a result of cavitation. Some authors have suggested that the increase in hydraulic resistance following cavitation will predispose the tree to further cavitation, resulting in catastrophic or "runaway" cavitation with complete dysfunction of xylem water transport (Tyree and Sperry 1988, Jones and Sutherland 1991). This hypothesis, however, overlooks the possibility that a decline in stomatal conductance in response to a chemical or hydraulic signal from the roots (Blake and Ferrell 1977, Davies and Zhang 1991, Tardieu and Davies 1993) reduces the transport of water in the xylem and hence avoids the critical tensions causing cavitation.

Much of the work that underlies present knowledge of the impact of soil water deficit on trees comes from experiments on seedlings and saplings (Gollan et al. 1985, Saliendra et al. 1995, Jackson et al. 1995*b*). In mature forests, there have been fewer experiments, and there are good reasons to suspect that mature trees may behave differently from juveniles. In mature trees signals from the roots are likely to take a long time to reach the canopy, and the roots may extract water from great depth (Canadell et al. 1996). In the present study, three specific questions were addressed.

(1) Does stomatal closure in mature trees occur in response to soil dryness in a similar manner to that suggested by studies on young trees? This question is not only of great theoretical interest, but is needed for models of forest growth and yield, and for parameterizing the various forest types that are currently used in Global Circulation Models (Sellers et al. 1997). (2) Can stomatal closure prevent cavitation by reducing transpirational flux, so that the critical tension for cavitation is rarely or never reached (Jones and Sutherland 1991)? (3) Does the hydraulic resistance in the soil–vegetation–atmosphere system increase during drought, and can it recover when drought ceases? The question of whether recovery occurs is important, because refilling of embolized tracheids is believed to occur only when tension in the water columns approaches

zero (Borghetti et al. 1991, Edwards et al. 1994).

These issues were addressed by artificially droughting a mature stand of Scots pine in central Scotland, and carrying out appropriate physiological measurements.

Materials and methods

Study site

The site was Compartment 474 of the Forestry Commission's Devilla forest in Fife, Scotland (see Table 1 for details), situated on one of a series of low hills of fine-grained carboniferous sandstone. The soil is a sandy loam, with occasional pockets of heavier less freely draining soil in the vicinity. Ground vegetation is dominated by *Deschampsia flexuosa* (L.) Trin., *Calluna vulgaris* (L.) Hull. and *Vaccinium myrtillus* L. Eight 10 × 10-m plots, each containing between eight and 15 trees, were selected. Each plot was isolated from the surrounding soil by a 1.5-m deep ditch, the side of which was lined with heavy black polyethylene sheet before being refilled with soil. The plastic film prevented lateral inflow of water and allowed rooting volumes to be subjected to drought or to be watered, as desired. Four plots were assigned to a drought treatment and the remaining four plots were periodically irrigated so as to represent the 20-year average summer rainfall conditions. This treatment is referred to as the control treatment throughout. Precipitation and stem flow were prevented from reaching the soil in the four drought plots by constructing clear polyethylene covers to deflect intercepted water beyond the ditch surrounding each plot. The covers were inclined, supported 1.5 m above ground at the center of the plots and 0.3 m at the edges, thus enabling access to the soil and boles of the trees, and allowing free movement of air above the plot.

To gain access to the forest canopy, a 0.6-m wide by 9-m long walkway was suspended between two 15-m high tripole mast towers at a height of about 11.5 m. This walkway spanned a neighboring drought and control plot and allowed access to the foliage on four or five trees per treatment.

The polyethylene covers and soil water barrier were installed in October 1994 and measurements began in April 1995. Soil water, growth, stem and shoot embolism measurements were made at 2-week intervals. Diurnal time courses of needle water potential were made at approximately 3-week intervals. At the beginning of November 1995, the covers on the drought-treated plots were removed and the plots were irrigated to bring soil water content back to pre-drought values.

Soil water

Soil volumetric water content (VWC) was determined by time domain reflectometry (TDR), with stainless steel probes of the two-pin balanced design. Three sets of 20-cm and two sets of 50-cm probes were left permanently installed in each plot. Measurements were made with a Tektronics 1502B cable testing oscilloscope (Tektronics Corp., Redmond, OR) fitted with an SDM1502 interface connected to a 21X data logger (Campbell Scientific, Leicestershire, U.K.).

Microclimate

Sensors to measure air temperature and relative humidity (HMP35AC, Campbell Scientific), photosynthetically active radiation (PAR, Skye 215, Skye Instruments, Llandrindod Wells, Powys, Wales) wind speed (A100R, Vector Instruments, Rhyl, Clwyd, Wales) and net radiation (Q7, Campbell Scientific) were left permanently installed above the canopy at a height of 17 m. Measurements were made at 1-min intervals and averaged and stored every hour on a 21X data logger (Campbell Scientific).

Stem and shoot embolism

The relative water content (RWC) of the sapwood in the bole of five trees per plot 0.5 m above ground was monitored with 0.05 m TDR probes as described by Irvine and Grace (1997). The degree of embolism in the xylem of shoots of current-year and previous-year growth was assessed by destructive sampling. Shoots were collected from the middle to lower canopy with pole pruners, and the needles immediately removed before the sample was wrapped tightly in sealing film to prevent water loss (Nescofilm). On return to the laboratory, the shoots were stored at 4 °C for a maximum of 24 h before their xylem RWC was assessed according to the method of Sobrado et al. (1992).

Needle water potential and turgor

Needle water potential was assessed at 3-h intervals between predawn and dusk. Shoots were randomly sampled from the middle to lower canopy (no distinction was made between needles exposed to sun or shade) by using pole pruners. Shoots were immediately placed in plastic bags with damp tissue paper to minimize water loss. One shoot per plot was sampled every measurement period and two water potential measurements were made with a pressure chamber (Model 1400, Skye Instruments) on single needles that had elongated the previous

Table 1. Site and stand characteristics. The climate data for the area were extracted from the Meteorological Office Climatological Memoranda 108 and 115 and the 20-year average rainfall from a local station (Grangemouth). Diameters at breast height and numbers of trees per hectare were based on measurements of all trees within 0.25 ha. Leaf area index was calculated from 28 hemispherical photographs taken throughout the compartment. Where available one standard deviation is given in brackets.

Latitude	56°2′ N
Longitude	3°43′ W
Elevation (m)	75
Average January temperature (°C)	2.5
Average July temperature (°C)	14.8
Average annual precipitation (mm)	820
Planting year	1954
Average height (m)	15
Average diameter at breast height (cm)	20.1 (4.9)
Leaf area index	1.92 (0.39)
Overbark basal area ($m^2 ha^{-1}$)	28
Sapwood basal area ($m^2 ha^{-1}$) (excluding heartwood)	21
Trees per hectare	836

year. Measurements were made within 20 min of sample collection. During the midday measurement period, once the needle water potentials had been determined, needles of the same age class were removed from the shoot and placed in a 2-cm^3 plastic syringe, which was then immediately frozen in dry ice. These samples were transferred to a freezer pending measurement of osmotic potential. Once thawed, osmotic potential was determined with a vapor pressure osmometer (Model 5100C, Wescor Inc., Logan, UT).

Sap flow and transpiration

Sap flux density was measured continuously by the heat pulse (compensation) method on four trees per treatment (one tree per plot) at a height of 1 m using a "Custom" system (Soil Conservation Centre, Palmerston North, NZ). Heat pulse velocity (HPV) was determined at different depths in the sapwood at four points around the circumference of the tree at 90° to each other. At each point, two thermistor probes were inserted in the xylem 10 mm above and 5 mm below a heating probe. Every 20 min, a 1-s heat pulse was applied and the HPV recorded. The HPV was converted to sap velocity based on the theory of Marshall (1958) with corrections as calculated by Swanson and Whitfield (1974) for inhomogeneities caused by sensor implantation wounds. The depth of sapwood, and hence inner boundary at which zero sap velocity was assumed, was determined from cores of wood taken with a Pressler borer at the end of the experiment. By inspecting the cores in strong diffuse light, a distinct color change was discerned, which marked the boundary between sapwood and heartwood. The sap velocity profile together with calculations of the area of conducting sapwood were used to calculate sap flux density.

Measurements of sap flux density within any 1-hour period were averaged for the four trees per treatment. This figure, together with an estimate of total sapwood area per unit ground area derived from wood core samples and basal area measurements (see Table 1), was used to estimate transpiration of the pine canopy on a ground area basis, *E*. Approximately 2500 hourly daylight measurements of transpiration were collected by this technique.

Soil-to-needle hydraulic resistance

On days when diurnal measurements of needle water potential were made, the hydraulic resistance between soil and needles was calculated from the relationship between needle water potential and sap flux per unit ground area:

$$R_{\text{soil-needle}} = (\Psi_L - \Psi_{L\text{predawn}})/E,$$

where $R_{\text{soil-needle}}$ is the hydraulic resistance between soil and needles (MPa s m^{-1}), Ψ_L is the needle water potential (MPa), $\Psi_{L\text{predawn}}$ is the predawn needle water potential, assumed to equal the soil water potential (MPa), and E is the estimate of transpiration of the pine canopy per unit ground area (m^3 m^{-2} s^{-1}), obtained from sap flux data. Linear interpolation between the hourly values of sap flux was used to estimate the value at the instant that water potential was measured.

Canopy stomatal conductance

Canopy stomatal conductance g_c, or its reciprocal canopy stomatal resistance, was computed from sap flux measurements on an hourly basis by inversion of the Penman-Monteith equation:

$$r_s = \frac{sr_a(A - \lambda E) + \rho_a c_p D}{\lambda E \gamma} - r_a,$$

where r_s and r_a are canopy stomatal and aerodynamic resistances, respectively (s m^{-1}), s is the rate of change of saturation vapor pressure with temperature (Pa K^{-1}), A is the net radiation available at the level of the pine canopy (W m^{-2}), λ is the latent heat of vaporization of water (J kg^{-1}), E is the canopy transpiration expressed on a ground area basis (kg m^{-2} s^{-1}), ρ_a is the density of dry air (kg m^{-3}), c_p is the specific heat of air (J kg^{-1} K^{-1}), D is the saturated vapor pressure deficit of air (Pa), and γ is the psychrometric constant (Pa K^{-1}). The canopy aerodynamic resistance was estimated from the horizontal wind speed above the canopy using the equation for the resistance to momentum transfer (Monteith and Unsworth 1990) with values for displacement height and roughness length taken from Grace (1981).

Growth and changes in LAI

Girth bands installed at 0.2 m above ground on all trees were used to assess the rate of sapwood growth. Current-year needle and shoot growth were determined by repeated measurements on three trees per treatment with vernier callipers. Six shoots per tree at mid-canopy level on trees within reach of the aerial walkway were identified and labeled, and needle length measurements were made on a sample of 10 current-year needles on each of these shoots on each measurement occasion. To estimate needle loss during the experiment, the bases of a sample of 1- and 2-year-old needles were marked with an indelible marker, and at points throughout the experiment a count was made of the marked needles remaining attached to the tree.

Statistical analysis

If graphical presentation of measured variables showed a clear interaction between treatment and measurement date for a particular variable, *t*-tests were performed to assess the significance of treatment at each date. If no clear interaction between treatment and date was evident, or if a confused picture was presented by the data, a two-way ANOVA with one repeated measure factor was made. In these instances a correction to the number of degrees of freedom using ε (Greenhouse-Geisser) was made as necessary. All tests were performed using the SAS package (SAS Institute Inc., Cary, NC).

Results

The experimental period was unusually dry for central Scotland. Between the beginning of March 1995 and the end of August 1995, rainfall was 128 mm less than the 20-year mean (Figure 1). To prevent the control plots from experiencing substantial soil water deficits, 125 mm of irrigation water was

provided during the experimental period.

As a result of winter rainfall being withheld, soil water integrated over the top 20-cm depth was significantly reduced in the drought-treated plots from the beginning of measurements in April 1995 (Figure 2, upper panel). Soil water content in the drought treatment fell steadily to a minimum of 5% VWC by the end of August 1995. The fluctuating soil water in the control treatment was mostly a result of periodic irrigation over the season, but water content never fell below 20% VWC. Soil water integrated over 50-cm depth (not presented) in the control treatment showed similar behavior to that over the upper 20 cm. In the drought treatment, the values over 50-cm depth fell steadily from 21% VWC in mid-May 1995 to 11% VWC by the end of August 1995.

Predawn needle water potential in the drought treatment was consistently more negative than in the control treatment throughout the season (Figure 2, panel 2). The greatest differences developed from mid-July 1995; all data from this date onward showed significant differences ($P < 0.05$) until the covers were removed from the drought-treated plots at the beginning of November 1995. Values in the control treatment never fell below -0.55 MPa, whereas a minimum value of -0.75 MPa was recorded toward the end of August 1995 in the drought treatment. The abrupt recovery of predawn water potential in mid-September 1995, which can be regarded as the termination of the drought treatment, coincided with a slight inflection in the curve of soil water content. At this time there were several heavy rain events, which may have lead to lateral movement of water below the installed soil water barrier.

The seasonal pattern of transpiration is evident in the control treatment (Figure 2, panel 3). Values of up to 2 mm day^{-1} occurred during the summer months. Day-to-day variation was large and consistent with variable weather conditions. To remove daily and seasonal effects, the ratio of transpiration rates

Figure 2. Seasonal variations in the volumetric soil water content integrated over the top 20-cm soil depth, the predawn needle water potential ($\Psi_{Lpredawn}$), and the daily transpiration for drought ($\bigcirc$) and control ($\bullet$) treatments during 1995 (upper panels). The lowest panel is the drought treatment daily transpiration divided by the control treatment daily transpiration. Error bars indicate ± 1 SE.
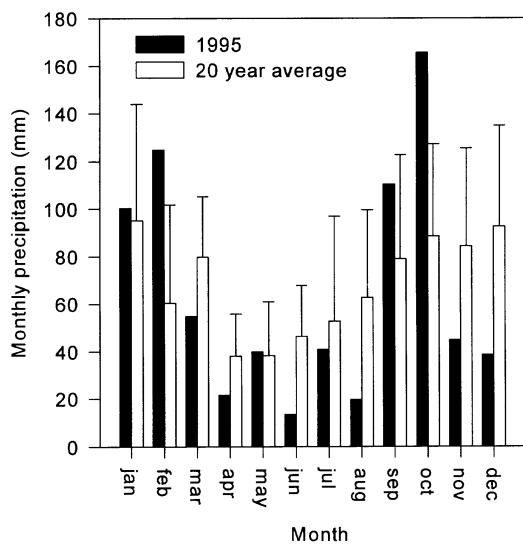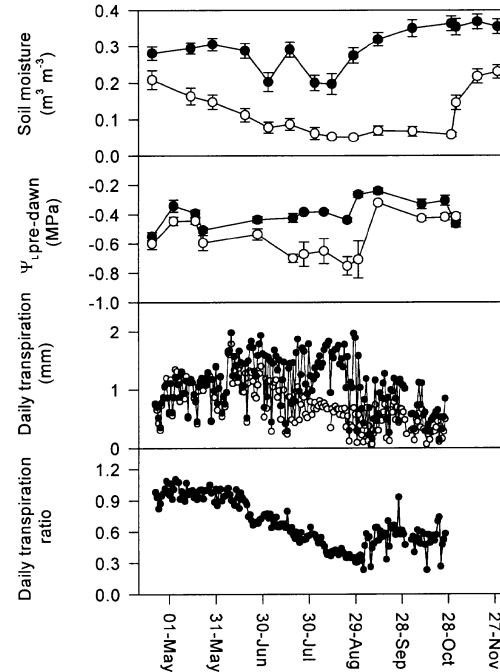

Figure 1. Mean monthly rainfall distribution (1977–1997) compared to rainfall received during the drought year (1995). The rain gauge was sited 4 km south of the experimental plots. Error bars indicate 1 SD.

in control and drought-treated plots is shown in the lowest panel (Figure 2). Transpiration in the drought treatment was largely unaffected until mid-June 1995 and then showed a steady decline to 30% of the control value by the end of August 1995, after which some recovery occurred. Between mid-May 1995 and the end of August 1995, 140 mm of water was transpired in the control treatment, whereas only 93 mm of water was transpired in the drought treatment. Soil water measurements in the drought treatment over the same time period showed that this corresponded to a change of 50 mm in water content in the top 50 cm of soil.

The minimum daily leaf water potentials were not significantly different ($P > 0.05$) between drought and control treatments except at the height of the drought at the end of August 1995 (Table 2). Midday bulk needle turgor was consistently greater in the control treatment than in the drought treatment, although the difference was not significant ($P < 0.05$) except at the height of the drought (Table 2).

The diurnal behavior of sap flux, canopy stomatal conductance, leaf water potential and meteorological variables on four selected days during the drought period are presented in Figure 3. On May 4, 1995, there were no significant differences between treatments with respect to any of the variables. The air saturation vapor pressure deficit (VPD) on this day was relatively high for the time of year in central Scotland. Canopy stomatal conductance showed an initial rise in the morning followed by a midday decline and partial recovery in the evening, a pattern that was repeated on other days (Figure 3).

Table 2. Plant water relations parameters during the development of the drought in 1995 and one day during the following spring (May 10, 1996) after the drought had been terminated. Values for minimum leaf water potential (Ψ_{Lmin}) and midday leaf turgor are the means of four values per treatment. Midday canopy stomatal conductance (g_c) was calculated from transpiration (sap flux) measurements from four trees per treatment. The *P* values refer to *t*-tests made between the treatments.

Date	Diurnal Ψ_{Lmin} (MPa)		*P*	Midday leaf turgor (MPa) and {osmotic potential}		*P*	Midday g_c (mm s^{-1})	
	Control	Droughted		Control	Droughted		Control	Droughted
4 May, 95	−0.97	−1.12	0.12	1.14 {−2.11}	1.07 {−2.18}	0.49 {0.50}	4.0	4.0
23 May, 95	−1.00	−0.95	0.71	1.04 {−1.97}	0.93 {−1.86}	0.52 {0.16}	4.5	4.6
13 June, 95	−0.98	−0.94	0.66	0.97 {−1.95}	0.85 {−1.79}	0.27 {0.10}	4.9	4.5
27 June, 95	−1.08	−1.17	0.44	0.76 {−1.84}	0.64 {−1.80}	0.37 {0.66}	4.5	3.3
27 July, 95	−0.96	−1.17	0.09	1.05 {−1.52}	0.88 {−1.64}	0.08 {0.28}	1.6	0.9
9 August, 95	−1.19	−1.41	0.11	0.73 {−1.71}	0.62 {−1.96}	0.09 {< 0.01}	3.9	1.6
31 August, 95	−0.68	−1.08	< 0.01	0.89 {−1.57}	0.64 {−1.72}	< 0.01 {0.07}	8.8	2.5
13 Sept., 95	−0.89	−1.11	0.11				3.7	2.4
11 October, 95	−0.79	−0.91	0.15	1.15 {−1.57}	1.05 {−1.60}	0.25 {0.79}	7.1	3.6
10 May, 96	−0.91	−0.98	0.53				8.4	7.2

On June 27, 1995, a day with similar meteorological conditions and patterns in bulk leaf water potentials to May 4, 1995, there was a significant decline in sap flux in the drought treatment, although there was no apparent difference between bulk leaf water potential in the two treatments (Figure 3). Between August 9 and 31, 1995, a continuing decline in sap flux in the drought treatment was evident. August 31, 1995, was a dull overcast day with low PAR and VPD. The apparent sensitivity of canopy stomatal conductance to VPD on this day was high.

The relationships between sap flux and leaf water potential on three days during the drought and one day in the following spring are illustrated in Figure 4. The relationships were more or less linear, with an increasing slope for the drought treat-ment over the period. The data for the drought treatment on August 9, 1995 suggest hysteresis in the relationship, a tendency that was noted on several other days when the drought was most extreme (data not presented). There was no significant difference between the slopes of this relationship on May 10, 1996.

The soil-to-leaf hydraulic resistance, obtained as the gradient of the relationships presented in Figure 4, was more or less constant in the control treatment but showed a progressive increase by a factor of approximately three in the drought treatment (Figure 5). Differences between treatments were significant ($P < 0.05$) between June 27 and August 31, 1995.

Trends in canopy stomatal conductance are best expressed as a fraction (i.e., g_c midday drought/g_c midday control). There
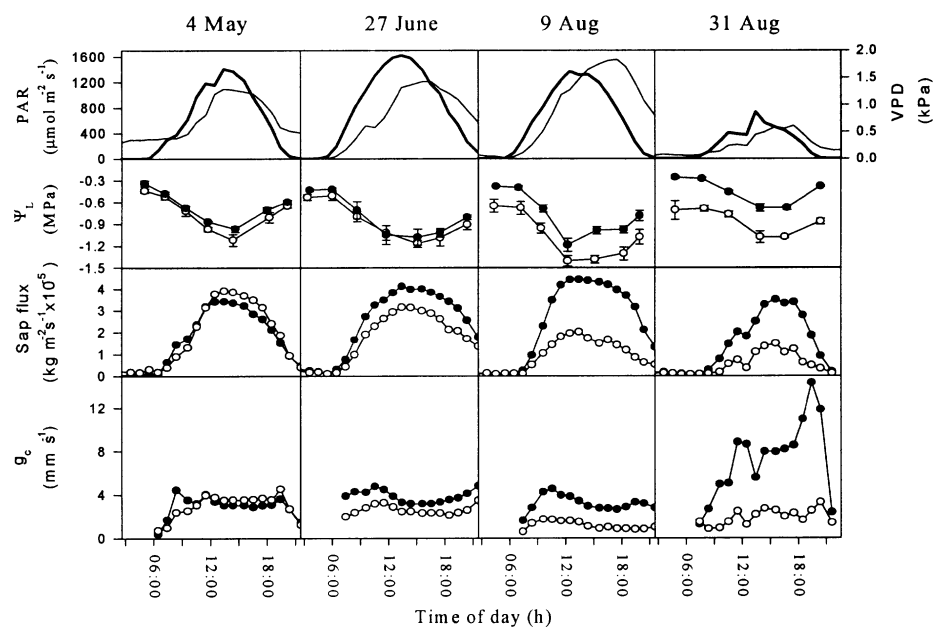

Figure 3. Diurnal courses of physiological and meteorological variables during four days as the drought progressed in 1995. Photosynthetically active radiation (PAR, heavy line), air vapor pressure deficit (VPD, fine line), needle water potential (Ψ_L), sap flux, and canopy stomatal conductance (g_c). Symbols: (○) drought treatment, (●) control. Error bars indicate ± 1 SE.
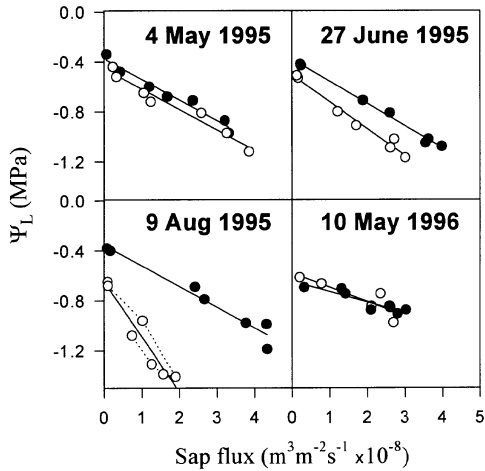
Figure 4. Relationship between needle water potential (Ψ_L) and sap flux (on ground area basis) for both drought ($\bigcirc$) and control treatments ($\bullet$) for 3 days during the development of the drought in 1995 and 1 day the following spring after the drought had been terminated (May 10, 1996). The dotted line shown on August 9 (drought treatment) illustrates a slight hysteresis in the relationship.

Figure 6. Midday canopy conductance in the drought treatment relative to that in the control treatment plotted against volumetric soil water content (integrated over the top 20 cm) in the drought treatment. The triangle refers to a measurement made one day in spring 1996 after the termination of the drought.

was no response of canopy stomatal conductance to soil water content as measured to 20-cm depth in the drought treatment until water content had declined to 12% VWC (Figure 6). Between 12 and 5% VWC, the decline in canopy stomatal conductance was linear. In spring 1996, after the termination of the drought, canopy stomatal conductance almost returned to its pre-drought value (triangular point in Figure 6).

Measurements of the RWC of the sapwood in the trunk over the drought period revealed a significant Treatment × Date interaction $F (8,48) = 7.21$, $P < 0.01$ (Figure 7, lower panel), which was the result of a significant increase in RWC of the control treatment $F (8,24) = 26.35$, $P < 0.01$, rather than a decline in RWC of the drought treatment $F (8,24) = 3.85$, $P > 0.09$. There was no evidence of a significant treatment effect at any date. The RWC of the xylem of the shoots was considerably higher than that of the bole (Figure 7, upper two panels) with a significant difference between treatments in previous years shoots, when grouped over all dates $F (1,42) = 8.61$, $P < 0.05$ (Figure 7, middle panel). There was no evidence of a
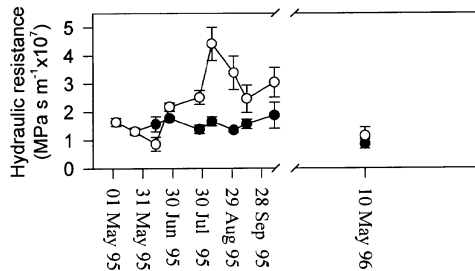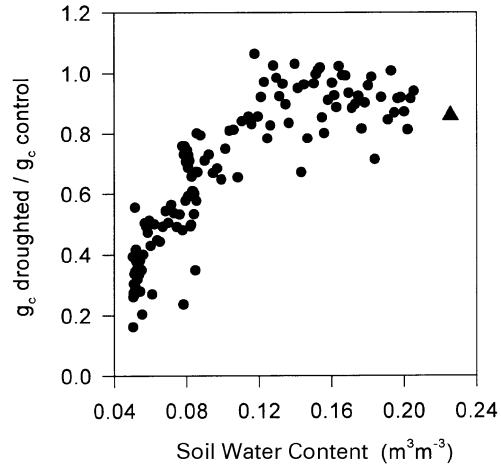
significant treatment effect on any date.

The imposed drought resulted in a 14, 34 and 20% reduction in basal area, shoot and needle growth, respectively, compared with the control by the end of the season (Figure 8, 1995). Needle growth was expressed relative to the final length of needles on the same shoot in 1994 in order to remove variability attributable to differing light environments. In the case of
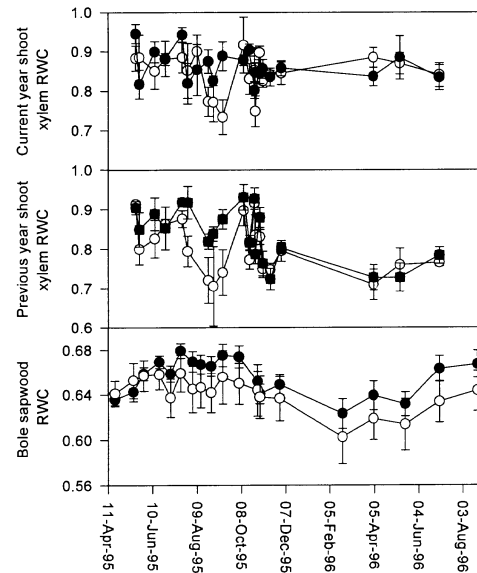

Figure 7. Seasonal changes in the relative water content (RWC) of the xylem in current-year (upper panel) and previous-year shoots (middle panel), together with the RWC of the sapwood (to 5-cm depth) in the bole of the trees during the drought year (1995) and the following year. Symbols: ($\bigcirc$) drought, and ($\bullet$) control treatment. Error bars indicate $1 \pm$ SE, $n = 4$.

Figure 5. Seasonal changes in the soil-to-needle hydraulic resistance in the drought ($\bigcirc$) and control ($\bullet$) treatments. Error bars indicate ± 1 SE.

shoot and needle growth, the differences between treatments were evident from an early stage in the drought (Figure 8, 1995, bottom two panels). However sapwood growth at the base of the tree showed a reduction in the drought treatment only from mid-August 1995, at a point when drought was becoming extreme (Figure 8, 1995, upper panel). There was no evidence of increased needle loss during the season in the drought treatment. Growth measurements in the year following the drought (Figure 8, 1996), when no significant soil water deficit developed, indicated no difference in needle growth by the end of the season between plants previously subjected to drought and plants in the control treatment, but basal area growth of the previously drought-treated plants was 23% less than in the control treatment.

Discussion

For the drought treatment, a significant decline in canopy stomatal conductance was observed once a threshold soil water deficit had been reached (Figure 6). Based on saturated soil water content and the minimum attained stable soil water content, approximately 57% of the extractable soil water had been removed from the top 50 cm of soil before transpiration was reduced below control-treatment values. Rutter (1967) reported a value of 54% based on water available between 0.01 and 0.1 MPa over a soil depth of 180 cm. Stewart (1988) found
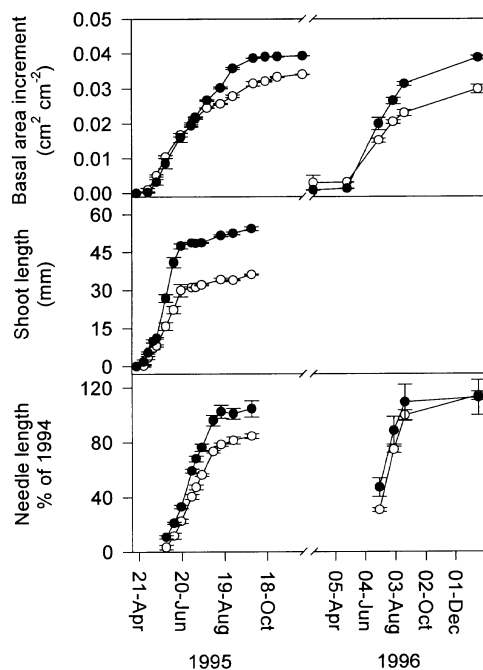

Figure 8. Seasonal changes in tree growth for the drought (○) and control treatments (●) during 1995 (the drought period) and the following year. Basal area increment (upper panel) is referenced to basal area measured in April 1995. Shoot length data (middle panel) were unavailable for 1996. Needle length was expressed relative to 1994 to remove effects of differing light environments between the sampled needles. Error bars indicate ± 1 SE.

no decline in canopy conductance until a soil water deficit of 78% was reached over 90-cm depth. More recently Kelliher et al. (1998) computed the threshold soil water deficit from various studies on pines as a fraction of the soil water when soil water potential was 5 kPa and reported a mean value of 50%. Studies on juvenile plants report similar threshold responses for both woody and herbaceous species (Gollan et al. 1985, Turner et al. 1985). In our study, 54% of the water transpired in the drought treatment was extracted from below 50-cm depth, and yet a strong decline in canopy stomatal conductance was evident that appeared to be in response to soil water deficit in the upper soil horizons. Because most roots are contained in the upper horizons (Roberts 1976a), the response of canopy stomatal conductance appears to be linked to the soil water deficit experienced by the majority of the roots, even if some water is being extracted from greater depth.

The range of midday values of canopy stomatal conductance (Table 2) is consistent with other data available for Scots pine (Hellkvist et al. 1980, Whitehead et al. 1984, Lindroth 1985, Beadle et al. 1985b, Stewart 1988, Jackson et al. 1995a, Kostner et al. 1996). Diurnal behavior of canopy stomatal conductance was dependent on microclimate and appears to be highly sensitive to VPD (Figure 3), which is consistent with other reports (Ng 1978, Beadle et al. 1985a). The partial recovery of stomatal conductance later in the day (Figure 3) is rarely reported in the literature for coniferous species, but is apparent in data presented for *Pinus pinaster* Ait. (Figure 7 in Loustau et al. 1996).

The tight stomatal control of transpiration appears not to be mediated by declining leaf water potential, because a clear reduction in canopy stomatal conductance was observed between May 4, 1995 and June 27, 1995 without any apparent differences between treatment bulk leaf water potential (Figure 3). It has been suggested that such a response is indicative of feed-forward signaling from root to shoot, perhaps involving a chemical signal (abscisic acid) (Blake and Ferrell 1977, Davies and Zhang 1991, Tardieu and Davies 1993). However, this interpretation would be contested by Saliendra et al. (1995) who suggested that bulk leaf water potential measurements mask the water potential gradients in the leaf that are likely be important in controlling stomatal behavior. We found no evidence for the feed-forward hypothesis for stomatal closure in response to air drought as proposed by Farquhar (1978), because there was no evidence of decreasing transpiration rates at high VPDs.

The values for RWC in the bole of the tree are consistent with values reported by Waring and Running (1978) for Douglas-fir, Running (1980a) for lodgepole pine, and Waring et al. (1979) for Scots pine, although Roberts (1976b) and Jackson et al. (1995a) report lower values for Scots pine during dry summer conditions. Needle water potential never fell below below −1.5 MPa (Table 2) and thus prevented the development of substantial xylem embolism (Figure 7) that would have resulted in an increase in the hydraulic resistance of the woody tissue. This view is consistent with the fact that no one has identified a mechanism by which refilling of embolized xylem can occur under significant tensions (Borghetti et al. 1991, Edwards et al. 1994). Thus, unlike some broad-leaved

Table 3. Data from the literature for the soil-to-needle hydraulic resistance expressed on a unit basal area sapwood basis, unit ground area basis and unit needle area basis.

Hydraulic resistance			Comments and source
Sapwood (MPa s m^{-1} × 10^4)	Ground (MPa s m^{-1} × 10^7)	Needle (MPa s m^{-1} × 10^7)	
3.2	1.5	2.8	41-year-old Scots pine, no drought, Devilla, U.K., this paper
2.5	1.2	2.8	41-year-old Scots pine (Plot 1), UK, Whitehead et al. 1984
1.9	0.5	1.5	41-year-old Scots pine (Plot 2), UK, Whitehead et al. 1984
1.7	–	–	21-year-old Norway spruce, Nancy, France, Granier et al. 1989
1.4	–	–	37-year-old maritime pine, Landes de Gascogne, FR, Granier et al. 1989
1.0	0.7	1.9	64-year-old maritime pine, Ribatejo, Portugal, Loustau et al. 1996
0.8	0.3	0.6	38-year-old Scots pine, Thetford, UK, Jackson et al. 1995*a*

species that show the ability to refill embolized xylem at the beginning of the season (Sperry et al. 1988, Sperry 1993, Sperry et al. 1994), Scots pine appears to have evolved mechanisms to prevent the development of widespread embolism.

In this study, transpiration and canopy conductance were expressed on a ground area basis. It might be thought that if they had been expressed on a foliage area basis, the reduced foliage area in the drought treatment, which was a consequence of reduced current needle growth (Figure 8), might explain the dramatic reduction in transpiration (Figure 2). However, it can be shown this is not the case. If we conservatively estimate that current-year growth accounts for 50% of canopy leaf area, (a figure of 36% is suggested by Beadle et al. 1982), the 20% decrease in needle length can account for only 10 of the 65% decrease in daily transpiration at the height of the drought (Figure 2, lowest panel). Thus, regulation of stomatal conductance appears to be the mechanism by which Scots pine maintains tight control over transpiration.

The linear relationships in Figure 4 and the lack of significant hysteresis suggest that the hydraulic capacitance of the trees is unimportant and that the treatment of the soil-to-needle water transport system as a simple resistor is appropriate. The direction of the rather small hysteresis on August 9, 1995 (Figure 4) indicates an increase in hydraulic resistance during the day and not a release of stored water from aboveground tissue. Because no significant diurnal changes in the RWC of the xylem were observed, this increase in resistance must be located either within the roots, due to cavitation (Sperry and Ikeda 1997), or in the bulk soil itself.

Values for the hydraulic resistance between soil and needles (Figure 5) are of similar magnitude to those reported for pine and other coniferous species (Table 3). Granier et al. (1989) reported a threefold increase in hydraulic resistance in *Abies bornmulleriana* Mattf. as predawn water potential declined from −0.18 to −1.14 MPa; Running (1980*b*) reported a threefold increase in resistance in 40-year-old Douglas-fir, and figures in Lu et al. (1996) suggest a twofold increase in resistance in 30-year-old Norway spruce, both over the same range of predawn water potentials as reported in this paper. In these studies it was suggested that the increase in resistance was probably located at the soil–root interface or in the soil itself. Because no substantial seasonal development of embolism

was observed in aboveground tissue, the majority of the increased hydraulic resistance in this study must be located below ground. This is consistent with the finding that hydraulic resistance returned to pre-drought values once the soil water deficit was eliminated (Figure 5, May 1996), and no substantial changes in plant xylem RWC were observed over the same period (Figure 7).

Needle, shoot and basal area growth were reduced during the drought period (Figure 8, 1995), although basal area increment was affected only when the drought became extreme. Shoots are known to be highly sensitive to water stress and a threshold soil water potential at which diameter growth declines has been reported for other pines (Dougherty et al. 1994). In 1996 when no significant soil water deficit developed, needle growth was unaffected by the end of the season, but a large reduction in basal area increment was observed in plants that had been subjected to drought in 1995 (Figure 8). The bole of the tree is a strong carbon sink and there were, perhaps, insufficient resources stored during exposure to drought or assimilated in the season following drought treatment to allow basal area growth comparable to that in the control treatment. Considering that both canopy stomatal conductance and needle water potential had recovered to pre-drought values in 1996 (Figure 6 and Table 2, respectively), reduced assimilation in the post-drought year seems unlikely. Partitioning of resources in favor of root rather than sapwood growth is an alternative explanation. It is likely that the drought treatment caused high root mortality, in which case resources may have been directed to rebuild the root system in 1996 at the expense of basal area growth.

Conclusions

In mature Scots pine, stomatal closure occurred in response to soil dryness at a threshold soil water deficit. This response appeared to be linked to the soil water experienced by the majority of the roots, even if substantial water was being extracted from greater depth. Stomatal closure prevented needle water potentials declining below −1.5 MPa. This response prevented the development of substantial xylem embolism in aboveground woody tissue. The large increase in the hydraulic resistance between soil and needles that developed as a conse-

quence of soil drought is likely to be located in the root or soil compartment of the hydraulic system. This increased resistance was not carried over into the following growing season when soil water had returned to pre-drought values. Reduced growth in the season following the drought is therefore unlikely to be a consequence of embolism carried over from one year to the next.

Acknowledgments

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