

Stomatal conductance, transpiration, and resistance to water uptake in a *Pinus sylvestris* spacing experiment

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Stomatal conductance was measured with porometers in two plots of *Pinus sylvestris* L. with markedly different tree spacings (plot 1, 608 stems ha⁻¹; plot 2, 3281 stems ha⁻¹), and hourly rates of transpiration were calculated using the Penman-Monteith equation at intervals throughout one growing season. Stomatal conductance varied little in relation to height or age of foliage. There was a linear decrease in canopy conductance with increasing water vapour pressure deficit of the air. Transpiration rates on both plots increased during the summer (maximum 0.3 mm h⁻¹); rates on plot 1 were always lower (ca. 0.7 times) than on plot 2. Needle water potentials were similar throughout the season and only slightly lower on plot 1 than on plot 2. The mean hydraulic resistance of the trees on plot 1 was 2.4 times that on plot 2. The results support a hypothesis that considers the changes in transpiration rate, conducting cross-sectional area, canopy leaf area, water potential, and hydraulic resistance following thinning as a set of homeostatic relationships.

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La conductance stomatique a été mesurée à l'aide de poromètres dans deux sites expérimentaux de *Pinus sylvestris* L. différemment espacés (placette-échantillon No. 1, 608 tiges ha⁻¹; placette-échantillon No. 2, 3281 tiges ha⁻¹) et les taux horaires de transpiration ont été calculés en utilisant l'équation de Penman-Monteith à intervalles tout au long d'une saison de croissance. La conductance stomatique a varié très peu en relation avec la hauteur ou avec l'âge du feuillage. Une diminution linéaire de la conductance de la couverture du feuillage a été notée suivant une augmentation du déficit de tension de vapeur. Les taux de transpiration, mesurés sur les deux sites, ont augmenté pendant l'été (maximum de 0.3 mm h⁻¹); les taux sur la placette-échantillon No. 1 étaient toujours inférieurs (ca. 0.7 fois) comparativement à la placette-échantillon No. 2. Les potentiels hydriques des aiguilles étaient semblables tout au long de la saison bien que les valeurs pour la placette-échantillon No. 1 étaient quelque peu inférieures comparativement à la placette-échantillon No. 2. Les résultats soutiennent une hypothèse que considère que les modifications des taux de transpiration, la surface conductrice en coupe, la surface du couvert, le potentiel hydrique et la résistance hydraulique à la suite d'un élagage du feuillage, constituent une mosaïque de paramètres en relation homéostasique.

[Traduit par le journal]

Introduction

Management of forest stands usually involves thinning operations after canopy closure with resulting changes in tree spacing, number and size (depending on type of thinning) of stems, with likely consequent changes in the hydraulic resistance between soil and canopy. Jarvis (1975) outlined the changes in volume flow, hydraulic resistance, and leaf water potential that might be expected to occur after thinning (Fig. 1). In a forest where there are n stems of resistance R_p per unit area, the resistance of the pathway between soil and canopy, R_p , is equal to R_p/n . The immediate consequence of removing one-half of the trees and leaf area at canopy closure, A_1 , is to double R_p and to allow more radiation to be absorbed by individual tree crowns than previously. This results in a fall in the transpiration from the stand ($E_1' < E_1$), but an increase in the flow of water in each remaining tree ($q' > q$). If Darcy's law applies, the resulting needle water potential will be lower than it was previously ($\psi_1' < \psi_1$). As the canopy regrows to the leaf area index at canopy closure, by a doubling of the leaf area on each tree, E_1' increases to E_1 again and q' to $2q$. Unless the stem resistance, R_p , is reduced in proportion, much lower values of ψ_1 would result with consequent physiological "stress" to the tree.

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In practice, however, this does not occur because the sapwood cross-sectional area also increases in proportion (Whitehead and Jarvis 1981), so that R_p falls to a new low value and R_p returns to its original value. The end result is that one-half of the number of trees have the original leaf area index, twice the leaf area, the sapwood area, the volume flow per tree, and half the resistance per stem. With ψ_1 remaining the same, low leaf water potentials which would have damaging physiological effects on growth processes are avoided.

Jarvis (1976) compared water potentials and transpiration rates for plantations of Scots pine (*Pinus sylvestris* L.) with 800 stems ha⁻¹ and Sika spruce (*Picea sitchensis* (Bong.) Carr) with 4100 stems ha⁻¹ at two different locations. In both canopies ψ_1 fell by the same amount during the day to a minimum of about -1.6 MPa, and transpiration rates from both canopies were about 0.55 mm h⁻¹ irrespective of tree spacing. The flow resistances were therefore identical for the two stands, although the hydraulic resistance of individuals was much larger in the *Picea* stand than in the *Pinus* stand and was proportional to the number of trees present per hectare. This surprising result for two such dissimilar species suggested that differences in leaf area, sapwood area, and permeability must compensate one another to lead to the same values in ψ_1 at the same stand transpiration rates.

The work reported here on *Pinus sylvestris* was done in a spacing experiment, in which thinning some time before the measurements had maintained different tree spacings. This

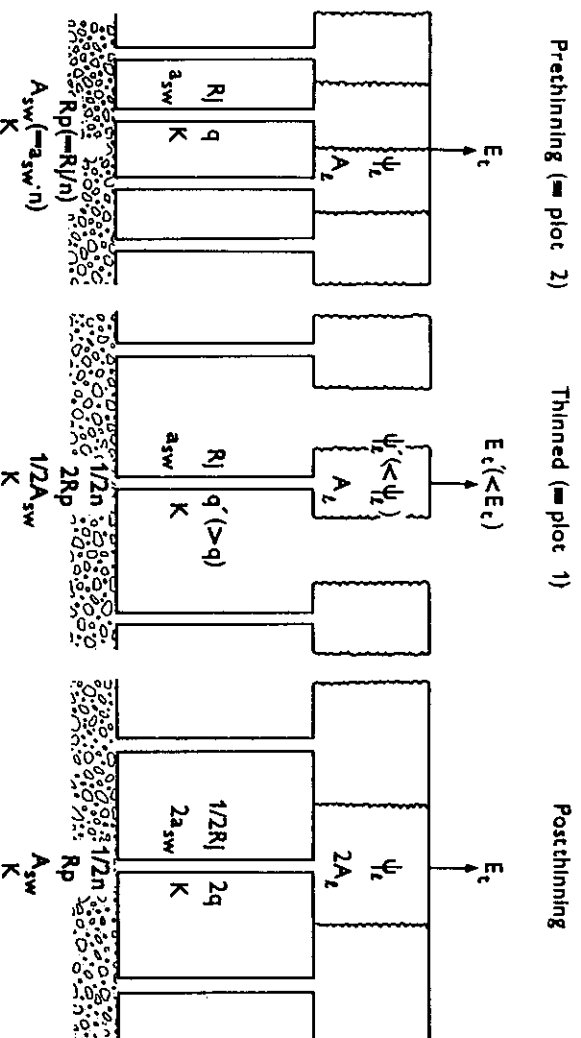


FIG. 1. Change in transpiration rate (E_t), foliage area (A_f), sapwood basal area (A_{sw}), foliage water potential (ψ_f), and resistance in the pathway between soil and canopy (R_p) following thinning as proposed by Jarvis (1975). q , a_{sw} and R_f refer to the transpiration flux, sapwood cross-sectional area, and stem resistance per unit area in n individual trees, respectively. K is the permeability for the stand and for an average individual tree.

TABLE 1. Description of the characteristics of the trees in the two forest plots from measurements made in 1976

	Plot 1	Plot 2	Plot 1 : plot 2
No. of trees per hectare	608	3281	0.2
Mean dbh \pm SE*	mm 233 \pm 37	146 \pm 32	1.6
Mean tree height \pm SE	m 15.0 \pm 0.3	15.0 \pm 0.2	1.0
Basal area	$m^2 ha^{-1}$ 26.6	57.7	0.5
Sapwood basal area	$m^2 ha^{-1}$ 21.0	39.8	0.5
Sapwood area per tree	m^2 0.035	0.012	2.9
Leaf area index	$m^2 m^{-2}$ 2.4	3.1	0.8
Leaf area per tree	m^2 39.5	9.5	4.2

*Tree diameter at breast height (1.3 m above ground) \pm standard error.

experiment provided an opportunity to test aspects of the hypothesis in two stands that were in conditions analogous to prethinning and postthinning.

Materials and methods

Site

Measurements were made on two plots, each consisting of approximately 0.1 ha of Scots pine (*Pinus sylvestris* L.) planted by the Forestry Commission in 1936 at Roseisle, part of the Laigh of Moray forest (latitude 57°42' N and longitude 3°30' W) in northeastern Scotland. The two adjacent plots were part of a spacing experiment and there were 608 and 3281 stems ha^{-1} on plots 1 and 2, respectively. Thinning had taken place in 1955, 1959, and 1963, and no subsequent treatment was carried out before measurements in this paper were made in 1977. The management of the trees, distribution of diameters within the plots, and vertical distribution of foliage have been described previously by Whitehead (1978) and a summary is given in Table 1.

Meteorological variables

Meteorological measurements were made at 5 min intervals, integrated over hourly periods, and recorded on magnetic tapes by an automatic weather station (Strangeways 1972) on a tower 5 m above the canopy on plot 2. Total incoming radiation, net radiation, dry and wet bulb air temperatures, wind speed and direction, and rainfall were measured.

Stomatal conductance

Measurements of stomatal conductance using a null-balance diffusion porometer (Beardstall et al. 1972) were made at 2-h intervals on shoots of both canopies during 25 complete days, spread throughout the growing season from March to October in eight measurement periods comprising 5–8 consecutive days. Additional data for parts of days were also collected.

The shoots sampled in the canopy for stomatal conductance were distributed among three levels and two needle age-classes within each stand. In level 1 at the top of the canopies all shoots were almost always sunlit; in level 3 at the bottom all shoots were almost always shaded and shoots at level 2 were sometimes shaded, sometimes sunlit. The two age-classes used were current year expanding shoots and 1-year-old fully expanded shoots. The same shoots were used for several days, then removed, and the projected surface area of the needles was measured using an optical planimeter (LI-3100, LI-COR Inc., Lincoln, NE). Generally, 20–30 shoots were sampled in each canopy at 2-h intervals during daylight in each measurement period. Stomatal conductance measurements are all expressed on a projected area basis. To convert to a total surface area basis for Scots pine stomatal conductances should be divided by 2.6 (based on geometrical measurements assuming needles are hemispherical).

Stomatal conductances of the canopies on a ground area basis (i.e., canopy conductances) were calculated from the sum of the stomatal conductances for each level, i , and age-class, j , of needles in the canopy. For three levels and two age-classes of needles of average stomatal conductance $g_{i,j}$ and leaf area index $L_{i,j}$, the canopy conductance is given by

$$[1] \quad g_c = \sum_{i=1}^3 \sum_{j=1}^2 (g_{i,j} L_{i,j})$$

Water potential

Needle water potential, ψ_n , was measured on three individual fas-

cicles from level 2 in each canopy in a pressure chamber (Roberts and Fourn 1977) during each set of conductance measurements. It was assumed that these values of ψ_s represented the average water potential of the canopy. Large variations in water potential do not usually occur between the top and bottom of open canopies of Scots pine (D. Whitehead, unpublished data). Fascicles were collected, stored in plastic tubes in a humid environment, and water potentials were measured within 10 min.

Stem temperatures

Stem temperatures were measured using copper-Constantan thermojunctions embedded into the centre of the sapwood at three heights (base, 1.3 m aboveground level, and midcrown) in one tree on each plot. Measurements were made before or soon after dawn and at midday.

Calculation of transpiration rates

Hourly rates of transpiration by the trees in the stands (not including the understorey), E_s , were calculated using the Penman-Monteith equation (Monteith 1965) where

$$[2] \quad \Omega E_s = \frac{sA + c_p p D g_a}{s + \gamma (1 + g_a/g_s)}$$

The rate of transpiration depends strongly on the available energy, A , the water vapour pressure deficit of the air, D , the canopy conductance, g_a , and the canopy boundary layer conductance, g_s . The physical coefficients c_p , p , γ , and λ are, respectively, the specific heat of the air, the density of the air, the psychrometric constant, and the latent heat of evaporation of water, all weak functions of air temperature (T_a). The slope (s) of the curve relates the saturated vapour pressure of water to temperature at the appropriate air temperature (for appropriate units see Monteith (1973)).

McNaughton and Jarvis (1983, Eq. 8) rewrote the Penman-Monteith equation in the form

$$[3] \quad \Omega E_s = \Omega \left(\frac{s}{s + \gamma} \right) A + (1 - \Omega) \frac{pc_p D g_e}{\gamma}$$

where

$$[4] \quad \Omega = \left(1 + \frac{\gamma}{s + \gamma} \cdot \frac{g_a}{g_s} \right)^{-1}$$

In [3] parameter Ω sets the relative importance of transpiration at the equilibrium rate (first term on the right-hand side) and at the imposed rate (second term on the right-hand side). The equilibrium rate is the rate that would be achieved if the surface were isolated from the regional airstream by a very large resistance; the imposed rate is the rate that would occur if the regional airstream were imposed at the surface with no local adjustment of the vapour pressure deficit. Thus Ω can be regarded as a coupling factor that describes how closely the vapour pressure deficit at the canopy surface is linked to the regional vapour pressure deficit. When $\Omega \rightarrow 1$ the coupling is weak and transpiration equals the equilibrium rate and is determined largely by incoming radiation and air temperature. When $\Omega \rightarrow 0$ the coupling is strong and transpiration is determined principally by the regional vapour pressure deficit.

Measurements of photon flux density (400–700 nm) using a quantum sensor (LI-COR Inc.) above and below the two canopies were used to calculate the proportions of net radiation absorbed by the two canopies. Photon flux densities under the canopies were calculated from the means of measurements made at 0.5-m intervals along five transects, each 10 m long. The proportions of absorbed radiation were 86.6 and 92.5% for plots 1 and 2, respectively. Values of A in [2] were calculated from net radiation measured by the weather station multiplied by these fractions. Although the transmission of canopies for visible and net radiation is not identical (see Table III of Jarvis et al. (1976)), the difference is not large and it will be shown later that this is a second-order correction that is being applied to net radiation to give A . It will be shown later that the transpiration rate is insensitive to the exact value of A .

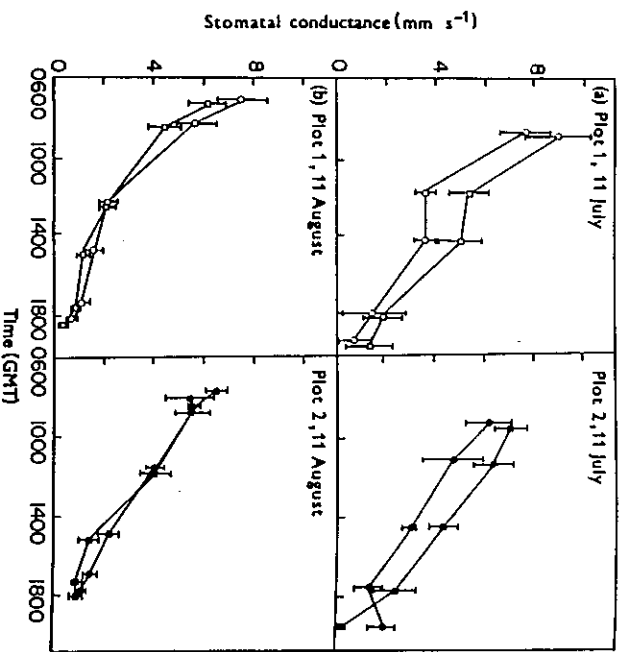


Fig. 2. Stomatal conductances for two age-classes of foliage in the canopies of plots 1 (open symbols) and plot 2 (closed symbols) for the dates shown in 1977. \circ and \bullet , current year shoots; \square and \blacksquare , 1-year-old shoots. The data shown are means of 10 measurements for current foliage and means of 6 measurements for 1-year-old foliage with ± 1 SE. GMT, Greenwich mean time.

Average hourly wind speeds at the top of the canopies at height h , $u(h)$ in metres per second, were calculated from measurements at 5 m above the top of the canopy assuming a logarithmic wind profile and neutral conditions. Values of zero plane displacement ($= 0.76$ h) and roughness length ($= 0.06$ h) were taken from Oliver (1971). Canopy boundary layer conductances were calculated from an empirical relationship based on 15 studies of wind profiles (Jarvis et al. 1976, Table V) as follows:

$$[5] \quad g_a = 0.1 u(h) \quad (\text{m s}^{-1})$$

While this estimate does not include the contribution to the mass transfer of the form drag at the leaf surfaces, the estimate of the transpiration rate is very insensitive to the value of the boundary layer conductance because it is so large (McNaughton and Black 1973).

Calculation of resistance and permeability

In a one-dimensional rigid flow system with no capacitance, the difference in water potential between soil and foliage is linearly dependent on the volume flow of water (e.g., Slatyer 1967). Ignoring branching, we may equate transpiration from the canopy, E_s , with the drop in potential (Jarvis 1975) and define the resistance of the entire pathway of parallel- and series-linked conduits from soil to leaves, R_p ,

$$[6] \quad R_p = (\psi_{pd} - \psi_l - hp_w g)/E_s \quad (\text{MPa s m}^{-1})$$

where ψ_l (megapascals) is the average leaf water potential in the canopy, ψ_{pd} is the average soil water potential (the average predawn leaf water potential which was assumed equal to the effective soil water potential in the major part of the rooting zone (Slatyer 1967)), and $hp_w g$ is the gravitational potential of a column of water of density ρ_w and height h (0.01 MPa m^{-1}). In the calculation of resistance for individual trees, $R_i = \Delta\psi/g$, where g is the average transpiration rate per tree ($= E_s/n$), and n is the number of stems per hectare. Thus $R_i = R_p/n$ (Fig. 1).

When comparing different stand structures, as in plots 1 and 2, it is desirable to isolate simple geometric properties of the flow pathway, such as the length, l , and the cross-sectional area from the overall

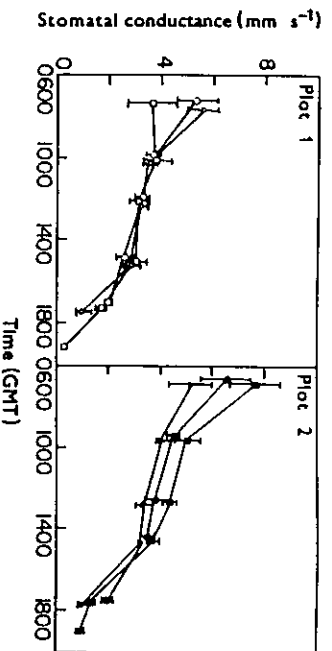


FIG. 3. Stomatal conductances at three levels in the canopies of plot 1 (open symbols) and plot 2 (closed symbols) on 10 August 1977. ● Level 1, top (○ and ●); level 2, middle (□ and ■); level 3, bottom (△ and ▲). The data shown are means of 6 measurements for levels 1 and 3, and 10 measurements for level 2 with ± 1 SE.

resistance. Thus following Darcy's law the permeability of the pathway between soil and leaves can be defined as

$$[7] \quad K = \frac{E_i}{(\psi_s - \psi_{pd} - hp_w g)} \cdot \frac{\eta l}{A_{sw}} = \frac{l}{R_p} \cdot \frac{\eta l}{A_{sw}} \quad (\text{m}^2)$$

where A_{sw} is the total cross-sectional area of the sapwood at 1.3 m above ground of all trees in the pathway that contribute to E_i and η is the viscosity of water at the stem temperature. In the calculation of permeability for an individual tree, the average sapwood cross-sectional area a_{sw} is given by A_{sw}/n . Since $q = E_i/n$, the permeability for an average individual is identical to that for a plot.

Results

Stomatal conductance

Stomatal conductances of two age-classes of foliage on 11 July and 11 August are shown in Fig. 2 and stomatal conductances at three levels in the canopy for 10 August are shown in Fig. 3. These results were chosen to represent the patterns which were measured throughout the season. Stomatal conductance was high in the early part of the day (maximum 9 mm s^{-1}) falling to a minimum by dusk, with an almost linear decline during the day. The differences in stomatal conductances between levels were small (Fig. 3) and level-1 shoots did not always have the highest stomatal conductances. One-year-old shoots tended to show higher stomatal conductances than current shoots soon after expansion in July and August (Fig. 2); however, this was not consistent at other times during the year. Differences between age-classes were again small.

In Fig. 4a median canopy conductance for each 0.1-kPa class of vapour pressure deficit shows a linear decrease in canopy conductance with increasing vapour pressure deficit. This observation is consistent with previous laboratory studies in which it has been shown that stomatal conductance in Scots pine and other conifers is very sensitive to vapour pressure deficit (see Whitehead and Jarvis 1981). The two points not lying on the line are based on very little data. Canopy conductances on plot 2 were higher than those on plot 1. In Fig. 4b canopy conductances have been divided by the leaf area indices for the two plots to give average stomatal conductances for the canopies. The slopes of the lines are very similar but stomatal conductances for plot 1 were slightly lower than those for plot 2.

Rates of transpiration

In Fig. 5 rates of transpiration during 4 days spread over the season are shown for plots 1 and 2. Transpiration rates were low in March and high in July and August, with those for plot 2

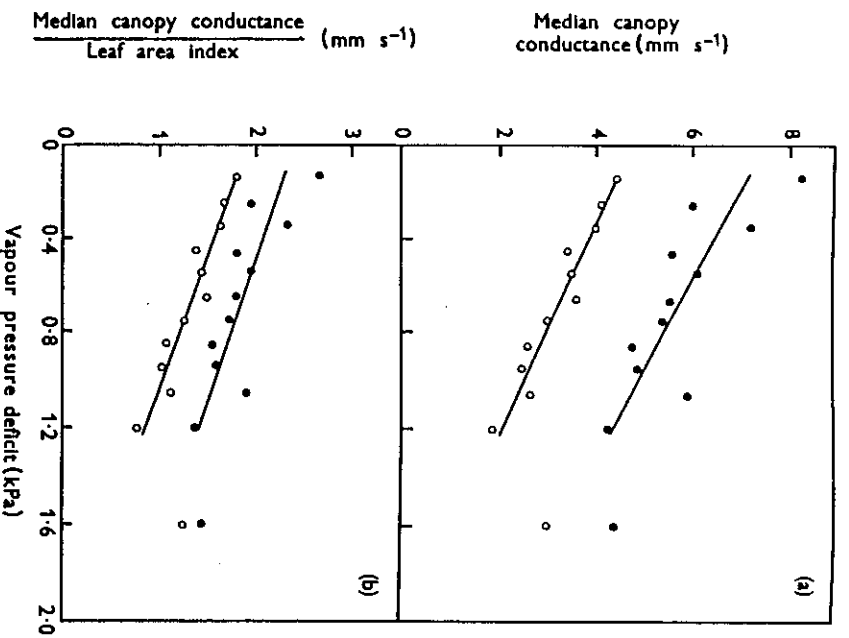


FIG. 4. Relationships between (a) median canopy conductance, and (b) median stomatal conductance calculated from (a) divided by leaf area index against vapour pressure deficit for the 1977 season for plot 1 (○) and plot 2 (●).

always being higher than those for plot 1. Maximum rates of transpiration in August approached 0.3 mm h^{-1} . The difference between the plots increased during the spring and summer.

Over the whole season rates of transpiration from plot 1 were 0.67 times those from plot 2 (Fig. 6). This ratio is smaller than the ratio of leaf area indices between the plots, but larger than the ratio of sapwood basal areas for the plots (Table 1).

The consequence of decreasing stomatal conductance with increasing vapour pressure deficit for rates of transpiration is shown in Fig. 7, where hourly transpiration rates from the measurements over the whole season (calculated from median canopy conductances in each 0.1-kPa deficit class) are plotted against increasing vapour pressure deficit. The straight lines show calculated rates of transpiration at constant canopy conductance for the conditions indicated. Consistent with Figs. 4 and 6, canopy conductances and transpiration rates are higher on plot 2 than on plot 1. Transpiration does not increase with increasing vapour pressure deficit as much as would be expected if canopy conductance were constant, because canopy vapour pressure conductance decreases as deficit increases.

In Fig. 8 the relationship between the actual transpiration rate and the imposed transpiration rate is shown, following [3]. The distribution of the data shows that Ω lies predominantly between 0 and 0.2, increasing to 0.4 at higher transpiration rates. Values for Ω are consistently higher for plot 1 than those for plot 2, but the difference is small and not significant. This analysis clearly shows the predominance of the imposed term, driven largely by D , in determining transpiration from these two stands.

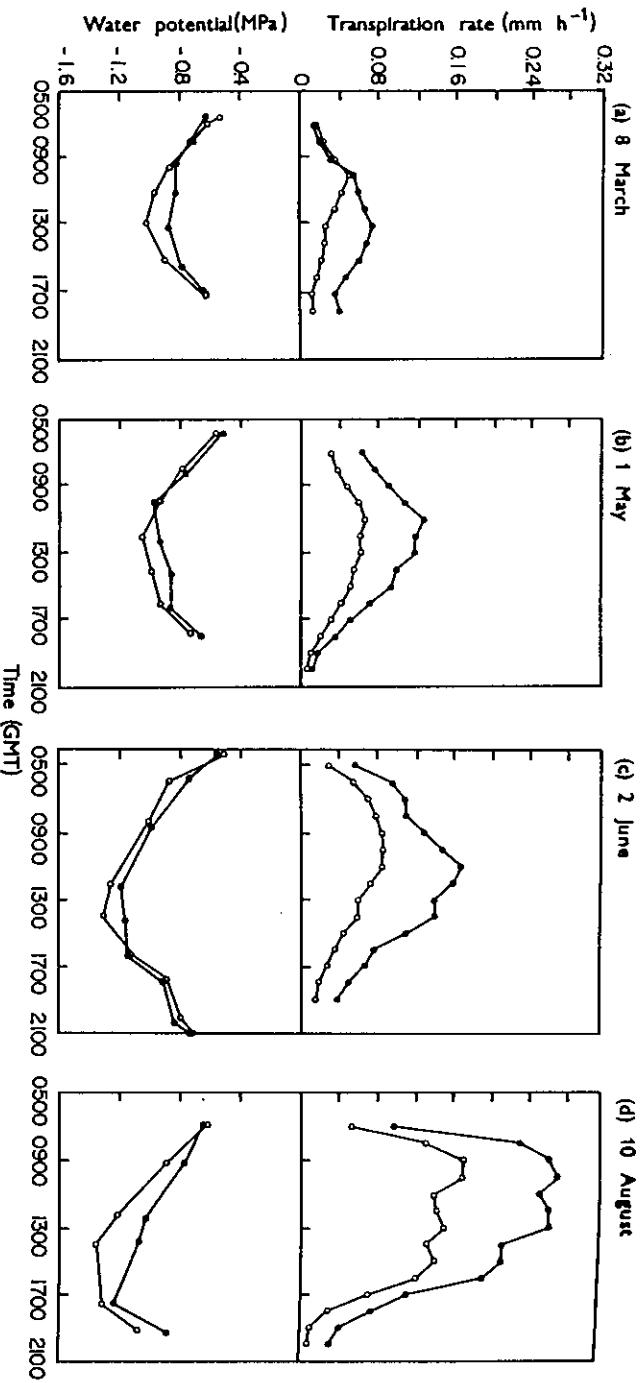


Fig. 5. Rates of transpiration and needle water potential during 4 days spread throughout the season for plot 1 (○) and plot 2 (●) for the dates shown in 1977. Water potential data shown are means of five measurements and standard errors (not shown) were less than ± 0.02 MPa.

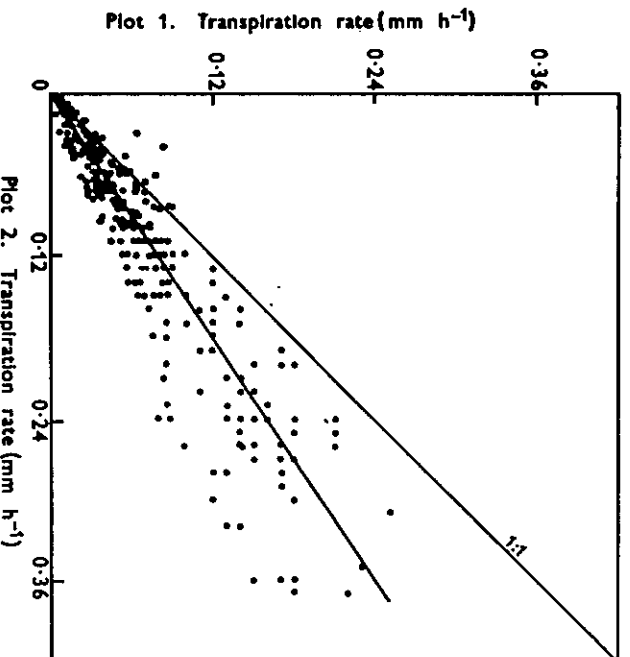


Fig. 6. Relationship between rates of transpiration on plots 1 (608 stems ha^{-1}) and plot 2 (3281 stems ha^{-1}) during the whole season. The slope of the regression line passing through the origin shown is 0.67 which is the overall ratio of transpiration rates on plot 1 : plot 2.

Water potential

Needle water potentials of midcanopy samples corresponding to the rates of transpiration on 4 days throughout the season are shown in Fig. 5. In Fig. 9 measurements of water potential are plotted against hourly rates of transpiration at the same time for data collected throughout the season for both plots in scatter diagrams. Predawn water potential did not fall below -0.6 MPa during the year, except during a few weeks in the winter when transpiration was significant but stems were frozen or close to freezing. Minimum water potentials during

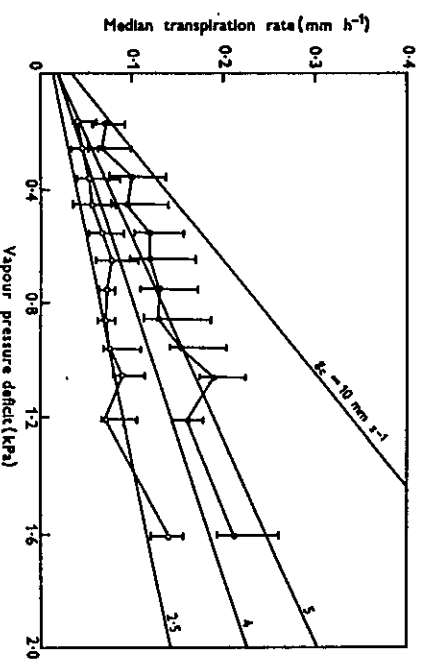


Fig. 7. The relationship between transpiration rate and vapour pressure deficit for plot 1 (○) and plot 2 (●). The straight lines show lines of transpiration rate at equal canopy conductance (g_c) when $A = 400 \text{ W m}^{-2}$, $g_a = 200 \text{ mm s}^{-1}$, and $T_a = 15^\circ\text{C}$. The vertical bars indicate interquartile ranges.

the day were between -0.8 and -1.4 MPa, with lower values during the summer. The values on plot 1 were usually slightly lower than those on plot 2.

Resistance and permeability

The slopes of the lines in Fig. 9 give the average hydraulic resistance to water transport (Table 2) for both plots from [6]. The slope of plot 1 is considerably steeper than that of plot 2. The average resistance for individual trees, R_i , obtained from $R_p \cdot n$ is also shown in Table 2. The corresponding permeabilities in Table 2 have also been calculated from these slopes using [7], where lengths l between the roots and the point of measurement of ψ_i were 10.5 and 12.5 m for plots 1 and 2, respectively. The resistance on plot 1 was 2.4 times the value for plot 2, but the average individual tree resistances were in the ratio of 0.5:1. The ratio of permeabilities was 0.6 for plot 1 relative to plot 2, and for the individual trees within the plots.

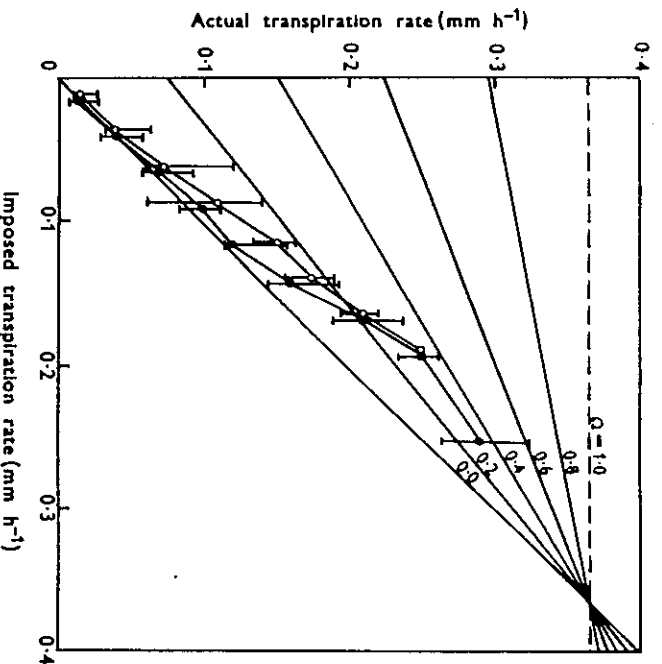


FIG. 8. The relationship between transpiration rate and imposed transpiration rate for plot 1 (○) and plot 2 (●). The straight lines show lines of transpiration rate at equal Ω when $A = 400 \text{ W m}^{-2}$ and $T_a = 15^\circ\text{C}$. The vertical bars indicate interquartile ranges.

Discussion

Stomatal conductances throughout the canopy are often very variable but stratification of the data into canopy levels and needle age-classes is useful in identifying patterns of stomatal conductance, as shown in Figs. 2 and 3. This is probably because environmental conditions at one level are reasonably uniform and do not change rapidly. Differences in stomatal conductance with depth in the canopy have often been attributed to gradations of irradiance. Warts et al. (1976) showed that stomatal conductance was highest at the top and lowest at the bottom of a *Picea sitchensis* canopy, although the differences were less on overcast days because diffuse light penetrated the canopy more uniformly. When water potential was high, stomatal conductance at three levels in a thinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) canopy were very similar; however, in an unthinned stand stomatal conductance decreased with depth more rapidly when water potential was low than when it was high (Tan et al. 1977).

Some observations have shown stomatal conductances at night to be very near zero (e.g., larch (*Larix decidua* Mill.) Benecke et al. (1981); *Pinus radiata* D. Don, D. Whitehead, unpublished data) and a rapid morning increase to a maximum that occurs near the top of the canopy first. All measurements of stomatal conductance of dry foliage in this study showed that stomatal conductance was similarly high soon after dawn, in both current and 1-year-old foliage in both plots (Figs. 2 and 3). Higher stomatal conductances in "sun" rather than in "shade" foliage (e.g., lodgepole pine (*Pinus contorta* ssp. *latifolia* Englm.) Fetcher (1976) and on the south side rather than on the north side (northern hemisphere) of an isolated silver fir (*Abies amabilis* Dougl. Forbes) tree (Hinckley and Ritchie 1970) have been reported. However, in this study stomatal conductances on plot 1, which had the lower leaf area index, were less overall than those on plot 2 (Fig. 4b) despite the better distribution of light through the canopy in the more open plot.

Warts et al. (1976) and Waggoner and Turner (1971) demonstrated seasonal differences in stomatal conductance among different age-classes of foliage of *Picea sitchensis* and red pine (*Pinus resinosa* Ait.), respectively. In this study, we found only small and inconsistent differences in stomatal conductance between age-classes (data other than those in Fig. 2 not given here).

In several recent studies of stomatal conductance in forest canopies, approximately three-quarters of the variation has been accounted for by variation in quantum flux density and vapour pressure deficit (see Whitehead and Jarvis 1981). In this study canopy conductance similarly decreased more or less linearly with increasing vapour pressure deficit on both plots (Fig. 4); however, further analysis not given here showed that there was no evidence of a response to radiation. Similar linear relationships have been measured for several other conifers (Table 3) although the sensitivity to vapour pressure deficit differs considerably between species. Coastal species seem to be more sensitive, possibly because they are adapted to oceanic influences and low vapour pressure deficit, whereas at inland continental sites, vapour pressure deficits can be much higher. *Pinus sylvestris* is characteristically an inland species, showing less sensitivity in response of stomatal conductance to deficit than oceanic species (Table 3). This response to vapour pressure deficit, in conjunction with site variation in climatic variables and leaf area index is instrumental in maintaining daily and annual transpiration rates from all coniferous forests in the same range (see Table 1 in McNaughton and Jarvis (1983) and Table 1 in Roberts (1983)).

In Fig. 4b canopy conductances are divided by leaf area indices to give average stomatal conductances, showing that values for plot 1 were lower than those for plot 2. This suggests a real difference in stomatal conductance between the plots, independent of leaf area index. However, the number of shoots sampled (30 per plot per occasion) was small in relation to the size of the sample (155 shoots) calculated by Leverenz et al. (1982) as a requirement to give an estimate of the mean stomatal conductance with a 95% confidence interval of $\pm 10\%$. Thus the difference between plots could be the result of a systematic sampling error. However, this is unlikely because a fresh sample of shoots was chosen for each of the eight measurement periods so that sampling errors should be random rather than systematic.

Rates of transpiration calculated throughout the season (Fig. 5) were within the range found for other conifers (see Table 1 in Whitehead and Jarvis (1981)). Rates from plot 1 were 0.67 times those from plot 2 (Fig. 6), the difference being attributable to higher canopy conductance on plot 2 (Fig. 4) and lower leaf area index on plot 1 (Table 1). Hourly transpiration rates in August (Fig. 5d) were three times the rates in March (Fig. 5a), following the typical pattern of a late summer maximum in transpiration rate. As pointed out by Jarvis (1981), actual transpiration rates do not reach those predicted from [2] at high values of A , D , g_a , and g_s because of the feedback response between g_c and D . In aerodynamically rough canopies such as forest, changes in A and g_a have only small effects on the transpiration rate, while changes in D and decreases in g_c caused by increases in D (Fig. 4) have a large effect on transpiration rate. The consequence of this is that rates of transpiration cross the lines of equal g_c as D increases (Fig. 7).

The analysis in Fig. 8 highlights the importance of the imposed term relative to the equilibrium term in driving transpiration from coniferous canopies. McNaughton and Jarvis (1983)

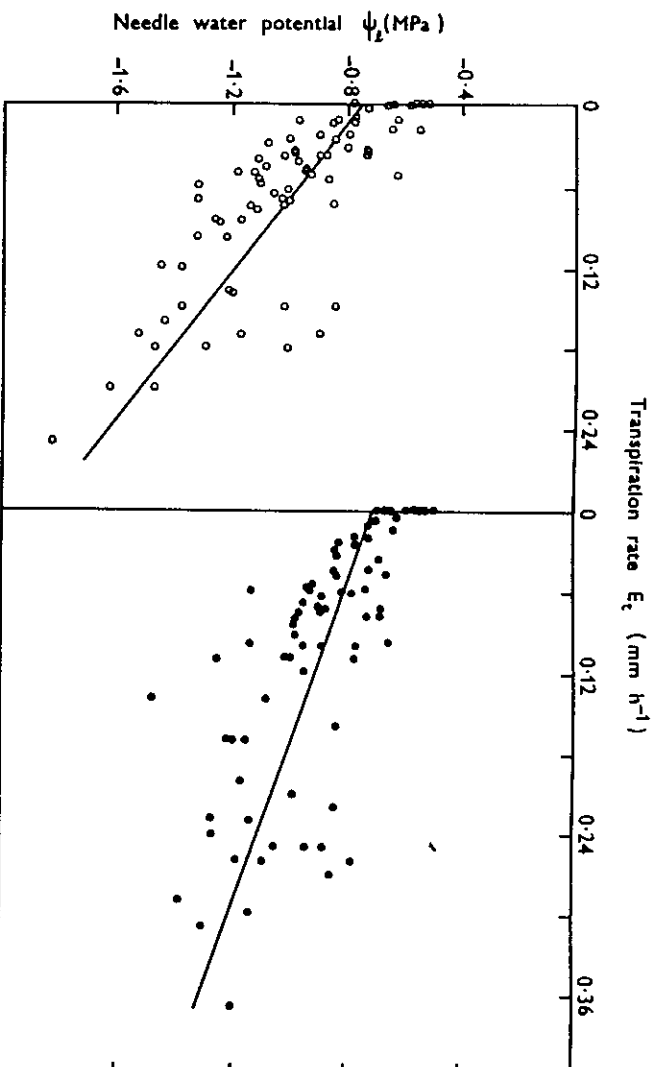


FIG. 9. The relationship between transpiration rate and needle water potential for all data for plot 1 (○) and plot 2 (●). The regression equations for the lines shown are ○, $\psi_2 = -3.69 E_t - 0.74$, $r^2 = 0.63$ and ●, $\psi_2 = -1.65 E_t - 0.71$, $r^2 = 0.50$.

TABLE 2. Calculated values of hydraulic resistance and permeability for both plots and individual trees in each plot

	Units	Plot 1	Plot 2	Plot 1 : plot 2
Resistance for plot	MPa s m ⁻¹	1.2 × 10 ⁷	0.5 × 10 ⁷	2.4
Resistance for one tree	MPa s m ⁻³	7.5 × 10 ⁵	16.0 × 10 ⁵	0.5
Permeability for plot and one tree	m ²	4.0 × 10 ⁻¹³	6.5 × 10 ⁻¹³	0.6

TABLE 3. Slope of relationships between stomatal conductance (g_s) and vapour pressure deficit (D)

Species	$\frac{g_s}{D}$ (mm s ⁻¹ /kPa)	Source
<i>Picea sitchensis</i>	-3.5	Watts (1977)
<i>Picea abies</i>	-2.2	Calder (1977)
<i>Pinus contorta</i>	-2.2	D. Whitehead and J. W. Levenez (unpublished data)
<i>Pinus radiata</i>	-1.5	D. Whitehead and J. C. Grace (unpublished data)
<i>Pseudotsuga menziesii</i>	-0.9	Tan et al. (1977)
<i>Pinus sylvestris</i>	-0.9	This study, Fig. 4

calculated an average value of $\Omega = 0.2$ for forest; the results from this study support this value. As a consequence of the low value for Ω , the transpiration rate after thinning a forest would be expected to be reduced in approximately the same proportion as the reduction in leaf area index (McNaughton and Jarvis 1983). The expectation that a sensitive response of stomatal conductance to the vapour pressure deficit is likely to be found in species which have evolved in conditions where Ω is low (see Fig. 4), leads to the conclusion that the characterization of canopy conductance is an important factor in the hydrology of

forested catchments.

Black et al. (1980) showed that transpiration rates from trees in thinned and unthinned stands of *Pseudotsuga menziesii* were "in general, remarkably similar," in contrast with our results (Fig. 6). At Roseisle, soil water supply did not appear to limit transpiration at any time during the year, as indicated by the measurements of predawn water potential which were no lower during the dry summer period. However, soil water was limiting at the sites of Black et al., and competition for water between the trees and salal undergrowth in the thinned stand led

TABLE 4. Summary of water flow characteristics for plot 1 in comparison with plot 2 (terms are defined in the equations in the text)

Water flow characteristics for plot 1	Plot 1 : plot 2
Lower transpiration rate (E_t)	× 0.7
Lower leaf area index (L)	× 0.8
Higher average transpiration rate per tree (q)	× 3.3
Higher leaf area per tree at canopy closure (A_l)	× 4.2
Smaller total basal area of sapwood for the plot ($A_{s,w}$)	× 0.5
Higher resistance for the plot (R_p)	× 2.4
Larger average basal area of sapwood per tree ($a_{s,w}$)	× 2.9
Lower resistance for one tree (R_t)	× 0.5
Lower permeability for the plot and one tree (K)	× 0.6

to a similar size of tree within the two stands. At Roseisle, average tree diameters and basal areas were very different in the two stands (Table 1). In addition, up to 30–50% of the water used for transpiration was available from the sapwood store over short periods up to several days in the summer (Waring et al. 1979), thus contributing to the avoidance of drought.

Despite the large differences in transpiration rates between plots 1 and 2 differences in needle water potential were small, and daily minima were not very different throughout the season (Fig. 5). This is consistent with Jarvis' (1975) hypothesis that water potential is conserved at a high value, even during periods of high transpiration with the avoidance of physiologically damaging water deficits. Hydraulic resistances were similar to those reported for other conifers (see Table IV in Whitehead and Jarvis (1981)) and differences between the two plots were probably associated with the roots and branches (Whitehead and Jarvis 1981). Permeabilities (Table 2) calculated from [7] are an order of magnitude lower than those measured on fully saturated stem segments in the laboratory, which is consistent with a reduction in permeability with decreasing sapwood relative water content (Edwards and Jarvis 1982). Apart from a short period in winter, average sapwood relative water contents were less than 85% on both plots (Waring et al. 1979).

Returning now to the hypothesis expressed in Fig. 1, we can identify plot 2 with the prethinning stage on the left and assess the measured properties of plot 1 in relation to it (Table 4). Plot 1 has clearly not reached the postthinning steady state implied by the right-hand side of Fig. 1, but is in an intermediate condition with many of the attributes of the central, transient stage. For example, the leaf area index has clearly not reached the value at canopy closure found in plot 2 and transpiration (per unit ground area) (E_t) of plot 1 is less than that of plot 2 by a proportionately similar amount (Table 4). However, because the leaf area per tree (A_l) is much larger on plot 1 than on plot 2, the average volume flow through each tree (q) is proportionately much larger in trees on plot 1 than on plot 2. The basal area of sapwood ($A_{s,w}$) is less than would be expected if the steady-state condition had been reached, commensurate with the subcelling leaf area index, and consequently the hydraulic resistance per plot (R_p) is higher than expected. On the other hand, the area of sapwood per tree shows that substantial adjustment has occurred, commensurate with the increase in leaf area per tree, and as a result the hydraulic flow resistance of the average individual tree is proportionately lower. The lower permeability of the sapwood on plot 1 rather than on plot 2 is consistent with this but somewhat surprising. This could reflect morphological changes in the sapwood resulting

from the very slow recovery to a complete canopy.

All of these observations are consistent with plot 1 being in a transient state, while leaf area increases slowly towards complete canopy closure again. The lack of precise agreement in the proportionalities discussed above probably results from some uncertainty in the relationship between leaf area per tree and sapwood basal area per tree as a result of the unexplained positive intercept on the x-axis of that relationship (Whitehead 1978). Had the relationship gone through the origin, much closer agreement would have been found between higher q and higher A_l , for example, in Table 4.

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