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Processes Controlling Understorey Evapotranspiration [and Discussion]

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Processes controlling understorey evapotranspiration

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The understorey often accounts for a significant proportion of forest evapotranspiration. In this paper we discuss the role of the understorey radiation régime, and the aerodynamic and stomatal conductance characteristics of the understorey in understorey evapotranspiration. Values of the McNaughton–Jarvis parameter Ω for the understorey in two mid-rotation Douglas-fir stands indicate considerable coupling between the understorey and the atmosphere above the overstorey. However, the stronger coupling between the overstorey and the atmosphere accounts for the observation that the fraction of stand evapotranspiration originating at the understorey increases as the water vapour pressure deficit increases and the soil dries. We also discuss the approaches to describing the process of evaporation from the forest floor and the results of understorey removal experiments. These show small decreases in stand evapotranspiration and root-zone soil water content, but significant increases in the transpiration and growth of the trees.

1. Introduction

Over the past 20 years, physical processes near the forest floor and within the understorey have been the subject of increasing study. The reason for the interest is the need to understand better the exchange processes of the forest as a whole and the competitive role of the understorey in terms of water, CO_2 and nutrient uptake. In silviculture, the goal is often to control or suppress the understorey by managing the overstorey cover (Black & Spittlehouse 1981; Jarvis 1985*b*). On the other hand, understorey is often important in providing browse and protection for wildlife, for example on deer winter range in British Columbia (Vales 1986).

The transfer of radiation, sensible and latent heat, momentum and precipitation through the overstorey play a major role in determining understorey microclimate as well as its evapotranspiration. The nature of the soil and forest floor, and the water table are also important. Spatial and temporal variability of these fluxes cause difficulties in studying the energy balance, transpiration and photosynthesis of the understorey vegetation. The presence of large scale eddies or gusts that penetrate the overstorey and enhance the vertical transport of heat, water vapour and CO_2 through the stand (see, for example, Denmead & Bradley 1985) implies more effective exchange between understorey or forest floor and the atmosphere than previously expected. Also, overstorey structure greatly affects the quantity (Gash 1979) and spatial distribution of throughfall of precipitation.

The aims of this paper are to discuss the role of the aerodynamic and stomatal conductances in controlling the rate of understorey evapotranspiration and to consider the effects of the presence of the understorey on both overstorey and forest evapotranspiration. In this paper, results from our research in stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with an understorey salal (*Gaultheria shallon* Pursh.) will be used to illustrate the concepts. The discussion emphasizes transpiration because it is much more important than evaporation of intercepted water, i.e. interception loss during the growing season in British Columbia. The two stands that will be mainly referred to are located near Courtenay and Nanaimo on Vancouver Island. The former (age 32 in 1982) was thinned from 1500 to 800 trees per hectare† in 1975 and has been slow to close; in 1982 the overstorey and understorey leaf area (projected) indices (a) were about 6 and 3, respectively (Kelliher *et al.* 1986). The latter (age 23 in 1985), an unmanaged stand located about 175 km south of the former, has a variable stand density (700–5000 trees per hectare) with overstorey and understorey leaf area index of 3–6 and 0.5–3, respectively (Osberg 1986).

2. UNDERSTOREY RADIATION REGIME

Radiative exchange at the understorey and forest floor is an important process influencing understorey evapotranspiration. Increased radiation transmittance by the overstorey can lead to increased understorey evapotranspiration as a result of the growth of understorey leaves, increased available energy for evapotranspiration and higher understorey stomatal conductance in response to higher quantum (light) flux densities (Roberts 1983). However, the growth response of the understorey to increasing radiation penetration is not easy to predict. Kelliher (1985) found at the Courtenay site that the average area of salal leaves increased from about 20 to 32 mm^2 and salal leaf area index decreased from 4 to 1 as stand basal area increased from 14 to 36 m^2 ha^{-1}. In contrast, at the Nanaimo site the leaf area index of the salal in an adjacent clearcut was less than 1.0, whereas in the stand it was 1–3. Moreover, the leaves in the clearcut were small and leathery, in contrast to the larger, greener leaves within the stand. In conifer stands in southern Vancouver Island, Vales (1986) found that the average shoot height and shoot basal diameter of salal tended to be largest for stands with intermediate values of solar radiation transmittance (figure 1).

The complex structure of forests has led to the use of both stationary sensor arrays (see, for example, Reifsnyder *et al.* 1971) and moving sensors (see, for example, Norman & Jarvis 1974; Baldocchi *et al.* 1986) in the measurement of radiation beneath the overstorey (see Jarvis *et al.* (1976) for a review for coniferous forests). Radiation-transfer models requiring quantitative

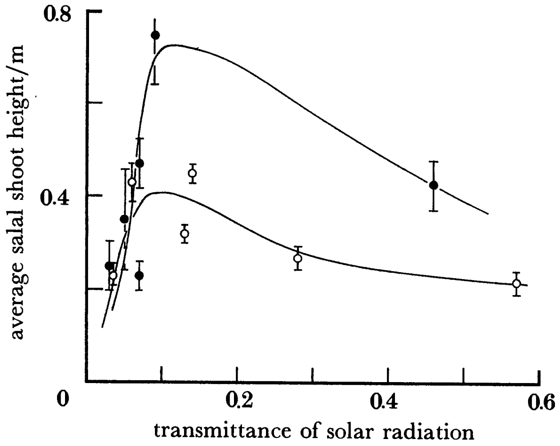

FIGURE 1. Average salal understorey shoot height against transmittance of solar radiation for conifer stands in the Coastal Western Hemlock dry (●) and wet (○) subzones on Vancouver Island (from Vales 1986).

† 1 hectare (ha) = 10^4 m^2.

descriptions of the overstorey canopy structure are essential in the development of understorey microclimate and transpiration models (Norman 1989).

Figure 2 illustrates the difficulty in measuring and modelling the net irradiance beneath the overstorey (R_{nb}) of the Courtenay Douglas-fir stand. A comparison is made between the ratios of time-integrated R_{nb} to the corresponding value above the stand (R_{na}) obtained by using (i) a stationary net radiometer, located beneath the overstorey in a 4.2 m wide plot in which the understorey had been cut and removed, and (ii) a net radiometer carried by a tram travelling at a speed of 0.5 m min^{-1} at a height of 1 m. The tram travelled back and forth across the plot and an adjacent section 5.8 m wide where salal understorey was present. It is clear that where values of spatially averaged net irradiance below the overstorey are required for 15 min or shorter time intervals the use of a stationary net radiometer is not adequate. In the case of average daytime values, stationary net radiometers indicated in August 1981 that values of $R_{\mathrm{nb}}/R_{\mathrm{na}}$ were 0.15 and 0.13 for salal understorey present and removed, respectively, whereas the corresponding values from the tram system operating on six days in August 1982 were 0.16 and 0.14 (table 1).

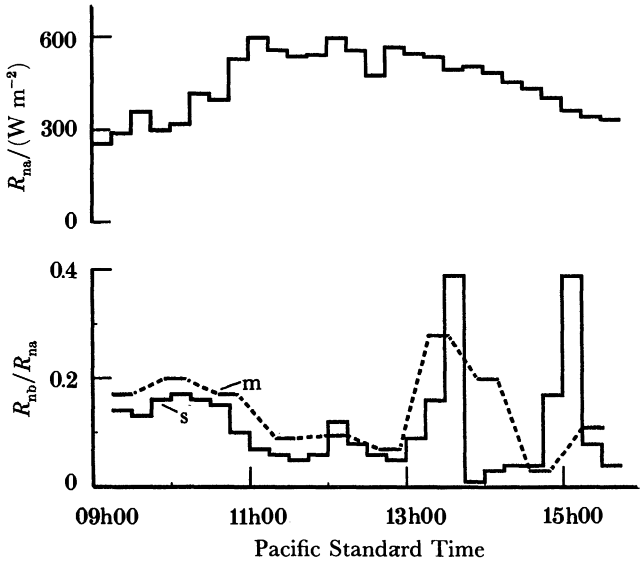

FIGURE 2. Ratio of below (R_{nb}) to above (R_{na}) overstorey net irradiance after salal understorey removal in the thinned Courtenay Douglas-fir stand on 1 Sep. 1982 measured with a moving (m) and a stationary (s) net radiometer. The broken lines indicate when the moving radiometer was over the understorey.

TABLE 1. RATIOS OF THE AVERAGE DAYTIME NET IRRADIANCE BELOW THE OVERSTOREY (R_{nb}) TO THAT ABOVE (R_{na}) IN THE SAME STAND AS IN FIGURE 2

net radiometer	understorey present	understorey removed
	Aug. 1981	
stationary	0.15	0.13
	Aug. 1982	
moving[a]	0.16	0.14
	1 Sep. 1982	
moving	0.13	0.14
stationary		0.12

[a] Average of six days including 1 Sep. using tram.

3. Partitioning understorey net irradiance

The Penman–Monteith equation can be used to describe how the net irradiance of understorey leaves (R_{nl}) is partitioned between sensible and latent heat flux densities (λE_l) (Monteith 1981*a*):

$$\lambda E_l = (\epsilon A_l + \rho_a c_p G_H D_b/\gamma)/(\epsilon + G_H/G_V), \tag{1}$$

where E_l is the sum of the water vapour fluxes from both sides of the leaf per unit projected leaf area (kilograms per square metre per second), D_b is the water vapour pressure deficit of the air outside the leaf's boundary layer below the overstorey, and A_l is the total available energy flux per unit projected leaf area, i.e. $R_{nl_1} + R_{nl_2}$ (two surfaces) minus the rate of energy storage in the leaf, ρ_a and c_p are the density and specific heat of the air at constant pressure, γ is the psychrometric constant and ϵ is the ratio of the slope of the saturation vapour pressure curve to the psychrometric constant. The total conductance for sensible heat transfer from both sides of the leaf, G_H, is given by $G_H = g_{H_1} + g_{H_2}$, where g_{H_1} and g_{H_2} are the boundary layer conductances for sensible heat transfer from each side of the leaf. Similarly, the total conductance for water vapour transfer, G_V, is given by $G_V = 1/(1/g_{s_1} + 1/g_{V_1}) + 1/(1/g_{s_2} + 1/g_{V_2})$, where g_{s_1} and g_{s_2} are the stomatal conductances of each surface of the leaf, and g_{V_1} and g_{V_2} are the boundary-layer conductances for water-vapour transfer from each side. In commonly occurring forced-convection conditions, we shall assume $g_{V_1} \approx g_{V_2} \approx g_{H_1} \approx g_{H_2} \approx g_b$.

The latent heat flux from the entire understorey canopy per unit ground area is the summation of (1) over the leaf area index (a) of the understorey canopy and requires measurements or approximations of the vertical distributions of R_{nl}, D_b, g_s, g_b and a within the understorey canopy. This gives a good approximation of the vertical latent heat flux beneath the overstorey (λE_b) because soil evaporation is usually small beneath the understorey (Kelliher *et al.* 1986).

It is sometimes convenient to use the 'big leaf' canopy version of (1) to estimate λE_b as follows:

$$\lambda E_b = (\epsilon A_b + \rho c_p D_b g_{AH}/\gamma)/[\epsilon + (g_{AH}/g_{AV})\,(1 + g_{AV}/g_c)], \tag{2}$$

where A_b is the flux density of available energy to the understorey canopy per unit ground area, i.e. net irradiance just above the understorey canopy (R_{nb}) minus the soil heat-flux density and rate of canopy energy storage. The canopy aerodynamic conductance for sensible heat transfer (g_{AH}) can be expressed as

$$g_{AH} = 1/(1/g_a + 1/(2a\bar{g}_b)), \tag{3}$$

where $\bar{g}_b$ is the average leaf boundary-layer conductance and g_a is the 'eddy conductance' of the bulk air in and just above the canopy. Inclusion of g_a in (3) follows Thom (1972) and is intended to account empirically for the usual measurement of D_b at a considerable distance beyond the boundary layer of many of the understorey leaves. It is emphasized that the use of (3) involves simplifying assumptions about turbulent transfer within the understorey canopy (Thurtell 1989). Similarly, the canopy aerodynamic conductance for water vapour transfer (g_{AV}) can be expressed as

$$g_{AV} = 1/(1/g_a + n/(2a\bar{g}_b)), \tag{4}$$

where $n = 1.0$ for symmetrical amphistomatous leaves and $n = 2.0$ for hypostomatous leaves. The canopy or surface conductance (g_c) is given by

$$g_c = 2a\bar{g}_s/n, \tag{5}$$

where $\bar{g}_s$ is the leaf area weighted, average stomatal conductance for the canopy. When $g_a \gg a g_b$, (2) reduces to

$$\lambda E_b = \frac{\epsilon A_b + 2\rho_a c_p D_b a \bar{g}_b / \gamma}{\epsilon + n(1 + \bar{g}_b / \bar{g}_s)}. \tag{6}$$

The errors involved in the procedures for averaging boundary layer and stomatal conductance over the canopy volume for use in (2) or (6) are discussed by Finnegan & Raupach (1987) and Baldocchi (1989).

The evaporation from wet understorey leaves can be estimated by using (1) with $G_H = G_V = 2g_b$ or (2) with $n = 1$ and $1/g_c = 0$. Shuttleworth (1979) presented theory that takes into account the presence of wet and dry amphistomatous leaves in a canopy. Kelliher *et al.* (1986) combined this theory with a simple canopy and soil water balance to investigate the effects of understorey removal on forest evapotranspiration in the Courtenay stand referred to earlier. The next three sections review studies of the relations required in the estimation of aerodynamic and stomatal conductances of understorey canopies and examine the use of (6) in estimating understorey transpiration.

4. AERODYNAMIC CONDUCTANCE WITHIN AND JUST ABOVE THE UNDERSTOREY CANOPY

The leaf boundary-layer component of the canopy aerodynamic conductance depends on leaf size and roughness, mutual sheltering between leaves, mean wind speed and turbulence intensity (Grace 1981; Finnegan & Raupach 1987). Analytical models of canopy wind profiles can be used to approximate mean wind speeds in the overstorey, but typically they do not accurately describe the wind profile near the understorey (Pereira & Shaw 1980). The eddy diffusive component of the aerodynamic conductance is related in a complex way to understorey canopy openness, roughness and the wind structure imposed from above.

The aerodynamic conductance of understorey leaves has been measured in the field by several methods. Roberts *et al.* (1980) measured the mass loss over 30 min periods of both cut, wetted bracken (*Pteridium aquilinum* (L.) Kuhn) fronds and wetted blotting paper replicas of bracken pinnae supported by cotton thread on wire frames in the configuration of a frond. Their measurements were made within the bracken understorey ($a \approx 1$) of a Scots pine (*Pinus sylvestris* L.) stand in Thetford Forest, England. Aerodynamic conductances ranged from 9 to 13 mm s^{-1} with a mean of 12 mm s^{-1}. (This is the sum of the upper and lower leaf surface boundary-layer conductances and includes the eddy diffusive conductance to the measurement location of D_b in the trunk space above.)

Spittlehouse & Black (1982) measured leaf boundary-layer conductance by the rate of movement of water in a capillary tube connected to a ceramic disc evaporating from one side and the rate of mass loss of a metal disc covered with wetted filter paper. The discs were located within the 0.6 m tall salal understorey ($a = 2.75$) of the Courtenay Douglas-fir stand. Discs of 37, 60 and 83 mm diameter were mounted at a height of 0.3 m and exposed to wind speeds that varied from 0.05 to 0.4 m s^{-1} and turbulent intensities from 5 to 50%. Wind speeds were about 50% of those just above the salal understorey. Boundary-layer conductances for water vapour were 1.2 to 2.0 times those calculated with the Polhausen equation for vapour transfer in parallel laminar flow (figure 3). Linear regression analysis of these field data, assuming $g_V \propto u^{\frac{1}{2}}$, gives

$$g_V = 5.7(u/d)^{\frac{1}{2}}, \tag{7}$$

where u (metres per second) is the wind speed near the artificial leaf within the salal canopy, g_V (one side of disc) is in millimetres per second and d is the disc diameter in metres. Although there is considerable variability in the data, (7) is similar to many results obtained in conditions of high turbulence intensity in plant canopies (see Finnegan & Raupach (1987) and Monteith (1981*b*) for reviews). Shown for comparison in figure 3 are the equations from Murphy & Knoerr's (1977) wind-tunnel measurements on broad leaves and Monteith's (1965) analysis of Raschke's field data on broad leaves.

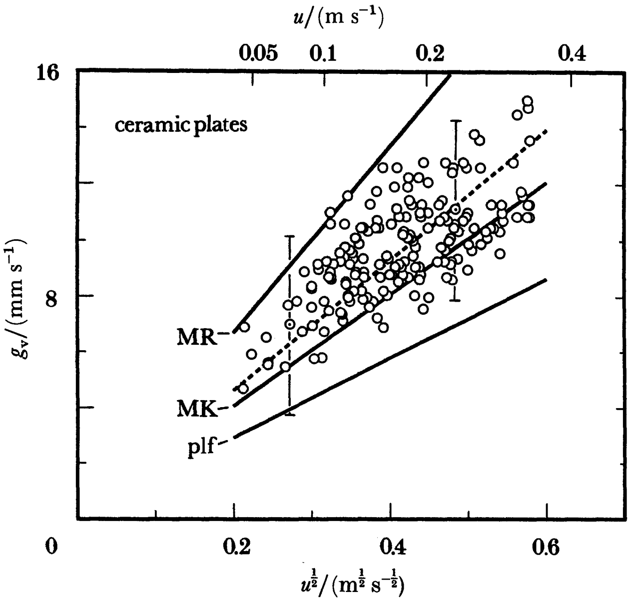

FIGURE 3. Boundary layer conductance of water vapour (g_V) from one side of 60 mm diameter ceramic plates located within the salal understorey at Courtenay in relation to the square root of the wind speed (u) at the same height. Also shown are the linear regression (7) (broken line), and the parallel-laminar flow (plf), Murphy & Knoerr (1977) (MK) and Monteith–Raschke (Monteith 1965) (MR) relations.

Osberg (1986), using a weighing lysimeter approach like that of Calder *et al.* (1984), determined the aerodynamic conductance of the salal understorey canopy ($a = 1.0$) in the Nanaimo Douglas-fir stand. He measured the mass loss of a 0.6 m diameter × 0.75 m deep lysimeter during 5 min periods for a range of wind speeds after the wetting of the salal understorey growing in, and for several metres away from, the lysimeter. He found that over 80 % of the upper and lower leaf surfaces remained wet for the 5 min periods. Osberg used (2) with $n = 1$ (i.e. leaves wet on both sides) and $1/g_c = 0$ to calculate the aerodynamic conductance, $g_{AH} = g_{AV} = g_A$ (i.e. $2a\bar{g}_b$ including the effects of any eddy diffusive conductance, g_a). He found that

$$g_A = (44 \pm 8)\, u_b^{0.66 \pm 0.10}, \tag{8}$$

where g_A is in millimetres per second, and u_b (measured 0.3 m above the salal canopy) is in metres per second (figure 4). This relation is very similar to that obtained by Calder *et al.* (1984) for heather (*Calluna vulgaris* (L.) Hull): $g_A = (50 \pm 6)\, u^{0.60 \pm 0.06}$. Equation (8) gives conductance values similar to those estimated from equation (7) (i.e. $2ag_V = 2 \times 1.0 \times 5.7 \times (0.7u_b/0.035)^{\frac{1}{2}} = 50u_b^{\frac{1}{2}}$) assuming wind speed in the salal is about 70 % of that above the understorey and salal leaf size is 0.035 m, both as reported by Osberg. This agreement and the

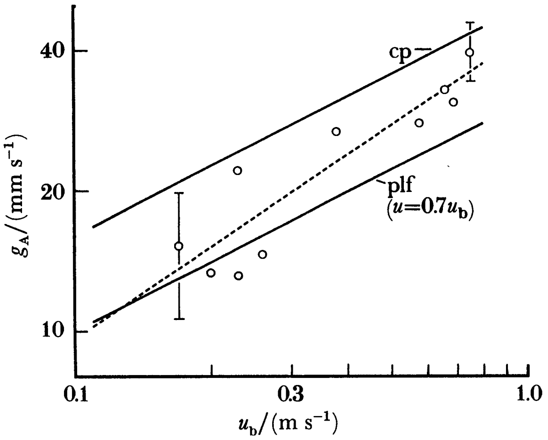

FIGURE 4. Aerodynamic conductance (g_A) of the salal understorey growing in a lysimeter in the Nanaimo Douglas-fir stand against wind speed just above the salal (u_b). Also shown are the regression (8) (broken line), and the parallel laminar flow (plf) and ceramic plate (cp) relations (figure 3), calculated assuming that the within-understorey wind speed was $0.7u_b$ and leaf diameter was 35 mm.

similarity of the exponent of u to 0.5 suggest that the aerodynamic conductance in Osberg's salal understorey was mainly determined by the leaf boundary layer conductance.

The most promising approach to the calculation of understorey transpiration and evaporation rates is the combination of (1) with either higher-order closure or random flight models of turbulent transfer within the understorey canopy (Raupach 1988; Wilson 1989). A simpler approach is the use of (2) with empirical relations like that in (8) incorporating the sheltering effects of canopy structure. The direct measurement of water-vapour fluxes from the understorey by the eddy correlation technique will be essential in validating these approaches.

5. STOMATAL CONDUCTANCE OF UNDERSTOREY SPECIES

A factor of major importance in determining the transpiration rate of the understorey is its stomatal conductance. Although affecting the water and energy balances of the understorey, stomatal conductance also plays a role in the photosynthesis and growth of the understorey. Woods & Turner (1971) showed how understorey species of differing shade tolerance had different speeds of stomatal opening and closing. They found that the most shade-tolerant species had the most rapid stomatal responses so that they were able to take advantage of sunflecks for photosynthesis.

Leaves of salal are hypostomatous. At Courtenay, Tan *et al.* (1977) found that the stomatal conductance of the lower surfaces of the leaves was mainly related to light, water-vapour pressure deficit and soil water potential, although they also found considerable unexplained variability in their data. The stomata of Douglas-fir and salal were fully open at solar irradiances higher than 100 W m^{-2}. Because this stand has been very slow to close over the years, light did not appear to limit understorey stomatal conductance during most of the daytime hours. Spittlehouse (1981) and Kelliher (1985) made further measurements confirming the general nature of the stomatal conductance characteristics of the salal as well as the unexplained variability observed by Tan *et al.* (1977). Figure 5 shows stomatal conductance data for the salal and the Douglas-fir overstorey from the three studies plotted against water-vapour

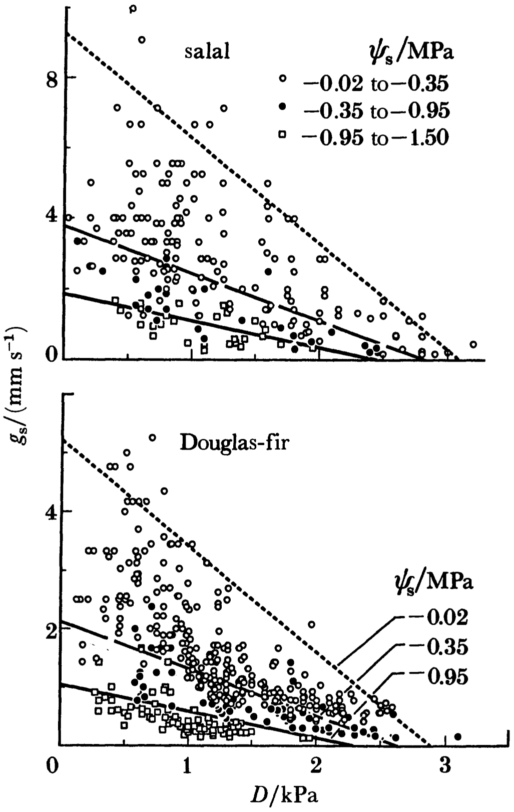

FIGURE 5. Comparison of relations between stomatal conductance (g_s) and vapour-pressure deficit (D) for the salal understorey and Douglas-fir overstorey in the Courtenay stand for three ranges of the average soil-water potential of the root zone (ψ_s). Lines are calculated from (9) and (10).

pressure deficit. The latter was measured just above the understorey in the case of the salal and within or just above the overstorey in the case of the Douglas-fir. The data have been separated into high, medium and low ranges of the average soil water potential of the root zone (ψ_s). The daytime stomatal conductance of the salal for $-1.5 \leqslant \psi_s \leqslant 0.02$ MPa can be estimated from the empirical equation

$$g_s/g_{s,\,\max} = -0.21\ln(-\psi_s/2.5) + 0.063D\ln(-\psi_s/3.5), \tag{9}$$

where $g_{s,\,\max} = 9.3\ \mathrm{mm\ s^{-1}}$ at $D = 0$ kPa and $\psi_s = -0.02$ MPa. The corresponding equation for the Douglas-fir is

$$g_s/g_{s,\,\max} = -0.21\ln(-\psi_s/2.5) + 0.067D\ln(-\psi_s/3.5), \tag{10}$$

where $g_{s,\,\max} = 5.2\ \mathrm{mm\ s^{-1}}$. The stomatal conductance of the understorey was approximately twice that of the overstorey. Both species showed similar sensitivity of the relative conductance, i.e. $g_s/g_{s,\,\max}$, to ψ_s, whereas $g_s/g_{s,\,\max}$ of salal was slightly less sensitive than that of Douglas-fir to D. Figure 5 illustrates the difficulty in determining reliably the relations between stomatal conductance and environmental variables. In large part this results from the difficulty in sampling adequately, given the marked spatial and temporal variability in the understorey environment (Leverenz *et al.* 1982). Some of the variability in these data may be a result of using D measured at a reference location some distance from the leaf instead of using either the leaf surface value (Jarvis & McNaughton 1986) or the leaf–air vapour-pressure difference (Choudhury & Monteith 1986).

Other workers have also found marked stomatal responses by understorey species to vapour-pressure deficit. Lindroth (1984) tentatively concluded that the canopy conductance of a heather-cowberry (*Vaccinium vitis-idaea* L.) understorey under a mature Scots pine stand at Jädraås, Sweden decreased linearly with increasing *D*. In a study to determine whether stomatal responses could help explain the distribution of understorey species along the northwest coast of North America, Marshall & Waring (1984) found that the relative conductance of salal decreased with increasing *D* slightly less rapidly than that of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Douglas-fir. Other understorey species, golden chinkapin (*Castanopsis chrysophylla* (Dougl.) A.D.C.), Pacific rhododendron (*Rhododendron macrophyllum* G. Don), vine maple (*Acer circinatum* Pursh), and Oregon grape (*Berberis nervosa* Pursh) were also less sensitive to *D* than the two overstorey conifers. On the other hand, snowbrush (*Ceanothus velutinus* Dougl. ex Hook.), a nitrogen-fixing shrub with high stomatal conductance, showed no response to *D*. They suggested that this lower sensitivity to *D* may be compensated for by greater sensitivity to soil water potential. In rigorous testing of this hypothesis, the difficulties of defining the appropriate root zone depth for the competing species must be recognized.

Roberts *et al.* (1984) studied the variables affecting the stomatal conductance of bracken below the Scots pine stand in Thetford Forest. They found that the conductance of the lower surfaces of the bracken pinnae was about three times that of the upper surfaces. As *D* increased, stomatal conductance of the bracken decreased much less than that of the Scots pine. Also, they found less than 50% of the variation in the bracken stomatal conductance could be explained by variation in the measured environmental variables, and felt that this may be the result of short-term fluctuations in light beneath the overstorey. They concluded that bracken stomatal conductance was light-limited at all times. Even though they used rain shelters throughout the growing season to dry the soil, they found relatively small effects of soil water potential on the leaf water potential and stomatal conductance of bracken.

Hollinger (1987) measured stomatal conductance and photosynthesis of a bracken understorey in a *Pinus radiata* (D.) Don plantation and a crown fern (*Blechnum discolor* (Forst. f.) Kegs) understorey in a southern beech (*Nothofagus truncata* (Col.) Ckn.) forest in New Zealand. He found that stomatal conductance of both the understorey species responded less than that of the overstorey species to changes in *D* (as Roberts *et al.* (1984) had found) and in light, but that there was a marked response to decreasing soil water potential. He suggested that the weak response to *D* is probably indicative of a low level of stomatal control in pteridophytes, whether growing as understorey or in open sites.

6. MEASUREMENTS AND CALCULATIONS OF TRANSPIRATION RATES OF UNDERSTOREYS

Understorey transpiration rates have been determined in various forest types by using a variety of methods. These methods include the use of lysimeters (Lindroth 1984; Osberg 1986), large ventilated chambers (Greenwood *et al.* 1985), eddy correlation measurements of the vertical flux of water vapour (Denmead 1984) and calculations using stomatal conductance measurements (1) or (2) (Roberts *et al.* 1980; Tan *et al.* 1978; Hollinger 1987). Measuring transpiration or evaporation rates from the understorey is difficult because the fluxes are much smaller than from the overstorey and are often spatially variable. Spatial variation occurs not only because of variability in overstorey cover, but also because of variability in understorey density, topography and soil. Soil evaporation has to be separated from lysimetric, ventilated chamber and eddy correlation measurements to determine the evaporation or transpiration from the understorey vegetation, but, as indicated earlier, this can often be neglected. In both the lysimetric and ventilated chamber methods, considerable care must be taken to reduce the effects of environmental modifications on transpiration or evaporation (see Leuning, this symposium).

Figure 6 compares the transpiration rate of the understorey in the Nanaimo stand calculated with (2) and (8) with the evapotranspiration rate measured by using the lysimeter described earlier (Osberg 1986). Even though this was a monolith or undisturbed-soil lysimeter, the salal was allowed nine months to recover fully from the installation. Soil evaporation was estimated to account for less than 10 % of the water loss from the lysimeter by measuring lysimeter mass loss after cutting the salal and determining the surface resistance of the forest litter. The reasonable agreement between the two methods in this experiment is not too surprising because the leaf area index of the understorey was only 1.0, so that the leaves would be expected to be quite well ventilated. Roberts *et al.* (1980) also found good agreement between two estimates of bracken transpiration obtained by pot weighing and by calculation using (2).

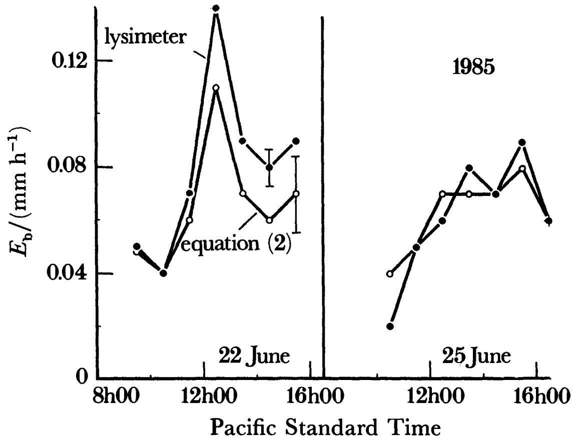

FIGURE 6. Comparison between understorey transpiration rate calculated by using (2) and the evapotranspiration rate beneath the overstorey (E_b) measured by a lysimeter in the Nanaimo stand. Calculated evaporation from the soil beneath the understorey was less than $0.1E_b$.

Eddy correlation measurements of understorey sensible heat flux, made 5–6 m away from the lysimeter in the Nanaimo stand by using two one-dimensional sonic anemometers, indicated that latent heat fluxes were almost twice those measured by the lysimeter. This is most probably a result of the marked spatial variability in understorey density and net irradiance in this stand and indicates the contribution that the eddy correlation technique can make to the study of understorey evapotranspiration.

7. COUPLING BETWEEN THE UNDERSTOREY AND THE ATMOSPHERE ABOVE THE OVERSTOREY

The relative importance of radiative and convective energy in driving understorey transpiration can be considered with the coupling concept of McNaughton & Jarvis (1983). Recognizing that the latent heat flux density from an understorey canopy can be written as

$\lambda E_b = \rho c_p g_c D_0/\gamma$, where D_0 is the value of vapour-pressure deficit at the 'big leaf' surface, it can be shown that D_0 can be expressed as

$$D_0 = \Omega_c D_{eq,b} + (1-\Omega_c) D_{imp,b}, \tag{11}$$

where $D_{eq,b} = [\epsilon A_b/(\epsilon + g_{AH}/g_{AV})]/(\rho c_p g_c/\gamma)$, the value of D_0 that would cause the understorey to transpire at a rate controlled by the net irradiance below the overstorey, namely, the equilibrium rate, $\lambda E_{eq,b} = \epsilon A_b/(\epsilon + g_{AH}/g_{AV})$. The value of the water-vapour pressure deficit imposed convectively on the understorey from above is $D_{imp,b}$ (here assumed to be the value measured just above the overstorey (D_a)), which would cause the understorey to transpire at the imposed rate, $\lambda E_{imp,b} = \rho c_p D_a g_c/\gamma$. The decoupling coefficient Ω_c, which indicates the relative importance of $D_{eq,b}$ and $D_{imp,b}$ in determining understorey transpiration rate, is given by

$$\Omega_c = (\epsilon + g_{AH}/g_{AV})/(\epsilon + g_{AH}/g_{AV} + g_{AH}/g_c). \tag{12}$$

If we consider the coupling of the understorey to the air above the overstorey, g_{AH} and g_{AV} must include the effects of the turbulent transport processes within the overstorey. As can be seen from (3) and (4), the value of g_{AH}/g_{AV} for a hypostomatous understorey canopy approaches unity from a value of two as the distance increases between the canopy and the height corresponding to $D_{imp,b}$ (Jarvis 1985*a*). It is difficult strictly to apply (11) and (12) because of the intervening sources or sinks for heat and water vapour in the overstorey.

The effectiveness of these processes of transport through the overstorey greatly affects the degree to which D_0 approaches $D_{imp,b}$ or D_a. Measurements made by Denmead & Bradley (1985) showed that in a 16 m tall ponderosa pine (*Pinus ponderosa* Laws.) stand (Uriarra Forest) gusts, which penetrated the canopy from above every 2–3 min, accounted for much of the sensible heat and water-vapour transport through the overstorey. Crowther & Hutchings (1985) observed gusts recurring every 20–40 s in an 11 m tall Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stand. Kelliher *et al.* (1989) determined turbulence intensity, kurtosis and skewness of the vertical wind velocity just above the understorey and above the overstorey of a 9 m tall *Pinus radiata* stand. They found turbulence intensities above the understorey were 0.30–0.48, slightly greater than above the stand. Values of kurtosis were 4–9, and greatly exceeded 3, the value (associated with a Gaussian distribution) found above the stand, whereas values of skewness were −0.6 to −1.5 compared with 0 found above the stand (figure 7). Similar results were obtained by Baldocchi & Hutchison (1987) just above the ground in an almond (*Prunus amygdalus* Batsch.) orchard, except that the skewness was much less negative. These results point to the occurrence of large intermittent downward gusts or sweeps in forests which would tend to impose D_a on the understorey and drive λE_b toward $\lambda E_{imp,b}$. McNaughton & Jarvis (1983) pointed out that the tendency of λE_b to approach $\lambda E_{eq,b}$ depends on the frequency with which these gusts penetrate the overstorey and displace air that is equilibrating with the understorey. Finnegan & Raupach (1987) showed theoretically that the quiescent periods between such gusts were too short for understorey transpiration to approach the equilibrium rate (i.e. Ω_c of the understorey would be expected to be less than 1.0).

The occurrence of gusting phenomena suggests that changes in the total heat content (sensible plus latent heat) of the air near the understorey would not be highly correlated with changes in the available energy flux density just above the understorey (McNaughton & Jarvis 1983). This is confirmed by daytime measurements of wet bulb temperature (proportional to the total heat content of the air) and available energy just above the salal understorey in the Courtenay Douglas-fir stand (figure 8). Consistent with the results in figure 8, Tan *et al.* (1978)

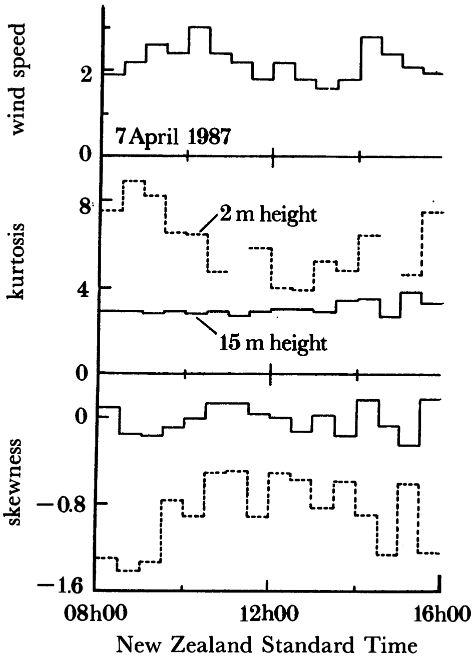

FIGURE 7. Kurtosis and skewness of the vertical wind velocity at the 2 m height (just above the understorey) and 15 m height in a 9 m tall *Pinus radiata* stand at Kiangaroa Forest, New Zealand. Also shown is the wind speed at the 15 m height (from Kelliher *et al.* 1989).

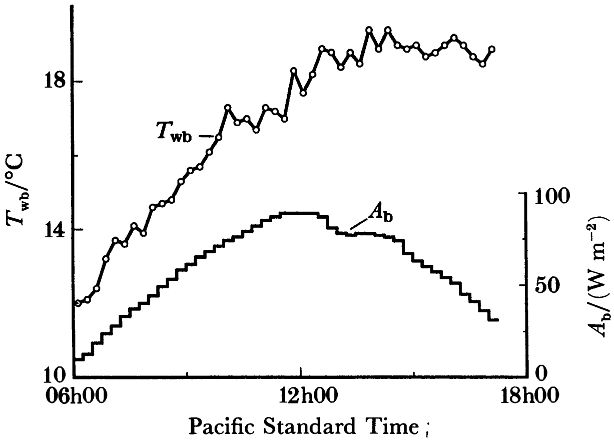

FIGURE 8. Daytime courses of wet bulb temperature (T_{wb}) and available energy flux density (A_b) beneath the overstorey in the 14 m tall Courtenay stand on 24 July 1981.

and Kelliher (1985) found D_b to be similar to D_a in this stand (table 2); Stewart (1984) also showed that D_b was similar to D_a in Thetford Forest. In the Nanaimo stand, however, the agreement was not quite as good (figure 9). In this stand during the summer, daytime air temperature just above the understorey was often 1–2 °C higher than that above the stand, whereas at night it was often 2–3 °C lower. This difference between the environments within the two stands is partly because of the higher transmittance of net radiation through the overstorey at Nanaimo than at Courtenay (daytime $R_{nb}/R_{na} = 0.16$ at Courtenay and 0.27 at Nanaimo). This points to the importance of the difference in the effectiveness of radiation

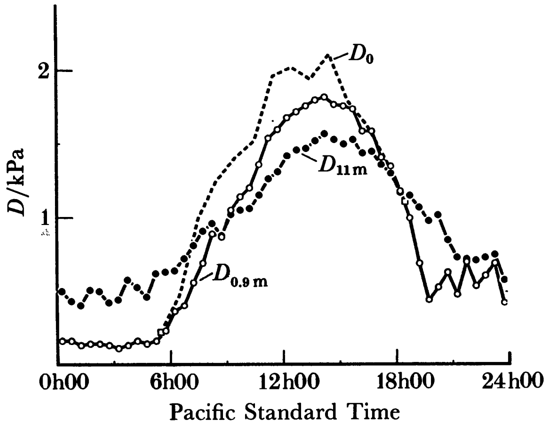

FIGURE 9. Comparison of vapour-pressure deficits (D) at heights of 0.9 m and 11 m in the 9 m tall Nanaimo stand on 26 June 1985. Also shown is the vapour-pressure deficit at the understorey leaf surface (D_0).

TABLE 2. ANALYSIS OF COUPLING OF THE UNDERSTOREY TRANSPIRATION TO THE ATMOSPHERE ABOVE FOR THE PERIODS IN FIGURE 10

(Ω_c was calculated by using (11) with $D_{\mathrm{imp,b}} = D_a$ (see text for definitions of symbols).)

date	Courtenay 24 Jly 1981	Nanaimo 26 Jun. 1985
ψ_s/MPa	−0.05	−0.3
D_a/kPa	1.31	1.5
D_b/kPa	1.14	1.7
$D_{\mathrm{eq,b}}$/kPa	0.32	5.0
D_0/kPa	0.69	2.0
λE_b/W m^{-2}	133	44
$\lambda E_{\mathrm{eq,b}}$/W m^{-2}	62	135
$\lambda E_{\mathrm{imp,b}}$/W m^{-2}	255	31
Ω_c	0.63	0.14

penetration and turbulent transport through the overstorey in affecting the understorey environment.

The values of Ω_c for the two understorey canopies calculated from (11) assuming $g_{AH}/g_{AV} = 1$ (tables 2 and 3) indicate quite strong coupling to the atmosphere above the overstorey. Daytime average values of Ω_c at Courtenay decreased with decreasing ψ_s (table 3). The value on 20 August was higher than expected because D was significantly lower than on the previous three days. The higher values for the Courtenay understorey is a consequence of its larger leaf area index which resulted in a higher understorey canopy conductance. For example, the values of g_c for the Courtenay and Nanaimo understoreys at midday in table 2 were 10.5 and 1.2 mm s^{-1} respectively. Some of the difference between the Ω_c values for the two understoreys may be attributable to the fact that g_c was determined by porometry at Courtenay and by using (2) with lysimeter measurements at Nanaimo. However, the effect is probably not large because good agreement was obtained between values of λE_b calculated by using (2) with porometer measurements and measured by using the lysimeter at Nanaimo (figure 6). The coupling to the atmosphere above the overstorey resulted in λE_b being markedly larger than $\lambda E_{\mathrm{eq,b}}$ in the Courtenay stand and smaller in the Nanaimo stand. Correspondingly, $D_{\mathrm{eq,b}} < D_a$ in the Courtenay stand, whereas $D_{\mathrm{eq,b}} > D_a$ in the Nanaimo stand.

The implications of coupling between the understorey and the air above the stand are evident in the comparison between the midday energy balances of the understorey in the Courtenay and Nanaimo stands during the summer shown in figure 10. In the Courtenay stand, λE_b from the understorey of high leaf area index exceeded A_b, indicating that sensible heat was drawn from above. The average leaf temperature of the understorey canopy was calculated to be 0.7 °C less than air temperature, although infrared thermometer measurements indicated leaf temperatures higher as well as lower than air temperature. The latent heat flux remained larger than A_b, even as the soil dried down. In contrast, in the Nanaimo stand λE_b was only a quarter of A_b as a consequence of the low leaf area index of the understorey and the dry soil. As a result, a good deal of sensible heat was generated by the understorey and the daytime air temperature just above the salal was higher than that above the stand (figure 9).

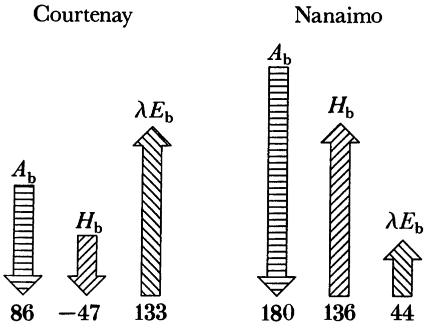

FIGURE 10. Comparison between the salal understorey energy balances (in watts per square metre) at 12h00–13h00 Pacific Standard Time in Courtenay (24 July 1981) and Nanaimo (26 June 1985) stands. See table 2 for conditions.

TABLE 3. AVERAGE VALUES OF $\lambda E_{eq,b}$, λE_b, $\lambda E_{imp,b}$ AND Ω_c FOR THE SALAL UNDERSTOREY IN DOUGLAS-FIR STANDS FOR 08h00–16h00 PACIFIC STANDARD TIME ON FOUR DAYS DURING A DRYING PERIOD AT COURTENAY (UNDERSTOREY $a = 2.75$) AND ON TWO DAYS NEAR THE MIDDLE OF A DRYING PERIOD AT NANAIMO (UNDERSTOREY $a = 1.0$)

(λE_b was obtained by porometry at Courtenay (soil evaporation beneath understorey was negligible) and weighing lysimeter at Nanaimo.)

date	ψ_s MPa	$\overline{\lambda E}_{eq,b}$	$\overline{\lambda E}_b$ W m^{-2}	$\overline{\lambda E}_{imp,b}$	$\bar{\Omega}_c$
			Courtenay 1981		
24 Jly	−0.05	52	122	242	0.63
31 Jly	−0.03	54	107	210	0.66
11 Aug.	−0.40	54	97	152	0.56
20 Aug.	−1.0	42	60	83	0.56
			Nanaimo 1985		
26 Jun.	−0.30	112	42	30	0.15
5 Jly	−0.50	85	34	25	0.15

8. IMPLICATIONS OF THE PRESENCE OF UNDERSTOREY VEGETATION TO STAND EVAPOTRANSPIRATION

Understorey transpiration rates can be as large as 3 mm per day and may often make a significant contribution to stand transpiration (table 4). Greenwood *et al.* (1985) found that understorey transpiration accounted for 32–36 % of the annual rainfall in a Jarrah (*Eucalyptus*

TABLE 4. MEASURED DAILY VALUES OF THE PERCENTAGE OF STAND EVAPOTRANSPIRATION ACCOUNTED FOR BY UNDERSTOREY TRANSPIRATION OR FOREST FLOOR EVAPORATION DURING THE GROWING SEASON

references	overstorey	understorey	%
Lindroth (1984)	*Pinus sylvestris*	heather and cowberry	6–22
Roberts *et al.* (1980)	*Pinus sylvestris*	bracken ($a \approx 1.0$)	25–60[a]
Kelliher *et al.* (1989)	*Pinus radiata*	shrubs, grass and slash	30–50
Denmead (1984)	*Pinus ponderosa*	sparse	10–18, 27[b]
Tan *et al.* (1978)	*Pseudotsuga menziesii*	salal ($a \approx 3.0$)	40–65[a]
Kelliher *et al.* (1986)	*Pseudotsuga menziesii*	salal ($a \approx 2.75$)	37–55[a]
	Pseudotsuga menziesii	none	21–13[a]
Osberg (1986)	*Pseudotsuga menziesii*	salal ($a \approx 1.0$)	30–42
	Pseudotsuga menziesii	none	15–18
Plamondon (1972)	*Pseudotsuga menziesii*	none	8–3[a]
Greenwood *et al.* (1985)	*E. marginata* and *E. calophylla*	acacia and other shrubs	32–36[c]

[a] First value moist conditions, second value dry conditions.
[b] First values spring, second value winter.
[c] Annual rainfall (%).

marginata Don ex. Sm.) forest in southwestern Australia. Kelliher *et al.* (1986) showed that when interception losses are also considered, 35 % of total forest transpiration and evaporation originated from the understorey during the growing season. These figures show that the understorey often plays an important role in the forest water and energy balances.

Differences in the responses of overstorey and understorey vegetation to environmental variables may affect their respective relative contributions to stand evapotranspiration. For example, Roberts *et al.* (1980) found that the proportion of total forest daily transpiration that came from the bracken understorey in their Scots pine forest increased from about 25 % under normal conditions to 60 % during exceptionally warm, dry periods because the bracken was less affected by vapour-pressure deficit than the pine trees. Immediately after thinning of the Courtenay Douglas-fir stand Tan *et al.* (1978) found that the proportion of daily stand transpiration originating from the salal understorey increased from 40 to 65 % as ψ_s decreased from -0.03 to -1.2 MPa. In the same stand in 1981, Kelliher *et al.* (1986) found that the proportion increased from 37 to 55 % for a similar decrease in ψ_s (table 4). The reason for this significant increase, when the relative stomatal conductance relations for the two species are similar (figure 4), is that the transpiration rate of Douglas-fir is approximately proportional to g_c because g_A is so large (i.e. a very small value of Ω_c), whereas the transpiration of salal decreases less rapidly than does g_c, because g_c is only slightly less than g_A (i.e. intermediate Ω_c). This is illustrated in figure 11, which shows the dependence of λE_b on g_c and g_A for typical midday understorey conditions in the spring.

In the Courtenay and Nanaimo stands, g_A was estimated to vary between 10 and 50 mm s^{-1} (see figures 3 and 4). Figure 12 shows how understorey and overstorey transpiration rates would be expected to vary with D_a and ψ_s for understorey $g_A = 50$ mm s^{-1}, with other conditions the same as in figure 11. The proportion of stand transpiration that originates with the salal understorey significantly increases with increasing D and decreasing ψ_s. Thus even with moderate coupling and relative stomatal conductance characteristics similar to those of the overstorey, the understorey contribution to stand evapotranspiration will usually increase as the vapour-pressure deficit increases and the soil dries.

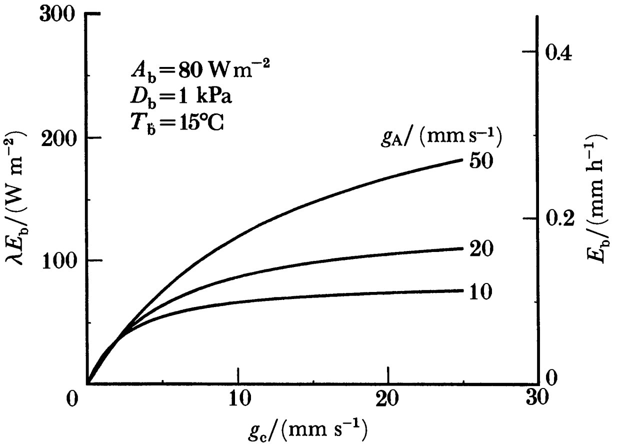

FIGURE 11. The relation between understorey latent heat flux density (λE_b), and transpiration rate (E_b) and understorey canopy conductance (g_c) for three values of understorey aerodynamic conductance and typical understorey conditions.

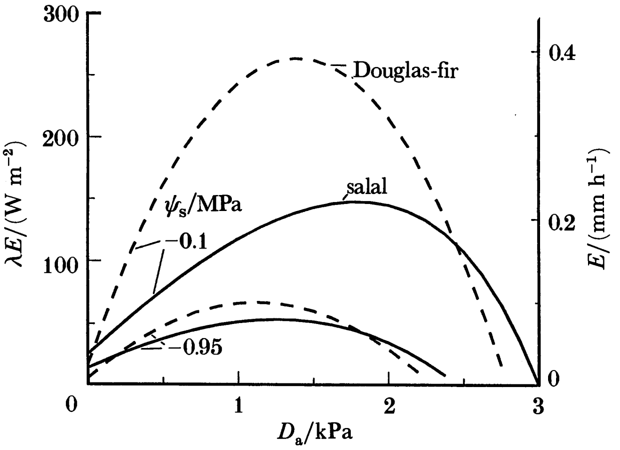

FIGURE 12. Understorey (salal, $a = 2.75$) and overstorey (Douglas-fir, $a = 6.0$) latent heat flux densities (λE) and transpiration rates (E) as a function of vapour-pressure deficit above the overstorey (D_a) for moderately high and low soil-water potentials (ψ_s). Conditions are: $A_b = 80$ W m^{-2}, $A_a = 500$ W m^{-2}, $T_b = T_a = 15$ °C, $D_b = D_a$, g_A (salal) = 50 mm s^{-1} and g_A (Douglas-fir) = 400 mm s^{-1}. Stomatal conductances were computed by using (9) and (10). (These conditions are typical of the Courtenay stand on a sunny day in spring except that in reality $D_b \approx 0.89\ D_a$.)

Black *et al.* (1980) found that the transpiration rates of individual trees and the evapotranspiration rates of the Courtenay stand and of a nearby unthinned stand (1870 trees ha^{-1}) with virtually no understorey were very similar during extended rainless periods of the growing season. They showed that transpiration of the salal in the thinned stand compensated for the reduction in the number of trees and they concluded that this largely explained the poor response of tree diameter growth to thinning in this stand. Black & Spittlehouse (1981) suggested that excessive thinning on dry sites with salal will reduce the soil water supply to the Douglas-fir, and that an overstorey should be maintained to suppress understorey transpiration.

In a comparison of evapotranspiration from Scots pine and Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melville) stands, Roberts *et al.* (1982) found that the soil water balance indicated similar stand evapotranspiration rates, although tree cutting experiments indicated that individual Corsican pine trees were transpiring at up to 28% faster than the Scots pine trees. They concluded that the understorey of bracken present only in the Scots pine stand compensated for differences in the tree canopies and that water yield was not likely to be reduced by planting the more productive Corsican pine. Roberts (1983) suggested that the presence of understorey is a contributing reason for the small variability observed in the annual evapotranspiration of different European forest stands.

9. EFFECTS OF UNDERSTOREY REMOVAL ON STAND EVAPOTRANSPIRATION

Discussion of the effects of understorey removal on stand evapotranspiration requires some understanding of the process of evaporation from the forest floor. Two semi-empirical approaches have been used to describe this process: (i) application of the Penman–Monteith equation using an empirical expression for estimating the surface conductance of the forest floor (g_{co}), and (ii) use of the lesser of the estimated energy-limited and soil-limited rates of evaporation. The former approach was used by Shuttleworth & Wallace (1985) and Choudhury & Monteith (1988) in studies of evaporation from sparse crops; Tanner & Jury (1976) used the latter in describing soil evaporation in row crops. Denmead (1984) found the Penman–Monteith equation more satisfactory than the energy or soil-limited approach in describing evaporation from the floor of the Uriarra Forest. He found the daily average value of g_{co} fairly well related to the square root of the number of days since rainfall. Kelliher *et al.* (1986) found the daily average surface conductance of the forest floor was highly correlated with the average volumetric water content (θ) of the tree root zone. They found g_{co} was about 1.2 mm s^{-1} for values of $\theta \geqslant 0.185$ m^3 m^{-3}, declining to about 0.3 mm s^{-1} at $\theta = 0.155$ m^3 m^{-3}. Using a single daily average value of surface conductance, with hourly values of R_{nb}, G, D_b and g_A, was moderately successful in calculating the course of soil evaporation over a 36 h period. The observed variation in forest floor evaporation is to be expected as a result of large fluctuations in A_b and u_b even at these low values of g_{co} (Monteith 1981*a*, p. 12) (figure 13). Both Denmead (1984) and Kelliher *et al.* (1986) demonstrated that their values of g_{co} could be

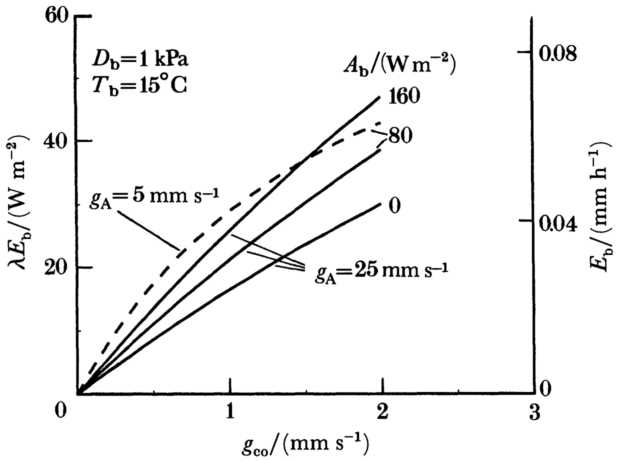

FIGURE 13. The relation between latent heat flux density (λE_b) or evaporation rate (E_b) from the forest floor and forest-floor conductance (g_{co}) for three values of available energy-flux density at the forest floor (A_b). Also shown is the effect of decreasing the forest-floor aerodynamic conductance (g_A).

calculated by considering the diffusion of water vapour through the observed thickness of the dry surface layer of litter and humus.

The surface conductance approach to soil evaporation must be considered empirical, however, because of the difficulty in predicting the thickness of the dry layer and the questionable validity of the assumptions that the layer is isothermal and the conductance constant over periods of one day. An alternative approach is the numerical solution of the heat and moisture flow equations for the soil and this requires the soil's thermal and hydraulic properties (see, for example, Bristow *et al.* 1986). In addition, there are obvious difficulties in calculating the aerodynamic conductance (g_A) immediately above the forest floor.

The effect of understorey removal on the vertical flux of water vapour below the overstorey depends on several factors including the species and leaf area index of the understorey, as well as the nature of the overstorey cover. Because we have seen that the vapour-pressure deficit during the daytime is quite similar above and below the overstorey in the Courtenay and Nanaimo stands, significant decreases in surface conductance beneath the overstorey would be expected to be accompanied by corresponding reductions in water vapour flux. An additional question is how water use by individual trees and by the stand as a whole responds to understorey removal over extended periods.

An understorey removal experiment was done in the thinned Douglas-fir stand in Courtenay in 1981–83 to address these questions (Kelliher 1985; Kelliher *et al.* 1986). The salal understorey was cut and removed from around one tree (or subplot) of each of four selected pairs of Douglas-fir trees. Soil water content and potential were intensively monitored during the first two growing seasons. On six selected days during a month-long dry period in 1981, soil evaporation was measured with two or three small lysimeters in one of the cut subplots and on five of these days salal transpiration in the corresponding uncut subplot was calculated with the Penman–Monteith equation using intensive hourly measurements of stomatal conductance and measured meteorological variables. Figure 14 shows that salal transpiration rates were two to four times higher than soil evaporation rates. Also shown in the figure are the soil evaporation and salal transpiration rates calculated from the water-balance model of Kelliher

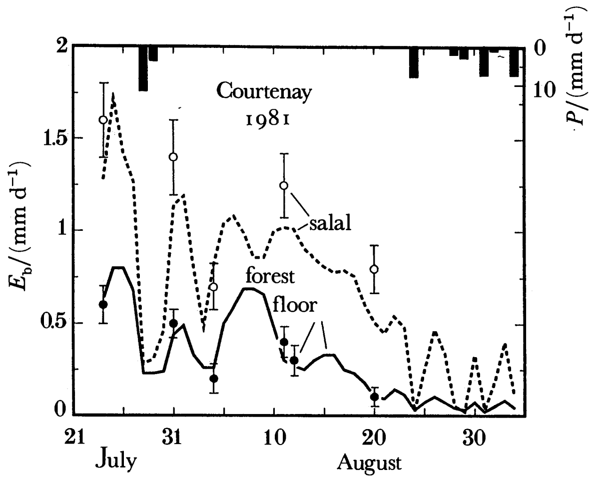

FIGURE 14. Salal understorey transpiration rates (○) calculated from (2) with measured stomatal conductances, and forest-floor evaporation rates (●) measured by small lysimeters in plots from which the salal was cut and removed. Lines are values calculated by the water-balance model of Kelliher *et al.* (1986). Also shown is the daily rainfall rate (P).

et al. (1986). The agreement between measured and calculated soil evaporation is not surprising, as the rates measured on the six days were part of the data set used to develop the relation between g_{co} and θ described earlier that is used in the model. As the soil dried, soil evaporation in the cut plots decreased from 21 % to 13 % of stand evapotranspiration, a trend also observed by Plamondon (1972) (table 4). The differences between salal transpiration rates calculated with the two procedures indicate that there is probably considerable spatial variability in stomatal conductance of the understorey, so that obtaining 'average' stomatal conductance characteristics is bound to be very difficult.

Nevertheless, measured values of θ in 1981 and 1982 were less than 0.02 $m^3\ m^{-3}$ larger where salal was removed than where it was present. The water balance model of Kelliher *et al.* (1986) showed that total stand evapotranspiration (which includes a small proportion of interception loss) in the cut plots was only 8 % (table 5) and 6 % less than in the uncut plots during 5 week drying periods in 1981 and 1982, respectively. However, the model also indicated that the trees in the cut plot transpired 31 % (table 5) and 52 % more than the trees in the uncut plots during the same periods. Stomatal conductance measurements in both years and heat pulse measurements of stem sap flow in 1981, both made on one pair of trees, confirmed this large difference (Kelliher 1985). Consequently, rather than a large accumulation of moisture in the root zone as a result of understorey removal, most of the additional water was taken up by the trees.

TABLE 5. COMPONENTS (%) OF EVAPOTRANSPIRATION FROM THE COURTENAY DOUGLAS-FIR STAND FOR 24 JULY TO 3 SEPTEMBER 1981 CALCULATED BY USING THE KELLIHER *ET AL.* (1986) WATER-BALANCE MODEL

	overstorey		understorey			
understorey	transpiration	interception	transpiration	interception	soil	total/mm
present	44	17	32	3.5	3.5	88
removed	63	19	—	—	17	81

As the soil dried the small differences in water content reported above were equivalent to root-zone water-potential differences of up to 0.3 MPa (Kelliher 1985; Kelliher *et al.* 1986). This is consistent with the steep soil-water retention curve (large $\Delta\psi_s/\Delta\theta$) for this coarse soil. As a result of this difference in ψ_s, the photosynthesis rates of the trees without understorey were, like their stomatal conductance, higher than those of the trees with understorey (Price *et al.* 1986), whereas average annual basal area increments of the trees without understorey were significantly larger than those with understorey over the three years of the study (Kelliher 1985; Price *et al.* 1986).

To confirm the small plot results at Courtenay, a three-year study was conducted using two 30 m × 40 m plots in an unthinned part of the Nanaimo stand (Black *et al.* 1986). The coarse soil at Nanaimo was similar to that at Courtenay. Understorey was cut and removed from one of the plots in 1984. During each of the three growing seasons θ was never more than 0.01–0.02 $m^3\ m^{-3}$ higher where salal understorey had been removed than where it was present, in agreement with the earlier results at Courtenay in small plots.

Fertilization at the time of thinning may affect the response to understorey removal (Jarvis 1985*b*). Brix & Mitchell (1986) found no effect of understorey removal on ψ_s for nine years after thinning and fertilization of a 24-year-old Douglas-fir stand near Shawnigan Lake about 300 km south of Courtenay. The difference in the results of the two studies is partly the *et al.* (1986). The agreement between measured and calculated soil evaporation is not surprising, as the rates measured on the six days were part of the data set used to develop the relation between g_{co} and θ described earlier that is used in the model. As the soil dried, soil evaporation in the cut plots decreased from 21 % to 13 % of stand evapotranspiration, a trend also observed by Plamondon (1972) (table 4). The differences between salal transpiration rates calculated with the two procedures indicate that there is probably considerable spatial variability in stomatal conductance of the understorey, so that obtaining 'average' stomatal conductance characteristics is bound to be very difficult.

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removed	63	19	—	—	17	81

As the soil dried the small differences in water content reported above were equivalent to root-zone water-potential differences of up to 0.3 MPa (Kelliher 1985; Kelliher *et al.* 1986). This is consistent with the steep soil-water retention curve (large $\Delta\psi_s/\Delta\theta$) for this coarse soil. As a result of this difference in ψ_s, the photosynthesis rates of the trees without understorey were, like their stomatal conductance, higher than those of the trees with understorey (Price *et al.* 1986), whereas average annual basal area increments of the trees without understorey were significantly larger than those with understorey over the three years of the study (Kelliher 1985; Price *et al.* 1986).

To confirm the small plot results at Courtenay, a three-year study was conducted using two 30 m × 40 m plots in an unthinned part of the Nanaimo stand (Black *et al.* 1986). The coarse soil at Nanaimo was similar to that at Courtenay. Understorey was cut and removed from one of the plots in 1984. During each of the three growing seasons θ was never more than 0.01–0.02 $m^3\ m^{-3}$ higher where salal understorey had been removed than where it was present, in agreement with the earlier results at Courtenay in small plots.

Fertilization at the time of thinning may affect the response to understorey removal (Jarvis 1985*b*). Brix & Mitchell (1986) found no effect of understorey removal on ψ_s for nine years after thinning and fertilization of a 24-year-old Douglas-fir stand near Shawnigan Lake about 300 km south of Courtenay. The difference in the results of the two studies is partly the

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Discussion

J. S. Wallace (*Institute of Hydrology, Wallingford, U.K.*). All the deductions about the contribution of the understorey are, I think, dependent on conventional diffusion theory (*K*-theory). However, according to Dr Raupach (this symposium), the understorey is within the so-called 'near field' where *K*-theory is said to be inappropriate. Does this mean that the above conclusions about the contribution of the understorey are in error?

T. A. Black. Our calculations are effectively at the leaf level, and *K*-theory is applicable to the laminar boundary layer of the leaf because within this layer transport is largely a result of molecular diffusion rather than eddy motion. (Of course, if we made our measurements within only a few molecular diameters of the leaf surface, the application of *K*-theory would give erroneous results because of the near-field effect on molecular diffusion (Thurtell 1989).) The errors in our calculations are mainly a result of vapour-pressure deficit and wind speed not being measured just outside the boundary layer of the individual leaves. The agreement between the lysimeter measurements and the Penman–Monteith calculations of understorey transpiration indicate that, for understoreys with a leaf area index near 1.0, measurement of the vapour-pressure deficit just above the understorey canopy is a good measure of the vapour-pressure deficit near the majority of the canopy leaves. For understorey canopies of larger leaf area index, the desirable approach would be the combination of energy balance and transfer equations at the leaf level (or the Penman–Monteith equation) with the canopy turbulent transfer theory discussed by Dr Raupach.

J. B. Stewart (*Institute of Hydrology, Wallingford, U.K.*). I wish to refer to Professor Black's results for the Courtenay site, where he showed that the evaporation from the understorey vegetation exceeded the available energy measured just above it. Is this result due to the vapour-pressure deficit measured below the tree canopy being much higher than expected in relation to the available energy measured below the tree canopy, and more closely related to the available energy measured above the tree canopy? Also, how does the relation between vapour-pressure deficit measured below the tree canopy and the available energy also measured below the tree canopy differ between the Courtenay and Nanaimo sites?

T. A. Black. The evaporation from the understorey vegetation at Courtenay exceeded the available energy measured just above it because the vapour-pressure deficit below the tree canopy (D_b) greatly exceeded the equilibrium value ($D_{eq,b}$). For example, at noon on 24 July

1981 (see table 2), $D_b = 1.14$ kPa and $D_{eq,b} = 0.32$ kPa. The vapour-pressure deficit above the tree canopy (D_a) was 1.31 kPa, only slightly higher than D_b. The ratio of D_b to A_b at Courtenay was larger than at Nanaimo. This appeared to be mainly because of the higher transmittance of solar radiation in the Nanaimo stand and the significant degree of coupling through the tree canopy in both stands. The fact that $D_b < D_a$ at Courtenay and $D_b > D_a$ at Nanaimo appears to be mainly a consequence of the canopy conductance of the Nanaimo understorey being less than that of the Courtenay understorey.

J. L. Monteith, F.R.S. (*International Centre for Research into Crops for the Semi-Arid Tropics, Hyderabad, India*). Professor Black's graph of conductance versus vapour pressure or saturation deficit (D) raised two questions in my mind.

First, was conductance a function of D as might be expected for a coupled system? Or was D a function of conductance as in an uncoupled system. Or did both régimes occur at different times as the range of Ω suggests?

Second, is Professor Black justified in drawing straight lines to represent the negative correlation between conductance and D? This forces the evaporation rate to increase to a maximum as D increases and then to decrease to zero as one of his figures shows. An alternative model would make resistance increase linearly with D, implying that the evaporation rate was constant, limited perhaps by soil-water content or by the size of the root system.

T. A. Black. The functional relation between stomatal conductance of the Douglas-fir overstorey to vapour-pressure deficit is a good example of the response in a well-coupled system. In this case, the measured vapour-pressure deficit was a good approximation of that at the leaf surface. On the other hand, the relation for the salal understorey was obtained under conditions of moderate coupling. We have not analysed the understorey conductance data using the calculated leaf-to-air vapour-pressure difference or the vapour-pressure deficit at the salal leaf surface mainly because of the errors involved in these calculations.

In the case of the understorey, we feel that the use of straight lines is justified. The relation may not be linear, but it is not possible, considering the scatter in the data, to suggest a better alternative relation. There is certainly evidence in the Douglas-fir data that the relation is curvilinear; however, we feel that the use of straight lines is adequate for the analysis in this paper. As Dr Monteith says, this forces the evaporation to be related to D as shown in figure 12 (see also Choudhury & Monteith 1986). Some years ago, we found that our energy balance: Bowen ratio measurements of evaporation from the Courtenay Douglas-fir stand, when plotted against D, showed the same relation as indicated in figure 12 (Tan *et al.* 1978). Our stomatal conductance data from the Douglas-fir does not support Dr Monteith's alternative model that resistance increases linearly with D. This appears also to be the case with the understorey; however, considering the limited understorey data and the fact that D has not been calculated for the leaf surface, this deserves further investigation.

P. G. Jarvis (*Department of Forestry and Natural Resources, University of Edinburgh, U.K.*). I am impressed by the quantitative evaluation of the decoupling coefficient (Ω) for the salal understorey. It is particularly useful to see values for Ω, whereas we have only guessed at the degree of coupling as in the references cited. I have the following comments.

1. The understorey is better coupled than I, for one, had anticipated, presumably as a result of frequent, deep penetration of gusts from above, as demonstrated by Denmead & Bradley (1985). The canopy above seems to offer but little shelter.

2. A range of values of Ω from 0.1 to 0.6 may reflect the intermittancy of the gusts and the structure of the tree canopy above, but it should not be regarded as particularly exceptional. A population of values of Ω for any uniform stand of vegetation may show a similar range of variation, depending upon the variation in wind speed and canopy conductance. Although we may talk about typical or median values for a particular kind of vegetation, there is, in fact, always a distribution of values.