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Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements*

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Summary. Tree transpiration was determined by xylem sap flow and eddy correlation measurements in a temperate broad-leaved forest of *Nothofagus* in New Zealand (tree height: up to 36 m, one-sided leaf area index: 7). Measurements were carried out on a plot which had similar stem circumference and basal area per ground area as the stand. Plot sap flux density agreed with tree canopy transpiration rate determined by the difference between above-canopy eddy correlation and forest floor lysimeter evaporation measurements. Daily sap flux varied by an order of magnitude among trees (2 to 87 kg day^{-1} tree^{-1}). Over 50% of plot sap flux density originated from 3 of 14 trees which emerged 2 to 5 m above the canopy. Maximum tree transpiration rate was significantly correlated with tree height, stem sapwood area, and stem circumference. Use of water stored in the trees was minimal. It is estimated that during growth and crown development, *Nothofagus* allocates about 0.06 m of circumference of main tree trunk or 0.01 m^2 of sapwood per kg of water transpired over one hour.

Maximum total conductance for water vapour transfer (including canopy and aerodynamic conductance) of emergent trees, calculated from sap flux density and humidity measurements, was 9.5 mm s^{-1} that is equivalent to 112 mmol m^{-2} s^{-1} at the scale of the leaf. Artificially illuminated shoots measured in the stand with gas exchange chambers had maximum stomatal conductances of 280 mmol m^{-2} s^{-1} at the top and 150 mmol m^{-2} s^{-1} at the bottom of the canopy. The difference between canopy and leaf-level measurements is discussed with respect to effects of transpiration on humidity within the canopy. Maximum total conductance was significantly correlated with leaf nitrogen content. Mean carbon isotope ratio was -27.76 ± 0.27‰ (average ± s.e.) indicating a moist environment. The effects of interactions between the canopy and the atmosphere on forest water use dynamics are shown by a fourfold variation in coupling of the tree canopy air saturation deficit to that of the overhead atmosphere on a typical fine day due to changes in stomatal conductance.

Key words: Canopy conductance – Canopy transpiration – Xylem sap flow – Humidity response of stomatal – *Nothofagus*

The role of stomata in controlling leaf water loss and regulation of stomatal aperture by the aerial environment is well documented for many plant species (Farquhar and Sharkey 1982; Schulze 1986). However, extrapolation from leaf-scale stomatal conductance to plant- and canopy-scale transpiration can be difficult especially in a natural forest, where canopy/atmosphere interactions result in a variable and complex environment. In particular, atmospheric humidity may be continually changing throughout the canopy by advection through turbulent imposition and by evaporation itself.

With leaf or shoot chamber measurements, detailed knowledge of leaf conductance in a number of steady-state humidity environments can be derived as one prerequisite for integration from leaf- to canopy-scale processes. However, this information is not only difficult to obtain but also difficult to interpret because of the turbulent feedback of transpiration on the canopy humidity environment (Raupach and Finnigan 1988). Complementary to chamber measurements, forest evaporation has also been measured by micrometeorological methods (e.g. Verma et al. 1986 for temperate broad-leaved forests, see also McNaughton and Jarvis 1983 for coniferous forests). While such measurements provide spatial integration, effects of stand structure and the physiology of different species is difficult to discriminate. Understory and forest floor evaporation can also confound interpretation of whole forest evaporation measurements with respect to tree canopy transpiration and stomatal behaviour. In this situation, xylem sap flow measurements link the large scale integration of forest micrometeorological methods with micro-scale leaf stud-

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* This paper is dedicated to Prof. Dr. O.L. Lange on the occasion of his 65th birthday

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ies using chambers (Cermak et al. 1984; Schulze et al. 1985). In combination with atmospheric humidity measurements, an integrated tree canopy conductance can be estimated from sap flow measurements as a basis to explore stomatal effects on transpiration more carefully with respect to tree species and canopy position.

The present study was undertaken to: (1) examine tree xylem sap flow and stomatal behaviour in a heterogenously-structured, temperate broad-leaved forest of *Nothofagus fusca* (Hook.f.) Oerst. and *N. menziesii* (Hook.f.) Oerst., and (2) make comparisons with concurrent eddy-correlation evaporation measurements above the canopy. We believe that our measurements also provide important data for considering larger scale evaporation processes where complex vegetation structure requires knowledge of surface parameters. In this sense, the present study aims at understanding the interaction of structural diversity at the stand level with physiological effects at the leaf level.

Table 1. Frequency distribution of tree diameters at height 1.4 m (trees ha^{-1}) in a 3600 m^2 pristine *Nothofagus* forest plot. Numbers in brackets indicate the frequency distribution of trees in the measuring plot

Diameter (m)	*Nothofagus*		
	fusca	*menziesii*	total
0 –0.2	239	642 (7)	881 (7)
0.2–0.4	25 (5)	108 (5)	133 (10)
0.4–0.6	14 (2)	25 (1)	39 (3)
0.6–0.8	19 (1)	0	19 (1)
0.8–1.0	19	0	19
1.0–1.2	11	0	11
1.2–1.4	3	0	3
1.4–1.6	3	0	3
1.6–1.8	3	0	3
Total	336	775	1111

Forest site and methods

Stand and plot description

Xylem sap flow was measured in trees representing different canopy strata and species in a pristine *Nothofagus* forest located in the South Island of New Zealand (Maruia forest: 42° 13′S, 172° 15′E, 400 m elevation; for the year ending 30 April 1991, there was 2054 mm rainfall on 197 rain days, December – March summer rainfall was 678 mm, and average annual air temperature was 9.4° C). The two tree species, red beech, *Nothofagus fusca* (Hook.f.) Oerst., and silver beech, *Nothofagus menziesii* (Hook.f.) Oerst. co-exist in a stand which varies greatly on a small scale of order $< 1000\ m^2$. This variation results from periodic tree fall events that remove old trees from the canopy and leave gaps now containing trees of various ages and sizes (Stewart and Rose 1990). The forest canopy is thus very rough. Even so, over larger scales beyond 1000 m^2, the forest is relatively uniform (Fig. 1).

Fig. 1. Pristine *Nothofagus* forest showing the characteristic large variation in tree size on a small scale (photograph by J.E. Hunt). On a larger scale ($> 1000\ m^2$), the forest is relatively uniform

The stand contained 0.111 stems m^{-2} and 0.0067 $m^2\ m^{-2}$ basal area derived from a plot of 3600 m^2 at the study site. Total above-ground biomass in a similar forest was estimated to be 30 kg m^{-2} (Beets 1980). The tree size distribution (Table 1) is characterized by about 20 large, regularly spaced *N. fusca* trees per hectare which may reach a diameter of more than 1.5 m. These "old giants" are estimated to be 300 to 400 years old (Stewart and Rose 1990). They emerge 2 to 5 m above the main canopy and reach a height up to 36 m. The main canopy is also formed predominantly by *N. fusca* of 26 to 31 m height, having a diameter of 0.3 m to 1 m. The subcanopy of suppressed trees is 20 to 25 m height. It contains a larger proportion of *N. menziesii* of < 0.4 m diameter. Below this canopy layer, regrowth of a large number of seedlings and saplings is found in a shrub layer (up to 8 m high). During late summer and autumn, stand leaf area index was 7 on a one-sided basis. *Nothofagus fusca* has hypostomatous leaves of about 4 cm^2, while leaves of *N. menziesii* are only 1 cm^2. Specific leaf weight was 0.014 $m^2\ g^{-1}$ for *N. fusca* and 0.008 $m^2\ g^{-1}$ for *N. menziesii*.

Measurements were made in a 337 m^2 plot with ground area being a polygon determined by connecting bisects of outer plot trees and their nearest neighbouring trees outside the plot (Fig. 2). Xylem sap flow was measured in 14 trees (emergent trees 32–36 m height, codominant trees of the main canopy 28 to 31 m height, and suppressed trees of the sub-canopy 20 to 25 m height) over a period of six fine days during March 1991, at the end of the southern hemisphere summer. The plot contains an additional 12 trees (height < 10 m) which do not significantly contribute to plot leaf area. During 11–15 April 1991, measurements were extended to an additional 7 emergent trees outside the plot. Gravimetric forest floor and soil samples indicated that the root zone water storage was near field capacity on all measurement days.

The plot may be characterized by the following tree dimensional correlations. There is a significant relation between histochemically determined sapwood area (Bromocresol green, Burrows 1980) and projected crown area (intercept 0.0297, slope $0.86*10^{-3}$, $r = 0.87$, $p = 0.0001$) suggesting a proportionality of water supply tissue in the stem and evaporative surface area in the crown. For trees > 20 m height, projected crown area and tree height were significantly correlated, independent of species (intercept -151.9, slope 7.08, $r = 0.76$; $p = 0.0001$). A correlation between tree height and diameter at breast height was significant ($r = 0.67$, $p = 0.0007$). However, there appeared to be an upper limit of tree height of about 36 m while diameter appeared to be unlimited for *N. fusca* in this habitat.

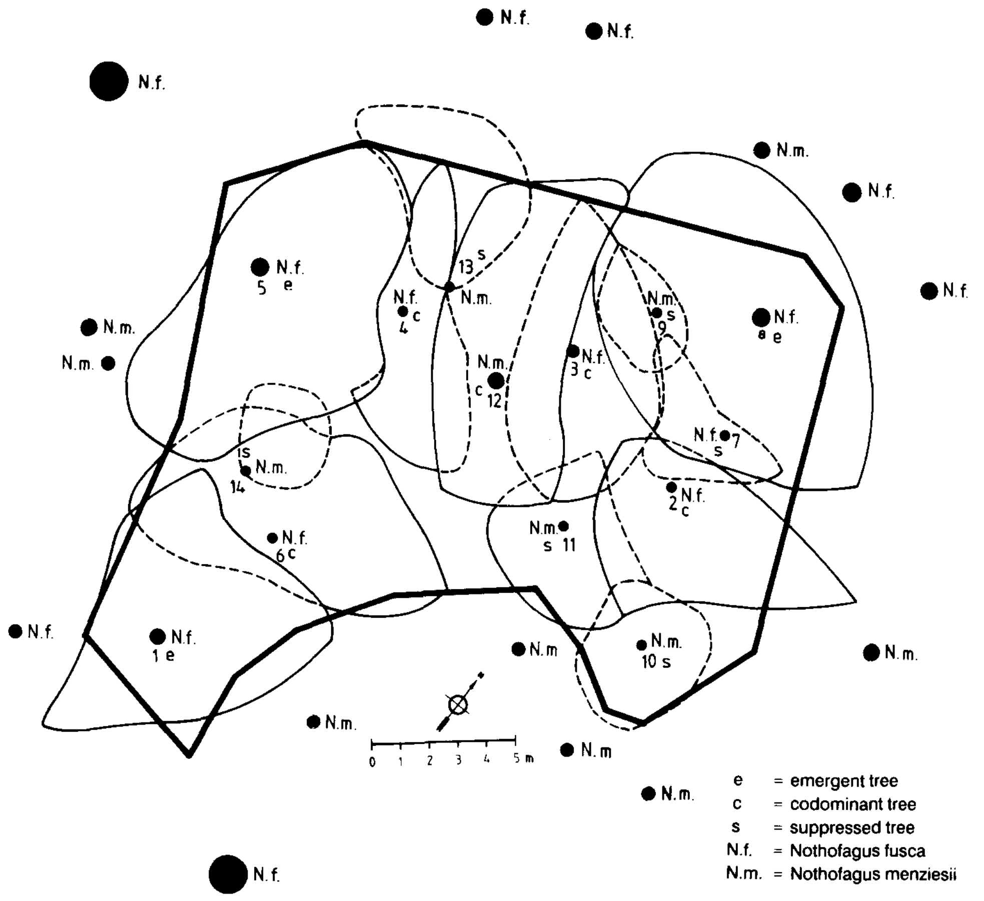

Fig. 2. Map of projected crown areas of the 14 measurement trees in the representative 337 m^2 (polygon) xylem sap flow plot during March 1991. The genus and species initials (N.f. = *Nothofagus fusca* and N.m. = *N. menziesii*), crown class (e = emergent, c = codominant, and s = suppressed), and stem location are given for each tree. Solid and dashed outlines are for emergent and underlying portions of tree crowns. Also shown are a scale and north arrow. The map also contains 15 neighbouring trees outside the plot

Sap flow measurements

A steady-state, null-balance method was used to measure xylem sap flux (Vieweg and Ziegler 1960; Cermak et al. 1973; Pearcy et al. 1989), by which a constant temperature difference of 3 K was maintained between a sapwood reference point and a heated stem area. Wood between pairs of electrodes was heated by the conduction of alternating current, electronically controlled with a time constant < 10 s (Steinwald Electronics, 8590 Marktredwitz, Germany). The mass flow of water through the xylem was thus proportional to the required amount of input energy, sampled every 10 s. No assumptions about wood structure were necessary because the heating current was proportionally converted into mass flow via the heat capacity of water (for details see Pearcy et al. 1989). The heated stem sector was approximately 72 mm wide including six 1-mm wide by 50-mm long and 10-mm high electrodes. The stem sector for water flux measurement was thus 66 mm including a small wound area in the vicinity of the electrodes. Preliminary temperature measurements indicated that sap flow was confined to the outer 20 mm of xylem although histochemical sapwood to extend up to 82 mm depth (Kelliher et al. 1992). Conductive heat losses were assumed constant and radial heat losses of the measuring point to the atmosphere were minimized by insulation. Total heat losses were determined from measurements on a night when fog was present and xylem sap flow was minimal. *Nothofagus* stomata are essentially closed in darkness (see later discussion).

The calculation of sap flux density was done for the plot by summing the 14 tree sap fluxes and (1) dividing by 337 m^2 ground area or (2) multiplying by the ratio of plot and stand summations of tree circumferences per unit ground area. The two estimates of plot sap flux density agreed with tree canopy transpiration from the difference between above-canopy eddy correlation and forest floor lysimeter evaporation measurements (Kelliher et al. 1992) (Fig. 3). For individual trees, sap flux density was calculated by division of sap flux by the ground area encompassed in a vertical projection of basal tree crown perimeter. The sum of the 14 measurement tree crown areas was 540 m^2 which exceeded plot ground area by the factor 1.6 so that the sum of individual sap flux densities are not directly comparable to the plot based calculations.

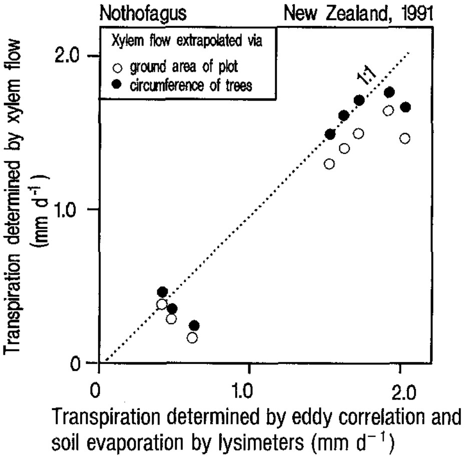

Fig. 3. Comparison of daily tree canopy transpiration rates (mm d^{-1}), determined from the difference between above-canopy eddy correlation and forest floor lysimeter evaporation measurements and by xylem sap flow measurements. Sap flux (l d^{-1}) was measured in 14 *Nothofagus* trees of a representative 337 m^2 plot. Extrapolation to stand sap flux density (l m^{-2} d^{-1}) was done either by dividing sap fluxes by plot ground area *(open circle)*, or by multiplying sap fluxes by the fraction of total stand tree circumference contained in the plot (i.e., m (cicumference) m^{-2} (plot) divided by m (circumference) m^{-2} (stand)) *(solid circle)*. Measurements were made during 12–17 March and 12–15 April 1991. Also shown is a 1 : 1 line

Theory and estimation of parameters

The Penman-Monteith equation describes how the relative importance of radiative and advective energy for tree transpiration rate (E, m s^{-1}), the dominant evaporation component in this study (Kelliher et al. 1992), depends on the ratio of the aerodynamic and canopy conductances (g_a and g_c, respectively, in units of m s^{-1}; g_c is the product of a "tree canopy average" stomatal conductance and leaf area index). This equation may thus be written in the instructive form of McMaughton and Jarvis (1983) as:

$$E = \Omega * E_{eq} + (1-\Omega) * E_{imp} \quad (1)$$

where E_{eq} is the transpiration rate obtained in equilibrium with an extensive, homogeneous wet surface via the energy balance expressed:

$$E_{eq} = (\varepsilon/(\lambda * \varrho * (\varepsilon+1))) * R_A \quad (2)$$

E_{imp} is the transpiration rate imposed by the effects of the air saturation deficit (D, kPa) given by:

$$E_{imp} = (D * g_c)/(\varrho * G_v * T_K) \quad (3)$$

and Ω is a coefficient indicating the degree of coupling between the canopy and D as

$$\Omega = (1+\varepsilon)/(1+\varepsilon+g_a/g_c) \quad (4)$$

In equation (2), the two terms ε and λ are properties of water in air and are only weakly temperature dependent; ε is the change of latent heat relative to the change in sensible heat of saturated air (1.27 at 10° C) and λ is the latent heat of vaporisation (2477 kJ kg^{-1} at 10° C). The density of water, ϱ, is 998 kg m^{-3}. The available energy, R_A, includes the net all-wave radiation, canopy biomass and air energy storage rates, and soil heat flux density. In equation (3), G_v is the gas constant for water vapour (0.462 m^3 kPa kg^{-1} K^{-1}) and T_K is air temperature in K. The above equations assume the similarity of aerodynamic conductances for the transfer of sensible and latent heat.

When aerodynamic conductance is much less than canopy conductance, Ω approaches 1, and E approximates E_{eq}. In this case, a thick boundary layer isolates the canopy from the effects of air saturation deficit in the air above, and stomatal control of canopy-level transpiration essentially is absent. This tends to be true for low vegetation, such as pastures and many crops, provided soil water and nutrients are adequate. Alternatively, the energy for transpiration may be advective, that is, it is brought by wind. Here, aerodynamic conductance greatly exceeds canopy conductance, Ω approaches zero, E approximates E_{imp}, and stomatal control of canopy-level transpiration is generally significant. Consequently, Ω quantifies the potential influence of stomatal behaviour on E for comparative purposes.

Use of Penman-Monteith equation requires measurement of environmental variables and estimation of aerodynamic and canopy conductances. We began by estimating the total water vapour conductance of individual trees, g_t, from the ratio of sap flux density (E) and air saturation deficit (D, measured above the canopy at height 32.5 m) with an units conversion faktor $k = (\varrho * G_v * T_K)$. When E is expressed in mm h^{-1} and D in kPa, k = 36.25 kPa at 10° C and g_t is derived in mm s^{-1} from

$$g_t = k * E/D \quad (5)$$

The total water vapour conductance includes stomatal, leaf boundary layer, and eddy diffusive conductance components because we are accounting for conductances from height of the "average" stomata in the tree canopy to the height of measurement of D above the canopy (Thom 1972). The canopy conductance, g_c, was determined from the difference between the inverses of g_t and the aerodynamic conductance, g_a.

$$1/g_c = 1/g_t - 1/g_a \quad (6)$$

Estimation of g_a involves additional measurements, some judgement, and confinement of calculations to emergent (principally *N. fusca*) trees to obviate complex within-canopy micrometeorology that is beyond the scope of this paper. We calculated g_a by combining the inverses of a canopy aerodynamic transfer conductance for momentum (g_{am}) as $1/g_a = 1/g_{bv} + 1/g_{am}$. Inclusion of the momentum component, g_{am}, in the estimation of g_a is intended to recognise that air saturation deficit was measured in this study at a height well above the boundary layers of the canopy leaves (Thom 1972).

Boundary layer conductance for water vapour transfer (on a onesided area basis) was 17 mm s^{-1} for a typical *N. fusca* shoot coated with gypsum, wetted, and placed in a ventilated porometer chamber with a wind speed of 0.25–0.50 m s^{-1} (Dr. David Whitehead, pers. comm.). We aproximated g_{bv} to be a constant 60 mm s^{-1} by multiplying the porometer measurement of 17 mm s^{-1} by one-sided tree canopy leaf area index = 7 and an approximation of the average leaf shelter factor = 0.5 after Black and Kelliher (1989). We estimated g_{am} from above-canopy wind speed (u) measurements and a relationship between g_{am}, measured by a 3-dimensional sonic anemometer above our tree canopy, and u as g_{am} (mm s^{-1}) = 100 u (m s^{-1}) after Kelliher et al. (1992).

With estimates of canopy conductance, g_c, and leaf area index, a_t, "tree canopy average" stomatal conductance (g_s) was calculated for emergent trees in the sap flow measurement plot. Calculation of g_s as $1.6 * g_c/a_t$ used a factor 1.6, the measurement plot ratio of projected tree crown area to ground area, to account for sap flux densities being normalised by projected tree crown areas. Comparative measurements of leaf-level stomatal conductance (g_l) were made at the top and bottom of the canopy of an emergent *N. fusca* tree using an open gas exchange system described by Hollinger (1987). The light response of g_l was determind using a sequence of neutral density filters at a constant air temperature of 20° C and an air saturation deficit of 1.0 kPa. The response of g_l to humitity was also measured at a constant air temperature of 20° C and a photon flux density of 1.0 mol m^{-2} s^{-1}. Because *N. fusca* and *N. menziesii* are hypostomatous, g_s, g_l, and comparative data from literature are all expressed in this paper on a one-sided leaf area basis.

Results

Maximum sap fluxes varied by an order of magnitude over the 14 plot trees (Fig. 4A). The range of daily transpiration in each crown layer was also large, being 58–84 kg tree^{-1} day^{-1} for emergents, 10–30 kg tree^{-1} day^{-1} for codominant trees, and 2–30 kg tree^{-1} day^{-1} for suppressed trees. Even so, differences in sap fluxes between the three canopy layers were consistently significant on a daily basis (ANOVA, $F = 29.67$, $p < 0.0001$, $n = 14$, $r = 0.918$). On average, trees of *N. menziesii* had lower maximum sap fluxes per tree than *N. fusca* (ANOVA, $F = 4.599$, $p = 0.043$, $n = 24$), but this was related to differences in average tree size. Corresponding maximum sap fluxes for different species of trees of the same height were not significantly different ($p = 0.22$, not shown).

Daily courses of sap flux were generally similar in the three canopy layers, although some individuals were divergent due to variable shading in the canopy. Sap flux was minimal in the early morning. After sunrise, sap flux of emergent trees began about 1 and 2 h earlier than for codominant and suppressed trees, respectively. Emergent trees were illuminated earlier than trees in the canopy. We also expect that early morning dew and fog (present on most days) evaporated first from emergent trees. Sap flux reduced to minimal levels in all canopy layers towards sunset and significant fluxes did not occur again until the following day.

On a clear day the daily course of sap flux appeared

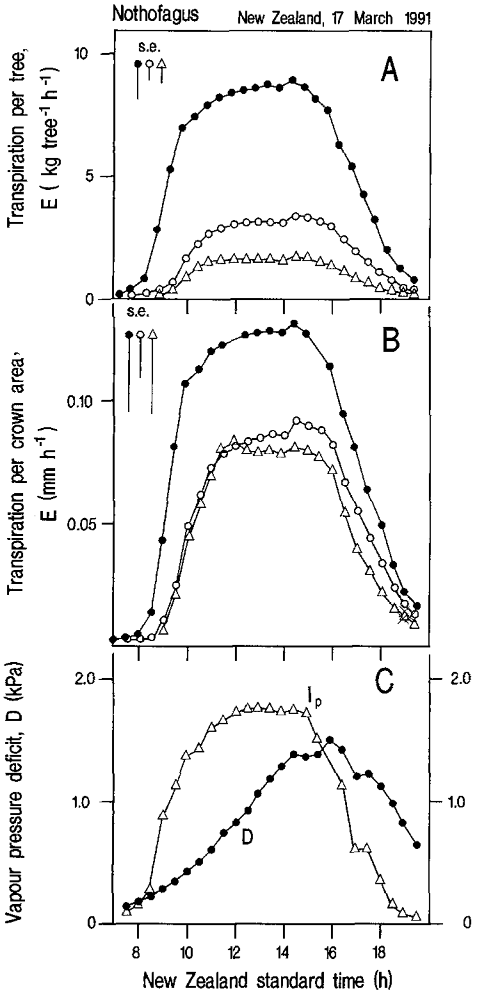

Fig. 4A–C. Half-hourly courses of sap flux (**A**) and sap flux density (**B**) of 14 *Nothofagus* trees, representing the 3 canopy layers (emergent *(solid circle)*, codominant *(open circle)*, and suppressed trees *(open triangle)*), on 17 March 1991. Sap flux density was determined for each tree by division of sap flux by an estimate of occupied ground area calculated from vertical projection of the crown perimeter. Standard errors (s.e.) are given in (**A**) and (**B**). Also shown in (**C**) are half-hourly courses of photon flux density (Ip, open triangle) and vapour pressure deficit *(D, solid circle)* measured above the tree canopy

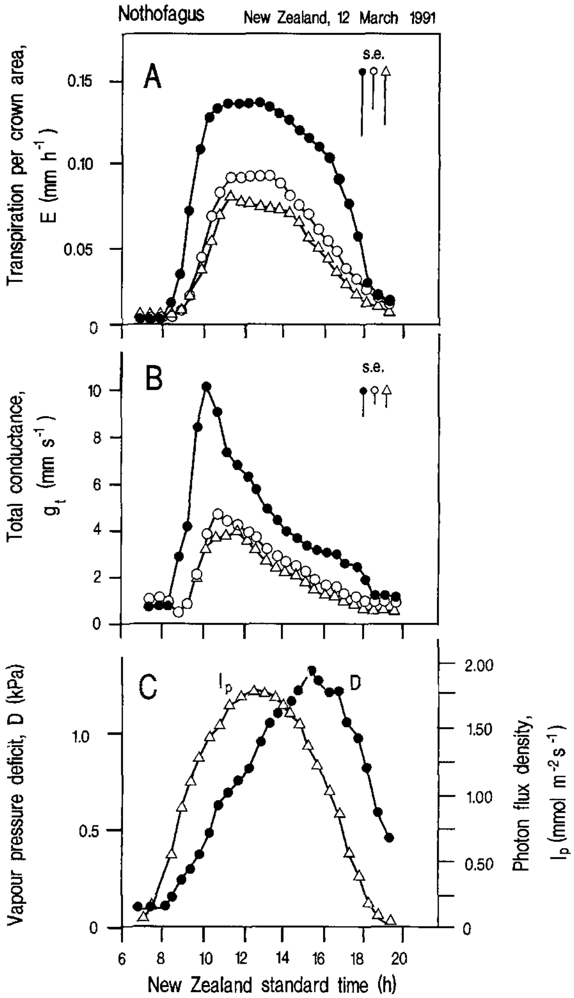

Fig. 5A–C. Half-hourly courses and standard errors of sap flux density (**A**) for 14 *Nothofagus* trees, representing the 3 canopy layers (emergent *(solid circle)*, codominant *(open circle)*, and suppressed trees *(open triangle)*, on 12 March 1991. Sap flux density (E) was determined for each tree by division of sap flux by an estimate of occupied ground area calculated from a vertical projection of the tree crown perimeter. Total water vapour transfer conductance (g_t), shown in (**B**), was calculated for each tree as k*E/D where D is vapour pressure deficit (kPa) and k is a units conversion factor (36.25 kPa) described in the text. Also shown in (**C**) are half-hourly courses of photon flux density *(Ip, open triangle)* and *(D solid circle)* measured above the tree canopy to be nearly parallel with the course of photon flux density (I_p) (Fig. 4A and C). However, the correlation of sap flux and I_p was poor on partly cloudy days (data not shown). It is known that air saturation deficit (D) is an additional determinant of forest evaporation (Jones 1983). Therefore, the interactions between I_p, D and sap flow are further examined below.

It is evident in Fig. 4B that mean sap flux densities of emergents greatly exceeded those of the other canopy layers on a representative day (17 March) and, for daily totals ($p < 0.025$, T-test). Thus, a vertical dimension, incorporating aspects of stand structure, is therefore necessary to fully understand and model tree transpiration in a natural stand.

Mean maximum g_t of all trees was 5.5 mm s^{-1} (± 0.59 s.e, $n = 24$, maximum: 13.2, minimum: 0.61 mm s^{-1}; Fig. 5B). There were no consistent differences in maximum g_t between species, canopy layers, or period of measurement (ANOVA; species effect: $F = 0.013$, sign. of F 0.9912; measuring period: $F = 0.610$, sign of F 0.610; canopy layer: F 0.647, sign. of F 0.535). Mean maximum g_t increased to 9.5 mm s^{-1} for emergent trees, but the sample of 3 emergent trees was too small for statistical analysis of variation.

During the course of a clear day, g_t was not constant, reaching a maximum in the early morning before sap flux reached its maximum at noon (Fig. 5B). Emergent trees obtained maximum g_t about an hour earlier than codominant and suppressed trees. Following the early morning maximum, g_t decreased in all canopy layers throughout the day. The similarity of g_t of codominant and suppressed trees suggests that the stomata of suppressed trees were more widely open than those of codominant trees, since the pathlength of water vapour through the main canopy was longer for this canopy layer. The data clearly demonstrate a strong regulation of canopy evaporation rate by the stomata. In the afternoon, there was a relatively constant or slightly decreasing rate of transpiration despite increasing D.

Total conductance of emergent trees was closely coupled with changes in I_p and D (Fig. 6) and it is difficult to separate independent effects of light and humidity without controlled experiments in the field (see later discussion of gas exchange measurements). During the morning, g_t of emergent trees increased linearly with I_p up to 1.2 mmol m^{-2} s^{-1}, while later, g_t decreased significantly even when I_p remained > 1.0 mmol m^{-2} s^{-1}. The decrease in g_t was associated with increasing D exceeding about 0.4 kPa after 10 h. However, after 16 h, g_t did not increase in response to decreasing D indicating some hysteresis in canopy response to humidity during the day. This may be caused by water stress in the tree even under well-watered conditions (Benecke and Evans 1986). Measurements of the stand energy balance show that evaporation was determined principally by advective energy (i.e., D imposed onto the tree canopy) and that the radiative energy regime was of lesser importance during most of the day (Kelliher et al. 1992). In support of this conclusion, the correlation of g_t and I_p was poor during days of variable cloudiness when D was low (data not shown). Furthermore, the March relationships in Fig. 6 were incorporated into an imposed transpiration rate model given by equation (3), which explained most of the daily variation in tree transpiration measured in April.

Total conductance contains an aerodynamic component and its removal for estimation of canopy conductance (g_c) was confined to emergent trees. For the emergent trees, estimates of g_a were 5–10 times larger than g_c so that g_c and g_t exhibited similar daily courses (g_t in Fig. 5B and g_c in Fig. 7A). The canopy-atmosphere coupling factor Ω varied by more than four-fold over a typical clear day with a maximum of 0.38 obtained at 10 h when g_c was largest and a minimum towards sunset when g_c was lowest because light was limiting (Fig. 7B). Among other changes in diurnal leaf metabolism, stomatal response to D strongly affected Ω with the afternoon decline of g_c corresponding with substantial decreases in Ω.

Mean maximum total conductance of emergent trees was 9.5 mm s^{-1} which is equivalent to 112 mmol m^{-2} s^{-1} at the scale of the leaf. Artificially illuminated *N. fusca* shoots measured in the stand with gas exchange chambers had maximum stomatal conductances (g_l) of 280 and

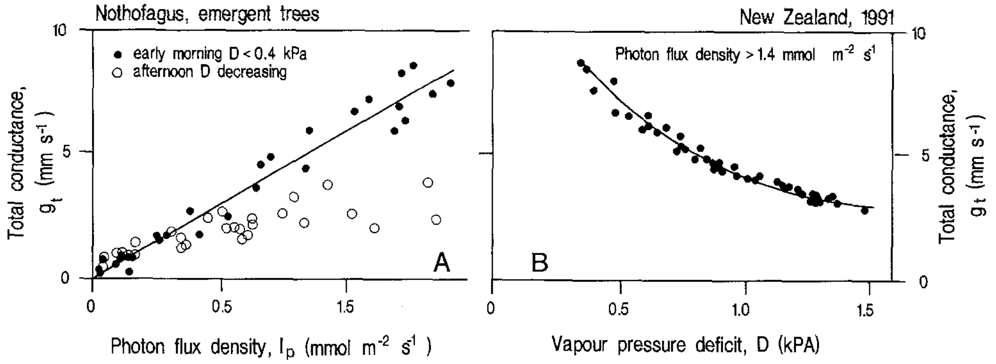

Fig. 6A, B. Relationship between averages of total water vapour transfer conductance (g_t) of 3 emergent *Nothofagus fusca* trees, derived from sap flow and humidity measurements in March 1991 as described in the text, and above-canopy photon flux density (Ip) when vapour pressure deficit (D) < 0.4 kPa (**A**). Maximum g_t (g_t max) in (**A**) was 7.5 mm s^{-1} for $Ip = 1.2$ mmol m^{-2} s^{-1}. For $I_p < 1.2$ mmol m^{-2} s^{-1} the line shown in (**A**) indicates $g_t = 0.83 * Ip * g_t$ max ($r^2 = 0.98$). The relationship between g_t and D is shown in (**B**), including morning data when $Ip > 1.4$ mmol m^{-2} s^{-1} and afternoon data when $Ip = 0.5$–0.6 and 0.8–1.1 mmol m^{-2} s^{-1}. For $D < 0.4$ kPa, $g_t = g_t$ max and the curve shown in (**B**) indicates for $D > 0.4$ kPa, $g_t = \mathrm{Exp}(2.45 - 1.71 * f(D))$ in which f(D) is a sigmoid function $f(D) = 1/(1 + \mathrm{Exp}(-(D - 7.36)/3.03))$ providing Ip is non-limiting ($r^2 = 0.97$)

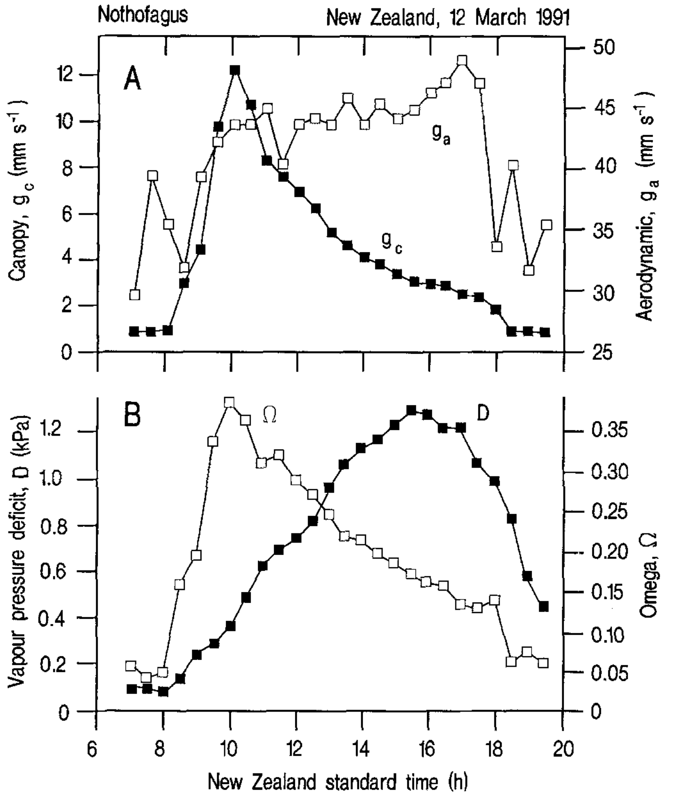

Fig. 7A, B. Half-hourly courses of canopy conductance (g_c, solid square) and aerodynamic water vapour transfer conductance (g_a, open square) of emergent *Nothofagus fusca* trees, derived from sap flow, humidity and wind speed measurements as described in the text, on 12 March 1991 (**A**). The atmospheric coupling parameter Ω (open square), shown in (**B**) and calculated according to equation (1), is proportional to the ratio g_a/g_c. Also shown in (**B**) is vapour pressure deficit above the tree canopy (D, solid square)

150 mmol m^{-2} s^{-1} at the top and bottom of the canopy, respectively (Fig. 8A). The decrease in g_l with increasing D was proportionally greatest at the top of the canopy. Stomata there closed by 50% as D increased from 0.5 to 1.2 kPa which is remarkably similar to results of the tree-scale analysis for emergent trees (Fig. 6B). However, stomatal light response curves were not so similar at shoot and tree scales. For the shoot, light response curves were hyperbolic, essentially reaching a maximum at about 0.7 mmol m^{-2} s^{-1} (Fig. 8B) in contrast with the linear curves derived from tree scale analysis (Fig. 6).

Since g_a was an order of magnitude larger than g_c, we use g_t in order to further explore the relations to plant internal parameters for different canopy layers. g_t was significantly correlated with nitrogen content of sun leaves ($p = 0.02$), in agreement with the *N. menziesii* porometer data of Körner et al. (1986) (Fig. 9A). These results may also explain the relatively low photosynthetic capacity of *Nothofagus* (Hollinger 1987b).

Carbon isotope ratios of sun leaves were −27.76±0.27% (mean ± s.e., n = 8) which corresponds to a photosynthetic carbon discrimination of 20.13‰. For a December 1990 – March 1991 summer rain fall of 611 mm at our site, the results agree remarkably well with the correlation between carbon discrimination in *Nothofagus* and summer rainfall of Read and Farquhar (1991). Our high carbon discrimination indicates a generally adequate supply of water for photosynthesis, in agreement with one-year leaf duration for the dominant species *N. fusca* and a positive site water balance calculated for the year ended April 1991.

The stand was characterized by a small number of regularly-spaced, large old "giant" trees of mainly *N. fusca* that contributed significantly to canopy transpiration. We investigated the contribution of water stored in stemwood to transpiration of these trees by measuring sap flux at two heights (1 and 15 m) in an emergent tree next to a 32 m tall tower built for access to the canopy. Radial variation in sap flux was assessed by measurements on opposite sides at the bases of four emergent trees. Differences of daily courses of sap fluxes at 1 and 15 m heights were not statistically significant (Fig. 10). However, sap flux at 1 m was consistently less than at 15 m in the morning and the converse occurred in the afternoon. These differences may indicate changes in water storage of order 0.5 l for a stem sapwood volume of 1.5 m^3, roughly equivalent to the quantity of water required for about 30 minutes of transpiration. In addition, sap flux was not zero during the first few hours of

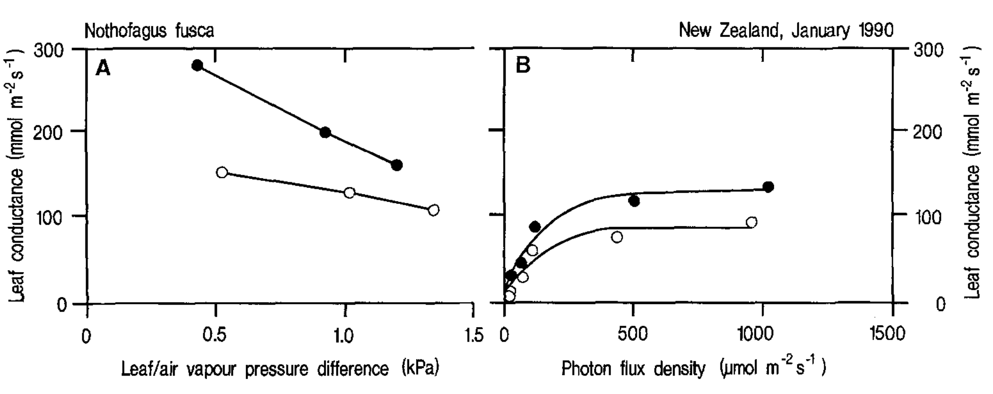

Fig. 8A, B. Stomatal conductance of artificially illuminated shoots at the top *(solid circle)* and bottom *(open circle)* of the canopy of a 30 m tall, emergent *Nothofagus fusca* tree at three imposed vapour pressure deficits. (**A**) Response to vapor pressure deficit at air temperature = 20° C and photon flux density = 1.0 mmol m^{-2} s^{-1}. (**B**) Response to photon flux density at air temperature = 20° C and vapour pressure deficit = 1.0 kPa. Measurements were made by enclosing shoots in a gas exchange chamber system described by Hollinger (1987a)

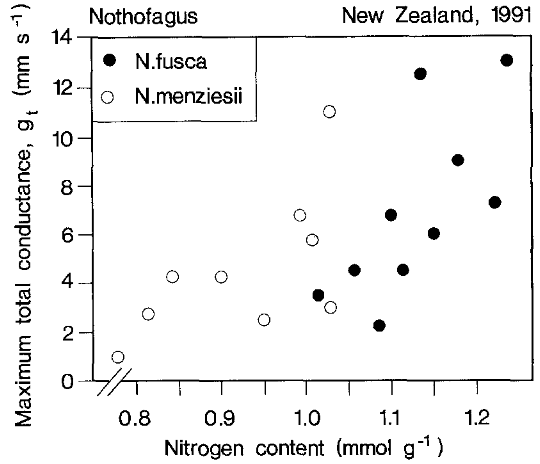

Fig. 9. The relationship between maximum total conductance and leaf nitrogen content of *Nothofagus fusca* and *N. menziesii* trees during 1991 ($r=0.6$, $p=0.02$). Each datapoint represents one of the measuring trees, the leaves of which were shot from the upper part of the crown

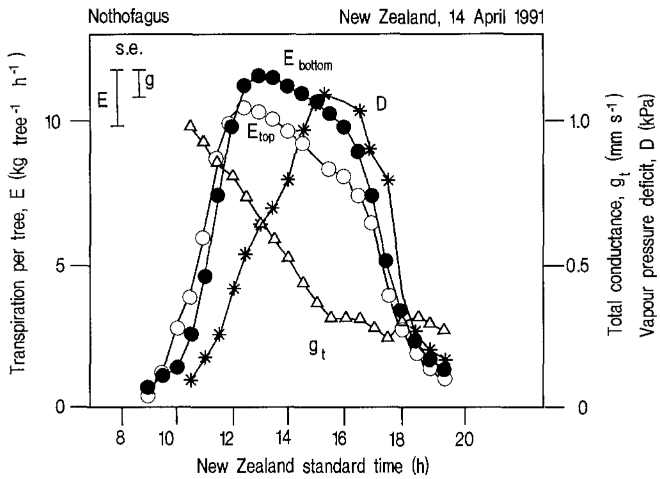

Fig. 10. Half-hourly courses of basal stem sap flux *(solid circle)*, the average of 1.3 m height measurements on two sides of three emergent *Nothofagus fusca* trees of total height 34 m and basal diameter 1.2 m, on a clear day 14 April 1991. Sap flux measurements made at height 15 m (at the bottom of the crown) in another, similar emergent *N. fusca* tree *(open circle)*, standard error (s.e.) and vapour pressure deficit above the tree canopy (*) are also shown

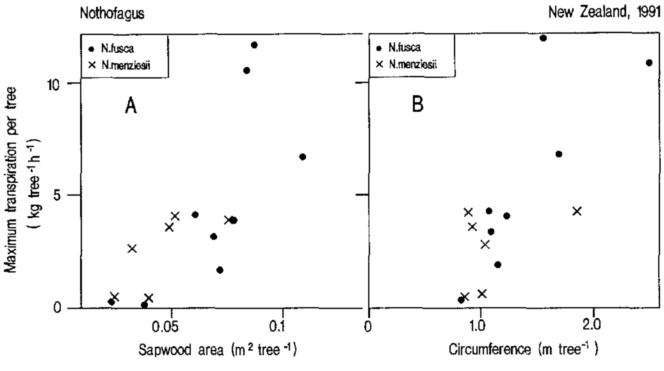

Fig. 11A, B. The relationship between 5-day averages of maximum halfhourly sap flux and histochemical sapwood area at height 1.3 m for 14 *Nothofagus fusca* (solid circle) and *N. menziesii* (x) trees during March 1991 (**A**). Linear regression indicated that the slope of the relationship $=0.011$, intercept $=-2.380$, $r^2=0.72$, and $p=0.0036$. Similarly, the relationship between maximum sap flux and stem circumference at height 1.3 m (**B**) was statistically significant (slope $=5.59$, intercept $=-3.02$, $r^2=0.59$, $p=0.0013$)

the night. Since stomata are nearly closed then (Fig. 8B) and air saturation deficit is very low, these measurements can also be interpreted as refilling of tree water storage. Nighttime sap flux was 5–10 l for emergent trees. These two, relatively small estimates of water use from storage suggest that this water probably originated mainly from leaves, twigs, and branches in the canopy and not from the stem.

The "pipe model" of Shinozaki et al. (1964) suggests that a proportional relationship will exist between tree transpiration and sapwood area (see also Waring and Running 1976). This relation was statistically significant in *Nothofagus,* independent of species, using histochemically determined sapwood area (Fig. 11 A, $r=0.72$, $p=0.004$). Since sap flux was found to be confined to the outer ca. 20 mm annulus of xylem (Kelliher et al. 1992), maximum rate of transpiration was somewhat more closely related to tree circumference (Fig. 11B, $r=0.77$, $p=0.001$). The slope of the relation between transpiration and sapwood area or circumference may be taken as an indication for the requirements for stem growth for water transport. The comparison of different trees indicates that the histochemically determined sapwood increased by 0.01 m^2 or by 0.06 m of circumference when maximum transpiration increased by 1 l per h. This may set the requirement for stem growth during expansion of the tree crown.

Discussion

The relation between energy exchange, canopy conductance and stomatal response to the aerial environment has generally been confined to coniferous plantations (e.g. Whitehead et al. 1984; Milne et al. 1985; Jarvis 1987; Werk et al. 1988; Gash et al. 1989). Information on natural, broad-leaved canopies is scarce (Verma et al. 1986; den Hartog 1987; Baldocchi 1985), and there is an obvious gap of knowledge between information about leaves and tree performance at the whole stand level.

Nothofagus exhibits a constant maximum tree canopy conductance that is independent of the two species and canopy position, in agreement with observations made in a *Pinus sylvestris* plantation (Whitehead et al. 1984). Maximum canopy conductance of *Nothofagus* is much lower than in a tropical, broad-leaf rainforest, a North American broad-leaf forest, and a number of temperate conifer plantations (Shuttleworth 1989) including *Pinus radiata* D. Don plantations in New Zealand (Kelliher et al. 1990). Furthermore, *Nothofagus* maximum canopy conductance was about a factor of two less than that derived in a similar manner from xylem sap flux density (expressed per unit all-surfaces leaf area) and humidity measurements of *Picea abies* trees in a German plantation (Werk et al. 1988).

From xylem sap flow measurements, *Nothofagus* reached an equivalent mean maximum stomatal conductance of 112 mmol m^{-2} s^{-1} (average of the whole crown) which is less than measured by gas exchange chambers. The low canopy conductance is related to the low assimilation rates (Hollinger 1987b) which in turn is due to low nitrogen contents of the leaves (Schulze and Chapin 1987). Maximum leaf-level stomatal conductance of artificially illuminated *N. fusca* seedlings in a growth chamber reached 160 ± 40 mmol m^{-2} s^{-1} (Hollinger 1987b) and fully illuminated sun leaves of *N. menziesii* trees in the field reached 125 to 190 mmol m^{-2} s^{-1} (Körner et al. 1986) at similar nitrogen content in *N. truncata,* a species closely related to *N. fusca*. Benecke and Evans (1986) measured an average leaf conductance of 102 mmol m^{-2} s^{-1} under field conditions tracking the ambient climate in a cuvette. Differences between maximum conductance derived from porometer and sap flow measurements may be explained by feedback of transpiration on D within the canopy and by the turbulent nature of water transport, both of which are not present within steadystate porometer chambers. Furthermore, at the scale of a tree, differences in stomatal conductance between leaf types and positions are integrated, and larger scale canopy structural effects can become more important. This may be a general observation which has previously been described for photosynthesis (Gifford 1974) and growth responses (Schulze et al. 1986).

Despite aerodynamic effects which diminish water vapour transfer conductances from leaf to canopy levels, canopy conductance dominated by *N. fusca* is very sensitive to changes in air humidity. Stomatal response to humidity regulates water loss of the forest stand and *N. fusca* response was more sensitive than that of *N. truncata* or *Picea abies* (Benecke and Evans 1986; Werk et al. 1988), but similar to that of *Picea sitchensis* or *Pinus pinaster* (Gash et al. 1989), and less sensitive than *Pinus radiata* (Whitehead et al. 1984). It is largely this response which causes a large daily variation in the Ω value (McNaughton and Jarvis 1983). It is apparent from our Ω analysis that *Nothofagus* forest responds to its aerial environment more like a meadow in the morning and like a coniferous forest in the afternoon (Fig. 7B).

Although humidity controlled stomatal behaviour is a dominant regulator of stand transpiration rate, there may also be a plant growth effect evident in the relationship between maximum hourly sap flux and sapwood area (Fig. 11). Such an effect has been suggested by the previously established surrogate relationship between sapwood area and leaf area (Waring et al. 1982; Whitehead et al. 1984). These relationships suggest coordination between stomatal and hydraulic conductances, and growth at the whole plant level (Schulze and Chapin 1987). This may be important for tree function in our forest on fine summer days because of the apparently minimal use of stored water for transpiration. It is evident that the opportunity cost for stem water storage in large trees may be less economic (Chapin et al. 1990) than previously considered (Waring et al. 1979).

Effects of structural diversity of a natural tree canopy on stand transpiration and energy balance have received scant attention in the literature. In our stand, there were statistically significant differences in sap flux density between the three canopy layers, with a 15 m range of tree height in the 337 m^2 measurement plot. Given the dominance of advective energy in driving tree canopy transpiration rate in our stand, one might intuitively surmise that the rough canopy would enhance mechanical generation of turbulence contributing to a higher forest evaporation rate than might be expected from a more uniform stand created by forest management. However, canopy-scale turbulence seems to have a number of universal characteristics that are independent of the exact canopy morphology. During the daytime, shear turbulence dominates with canopy height being a useful length scaling factor. Wake turbulence and horizontal heterogeneity, that might be expected to result from small-scale structural diversity, and buoyancy appear to be of considerably lesser importance (Raupach 1989). It is also noteworthy that, even for the small leaves of *Nothofagus,* leaf boundary layer conductance is about an order of magnitude smaller than stand aerodynamic conductance for momentum. Canopy conductance was generally much less than total aerodynamic conductance and it is likely then that physiological (stomatal) diversity in response to the imposed environment and, to a lesser extent, canopy height rather than structural heterogeneity, will be important determinants of stand transpiration rate in our forest.

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