

Characteristics of photosynthesis and stomatal conductance in the shrubland species mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*) for the estimation of annual canopy carbon uptake

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Summary Responses of photosynthesis to carbon dioxide (CO₂) partial pressure and irradiance were measured on leaves of 39-year-old trees of mānuka (*Leptospermum scoparium* J. R. Forst. & G. Forst.) and kānuka (*Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson) at a field site, and on leaves of young trees grown at three nitrogen supply rates in a nursery, to determine values for parameters in a model to estimate annual net carbon uptake. These secondary successional species belong to the same family and commonly co-occur. Mean (\pm standard error) values of the maximum rate of carboxylation (hemi-surface area basis) (V_{cmax}) and the maximum rate of electron transport (J_{max}) at the field site were $47.3 \pm 1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $94.2 \pm 3.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, with no significant differences between species. Both V_{cmax} and J_{max} were positively related to leaf nitrogen concentration on a unit leaf area basis, and the slopes of these relationships did not differ significantly between species or between the trees in the field and young trees grown in the nursery. Mean values of $J_{\text{max}}/V_{\text{cmax}}$ measured at 20 °C were significantly lower ($P < 0.01$) for trees in the field (2.00 ± 0.05) than for young trees in the nursery with similar leaf nitrogen concentrations (2.32 ± 0.08). Stomatal conductance decreased sharply with increasing air saturation deficit, but the sensitivity of the response did not differ between species. These data were used to derive parameters for a coupled photosynthesis–stomatal conductance model to scale estimates of photosynthesis from leaves to the canopy, incorporating leaf respiration at night, site energy and water balances, to estimate net canopy carbon uptake. Over the course of a year, 76% of incident irradiance (400–700 nm) was absorbed by the canopy, annual net photosynthesis per unit ground area was 164.5 mol m^{-2} (equivalent to 1.97 kg C m^{-2}) and respiration loss from leaves at night was 37.5 mol m^{-2} (equivalent to 0.45 kg m^{-2}), or 23% of net carbon uptake. When modeled annual net carbon uptake for the trees was combined with annual respiration from the soil surface, estimated net primary productivity for the ecosystem (0.30 kg C m^{-2}) was reasonably

close to the annual estimate obtained from independent mensurational and biomass measurements made at the site ($0.22 \pm 0.03 \text{ kg C m}^{-2}$). The mean annual value for light-use efficiency calculated from the ratio of net carbon uptake (net photosynthesis minus respiration of leaves at night) and absorbed irradiance was $13.0 \text{ mmol C mol}^{-1}$ (equivalent to $0.72 \text{ kg C GJ}^{-1}$). This is low compared with values reported for other temperate forests, but is consistent with limitations to photosynthesis in the canopy attributable mainly to low nitrogen availability and associated low leaf area index.

Keywords: carbon exchange, light-use efficiency, modeling, nitrogen response, shrubland forestry, water balance.

Introduction

Woody shrubland communities dominated by mānuka (*Leptospermum scoparium* J. R. Forst. & G. Forst.) and kānuka (*Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson) are widespread throughout New Zealand, occupying about 13,200 km², equivalent to 5.2% of the total land area (Newsome 1987). These light-demanding, secondary successional species belong to the same family and co-occur commonly. Both species establish rapidly on disturbed sites and are important components in the establishment of both primary and secondary forests. Mānuka is more tolerant of low fertility and poorly drained soils, whereas kānuka is more successful on fertile well-drained soils. The success of both species is attributable to abundant flowering when the trees are young, copious production of light seeds that are easily dispersed by wind, the unpalatability of the leaves to grazing mammals, and the tolerance of the species to a range of climatic and edaphic conditions (Wardle 1991). During the first 20–30 years of succession following a disturbance, stands are usually dominated by mānuka, which forms a thick uniform canopy that excludes other species. From 30 to 50 years, the taller, longer-lived

kānuka becomes dominant (Bergin et al. 1995) and, after about 70 years, the canopy may begin to break down, allowing the appearance of other long-lived forest species (Allen et al. 1992). However, the rate of stand development is strongly dependent on temperature and the periodicity of disturbance (Leathwick and Rogers 1996).

Recently in New Zealand, shrublands dominated by mānuka and kānuka have attracted attention because they are replacing large areas of pastoral hill country that have become uneconomic for animal farming, and the resulting uptake and storage of carbon could provide an important sink at the national scale (Tate et al. 2003). To quantify the size of this sink and to predict future changes, there is an urgent need to determine the rate of carbon uptake and storage by these shrublands, and to identify the environmental and site factors that regulate carbon sequestration. Previous modeling studies have identified the importance of climate, root-zone water deficit and nutrient availability as the principal sources of variation in the productivity of forests (Landsberg and Waring 1997) and shrublands (White et al. 2000a).

Although the ecology (Wardle 1991) and structural dynamics (Egunjobi 1969) in mānuka and kānuka stands are well documented, data on the rates of canopy photosynthesis in relation to nutrient and water availability are lacking. Also unknown is the sensitivity of photosynthesis to leaf nitrogen concentration and stomatal conductance to humidity. The principal objective of our work was to determine values for parameters describing the biophysical processes of photosynthesis in mānuka and kānuka leaves, and then use the values in a model incorporating appropriate scaling procedures to estimate annual net carbon exchange for a mixed canopy. The model incorporates a coupled photosynthesis–stomatal conductance model for leaves (Leuning 1995) with a radiation transfer model to allow scaling to the canopy (Leuning et al. 1995) and a model of daily site water balance (Whitehead et al. 2001). Measurements of photosynthesis and stomatal conductance in response to carbon dioxide (CO_2) partial pressure and irradiance were made on 39-year-old mānuka and kānuka trees growing at a field site in the central North Island, New Zealand. The estimate of annual net carbon uptake from the model, adjusted for respiration from leaves and soil, was compared with the mean rate of carbon accumulation for the ecosystem obtained from independent mensurational data. A further objective was to investigate the response of photosynthesis to leaf nitrogen concentration so that the model could be applied at more fertile sites. To achieve this objective, similar measurements were made on young trees of both species growing in a nursery and irrigated with nutrient solution at three nitrogen concentrations.

Materials and methods

Field site

Measurements were made at a site in the Tongariro National Park, central North Island, New Zealand (39.15°S , 175.78°E , elevation 800 m above sea level), comprising dense shrubland

vegetation dominated by mānuka and kānuka resulting from regrowth after burning about 39 years previously. The stand consisted of approximately 1.0 stem of mānuka and 1.4 stems of kānuka per square meter. Mean tree height ($\pm \text{SE}$) was $5.0 \pm 0.1 \text{ m}$ and mean canopy depth was $1.7 \pm 0.3 \text{ m}$ with no significant differences between species. The soil is derived from a series of recent rhyolitic and andesitic volcanic eruptions and is classified as Podzolic Orthic Pumice soils of the Rangipo series (Hewitt 1993), roughly similar to the Vitrandis classification in the USDA soil taxonomy series (Soil Survey Staff 1990). Destructive measurements on 48 trees in the stands provided equations for estimating the aboveground and coarse root biomass at the site from measurements of tree diameter (Scott et al. 2000). Mean biomass for the site was 7.2 kg C m^{-2} and leaf area index (hemi-surface area basis) was estimated to be 2.8 (C.M. Trotter, unpublished data). Mean leaf nitrogen concentration was $124.8 \text{ mmol m}^{-2}$ and there were no significant differences between species or with depth in the canopy.

The 30-year mean annual temperature at the nearest weather station at Turangi (39.0°S , 175.8°E , elevation 366 m above sea level, 17 km from the site) is 12.0°C and mean annual rainfall is 1586 mm (New Zealand Meteorological Service 1983). During the year in which measurements were made, daily minimum and maximum air temperatures, solar irradiance (400–700 nm) and rainfall were measured at Turangi. The temperature data were extrapolated to the field site assuming a wet adiabatic lapse rate of 6°C km^{-1} to account for the increase in elevation (Miller and Anthes 1985) and rainfall was adjusted orographically at the rate of 30 mm km^{-1} , based on comparisons of meteorological data from stations located at different elevations (J.D. White, Baylor University, Waco, TX, personal communication). So, for the field site, calculated mean annual temperature was 9.3°C and mean annual rainfall was 1523 mm.

In addition to the physiological measurements made at the field site, measurements were made on 2-year-old trees (about 0.4 m tall) of mānuka and kānuka grown from seed in full sunlight in a nursery. Trees were grown in 9-l pots containing coarse sand, and were watered to field capacity three times each week with nutrient solution containing either 6, 3 or 0.5 mM nitrogen as NH_4NO_3 for 6 months before measurements were made. The other nutrients in the solution were the same for all trees and consisted of a balance of macro- and micro-nutrients as recommended by Millard and Proe (1991) for the 3 mM solution. On the night before measurements, trees were transferred from the nursery to a controlled environment cabinet providing an irradiance of $650 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (400–700 nm) at tree height, day and night temperatures of 20 and 10°C , respectively, and an air saturation deficit of $3.5 \text{ mmol mol}^{-1}$.

Measurements of photosynthesis and stomatal conductance

At the field site, measurements for the response of the rate of photosynthesis (A) to intercellular CO_2 partial pressure (c_i) and to irradiance (Q) were made on nine and six shoots, respectively, spread between four trees for each species. Mea-

measurements of A and stomatal conductance to water vapor (g_s) were made with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE) and an artificial light source (LI-6400-02B, Li-Cor). Individual shoots comprising about $2 \times 10^{-4} \text{ m}^2$ hemi-surface leaf area were placed in the chamber and left to equilibrate for 15 min at a saturating CO_2 partial pressure of 36 Pa, saturating irradiance of $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and constant chamber temperature of 20°C . This temperature was close to the maximum ambient daytime temperature of 19°C when the measurements were made. Ambient CO_2 partial pressure in the chamber was reduced to 0.5 Pa and increased automatically in 14 steps to 150 Pa using the CO_2 mixer on the instrument for the determination of the A/c_i curve. The shoots were then left to equilibrate at saturating irradiance, a constant temperature of 20°C , and a constant CO_2 partial pressure of 36 Pa for 15 min, after which measurements of A were made as Q was reduced automatically in 12 steps to darkness.

An identical procedure was used to determine the A/c_i curves for the young trees placed in the controlled environment cabinet. Measurements for 12 curves for each species were made on four trees per nutrient treatment.

Because of difficulties in controlling air saturation deficit at fluctuating temperatures under field conditions, it was possible to determine the response of g_s to the air saturation deficit at the leaf surface (D_s) only in the young trees, which were small enough to be placed in the controlled environment cabinet. The supply of air to the portable photosynthesis system was pumped from a dew point generator (LI-610, Li-Cor) to maintain a constant value of air saturation deficit in the chamber. Each shoot was placed in the chamber and left to equilibrate at ambient CO_2 partial pressure, saturating irradiance, chamber temperature of 20°C and low air saturation deficit (about 4 mmol mol^{-1}) until maximum g_s was reached. Air saturation deficit in the leaf chamber was increased in about 12 steps by adjusting the output humidity from the dew point generator. Simultaneous measurements of photosynthesis were used to describe the coupling between stomatal conductance and photosynthesis given by Equation 6. Measurements were made on three of the young nursery-grown trees from the high nitrogen treatment for each species and it was assumed that the responses of g_s to D_s would be similar for trees in the other nitrogen treatments and at the field site.

After the response curves had been completed, leaves from each shoot were removed and pressed flat between plastic sheets and their hemi-surface area measured with a leaf area meter (LI-3100, Li-Cor). The leaves were dried at 70°C , weighed, and then finely ground for determination of total nitrogen concentration with a CNS analyzer (Carlo Erba/Thermo Electron, Milan, Italy).

Analysis of photosynthesis and stomatal conductance

Photosynthesis and stomatal conductance data for individual leaves were analyzed with the coupled model described by Leuning (1995), where the rate of photosynthesis (A) is given by the minimum of the rates limited by carboxylation (A_c) and electron transport (A_q) as:

$$A = \min\{A_c, A_q\} - R_d \quad (1)$$

where R_d is rate of daytime respiration resulting from processes other than photorespiration (Farquhar et al. 1980). The rate of assimilation limited by carboxylation (A_c) is given by:

$$A_c = V_{c\text{max}} \frac{c_i - \Gamma^*}{c_i + K_c(1 + (o_i/K_o))} \quad (2)$$

where $V_{c\text{max}}$ is maximum rate of carboxylation by Rubisco with saturating substrate and CO_2 partial pressure, c_i and o_i are the intercellular CO_2 and oxygen (O_2) partial pressures, Γ^* is the CO_2 partial pressure at compensation in the absence of photorespiration, and K_c and K_o are the Michaelis constants for CO_2 and O_2 , respectively. The assimilation rate limited by electron transport (A_q) is given by:

$$A_q = \frac{J(c_i - \Gamma^*)}{4(c_i + 2\Gamma^*)} \quad (3)$$

where J is electron transport rate at a given Q , and the response of J to Q is given by a non-rectangular hyperbola (Farquhar and Wong 1984) as:

$$\beta J^2 - (\alpha Q + J_{\text{max}})J + \alpha Q J_{\text{max}} = 0 \quad (4)$$

where J_{max} is maximum rate of electron transport at saturating irradiance, α is the quantum yield of electron transport and β defines the convexity of the hyperbola. The intercellular partial pressure of CO_2 (c_i) is given by:

$$c_i = c_s - (A/g_{sc}) \quad (5)$$

where c_s is CO_2 partial pressure at the leaf surface and g_{sc} is stomatal conductance to CO_2 transfer ($= g_s/1.6$ where g_s is stomatal conductance to water vapor transfer and 1.6 is the ratio of the diffusivities of water vapor and CO_2 in air). The coupling of photosynthesis with stomatal conductance is completed by the expression describing the relation between g_{sc} , A , c_s and air saturation deficit at the leaf surface (D_s) as:

$$g_{sc} = g_{sc0} + \frac{aA}{(c_s - \Gamma)(1 + (D_s - D_{s\text{min}})/D_{s0})} \quad (6)$$

where g_{sc0} is the residual conductance at the light compensation point, D_{s0} is a parameter describing the sensitivity of g_{sc} to D_s when $D_s > D_{s\text{min}}$, $D_{s\text{min}}$ is the minimum value of D_s below which g_{sc} remains at its maximum value (Lohammar et al. 1980), Γ is the CO_2 partial pressure at compensation in the presence of photorespiration and a is a parameter describing the stomatal sensitivity to environmental variables. Measurements were made in well-ventilated canopies with small leaves (about 5 mm long and 3 mm wide), and values of D_s and c_s were calculated from measurements of air saturation deficit (D) and CO_2 partial pressure above the canopy (c_a) and from the energy balance and boundary layer conductance (Leuning et al. 1995).

Values for V_{cmax} and R_d were derived by fitting Equations 1 and 2 to data from the A/c_i response curves when $c_i < 20$ Pa. Values for J_{max} were derived by substituting Equations 2 and 3 into Equation 1 and fitting this to the entire A/c_i response curve based on previously determined values for V_{cmax} and R_d . Values for α and β were derived by fitting Equation 4 to data from the A/Q response curves.

Statistical significance between values of parameters for the two species was tested by analysis of variance. Differences between slopes and between intercepts of the linear relationships between photosynthetic parameters and leaf nitrogen concentration were tested for significance by analysis of covariance (Sokal and Rohlf 1995). Parameter values in nonlinear relationships were estimated by a least squares routine (Sigma-Plot 2001, SPSS, Chicago, IL) and differences were tested for significance by the Student's t statistic.

Modeling canopy net carbon uptake

Parameter values derived from our measurements were used with a canopy model to estimate annual net carbon uptake at the field site. The one-dimensional multi-layer model incorporating radiative transfer, energy balance, evaporation and photosynthesis (Leuning et al. 1995), and water balance (Whitehead et al. 2001) has been described fully elsewhere (Whitehead et al. 2002, 2004), so only brief details will be provided here. The canopy was divided into 20 homogeneous layers based on the vertical distribution of cumulative canopy leaf area index. Leaf energy balance and the coupling of photosynthesis with stomatal conductance (Leuning 1995) were used to calculate photosynthesis for sunlit and shaded foliage separately in each layer (Leuning et al. 1995). Total photosynthesis was summed across layers within the canopy and daily values were obtained by Gaussian integration following Goudriaan and van Laar (1994).

Net carbon uptake was calculated with Equations 1–6 from measurements of photosynthesis, respiration and stomatal conductance for leaves in the canopy. With the lack of measured responses of photosynthesis to temperature for mānuka and kānuka, the temperature dependence of K_c , K_o and Γ^* in Equations 2 and 3 were calculated based on the functions described by Walcroft et al. (1997). Values for the parameters were calculated from measured temperature responses given by Bernacchi et al. (2001) and are shown in Table 1.

The response of respiration, R_d , to temperature during the day and at night was determined by an Arrhenius-type relationship following Turnbull et al. (2003) with the value for the energy of activation taken from Walcroft et al. (1997). Leaf temperature was estimated from air temperature using energy balance calculations and mean leaf width (l).

On wet days, the proportion of net rainfall penetrating the canopy was set at 0.8 (R.J. Jackson, Landcare Research, Lincoln, New Zealand, personal communication). The root-zone water storage capacity of the soil (W_{max}) was estimated from measurements of root-zone depth (Scott et al. 2000) and soil texture (Anonymous 1968). Daily calculations of water balance, including components of transpiration from the tree canopy, evaporation from the wet tree canopy and evaporation from the understory vegetation and soil, were used to define a

coefficient to reduce photosynthesis and respiration when daily root-zone water storage fell below 50% of its capacity. Maximum and minimum root-zone water storage was 187 and 115 mm, respectively, so the coefficient was set to reduce photosynthesis when water storage fell below 151 mm. This was done by reducing the value of A in Equation 1 in accordance with Equation 7 from Wang and Leuning (1998).

Parameter	Value	Units
γ_0	32.6	$\mu\text{mol mol}^{-1}$
γ_1	0.0571	–
γ_2	0.001321	–
K_{c0}	223	$\mu\text{mol mol}^{-1}$
K_{o0}	216	mmol mol^{-1}
$H(K_c)$	85923	J mol^{-1}
$H(K_o)$	37990	J mol^{-1}
$H_v(V_{\text{cmax}})$	45027	J mol^{-1}
$H_d(V_{\text{cmax}})$	203594	J mol^{-1}
$H_v(J_{\text{max}})$	45977	J mol^{-1}
$H_d(J_{\text{max}})$	199345	J mol^{-1}
$H(R_d)$	10315	J mol^{-1}
S_v	650	J mol^{-1}

coefficient to reduce photosynthesis and respiration when daily root-zone water storage fell below 50% of its capacity. Maximum and minimum root-zone water storage was 187 and 115 mm, respectively, so the coefficient was set to reduce photosynthesis when water storage fell below 151 mm. This was done by reducing the value of A in Equation 1 in accordance with Equation 7 from Wang and Leuning (1998).

Daily weather data required to drive the model were solar irradiance, minimum and maximum air temperature and rainfall with hourly values of irradiance, temperature and air saturation deficit calculated following Goudriaan and van Laar (1994). The values of the parameters required by the model, V_{cmax} , J_{max} , R_d , α , β , D_{s0} , $D_{s\text{min}}$, a , $g_{\text{sc}0}$, W_{max} and l , were derived from measurements made in this study or from other published values and are listed in Table 2.

Results

Photosynthesis and stomatal conductance for leaves

Mean (\pm standard error) values of V_{cmax} for leaves in the canopy at the field site were 50.1 ± 2.2 and $44.9 \pm 2.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for mānuka and kānuka, respectively. Equivalent mean values of J_{max} were 100.2 ± 4.2 and $88.9 \pm 5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for mānuka and kānuka, respectively. Analysis of variance showed that there were no significant differences in V_{cmax} or J_{max} between species. There was no significant difference in specific

Table 2. List of parameters derived from measurements and used in the model to estimate annual net carbon uptake at the field site. As required by the model, V_{cmax} , J_{max} and R_d are maximum values measured at 20 °C for leaves at the top of the canopy for the field measurements from Figure 1. Values for α and β are means from the field measurements, D_{s0} is the mean value from the responses for the trees grown in the nursery shown in Figure 2 and D_{smin} is estimated as the value of air saturation deficit at the leaf surface (D_s) when g_s is maximum. Values for a and $g_{\text{sc}0}$ were taken from the slope and intercept in Figure 3 for the trees grown in the nursery. The value of W_{max} is the difference between maximum (187 mm) and minimum (115 mm) values of root-zone water storage at the field site.

Parameter	Definition	Value	Units
V_{cmax}	Maximum rate of carboxylation at top of canopy	60.0	$\mu\text{mol m}^{-2} \text{s}^{-1}$
J_{max}	Maximum rate of electron transport at top of canopy	120.0	$\mu\text{mol m}^{-2} \text{s}^{-1}$
R_d	Rate of daytime respiration	1.5	$\mu\text{mol m}^{-2} \text{s}^{-1}$
α	Quantum yield of electron transport	0.24	mol mol^{-1}
β	Convexity of the light response curve	0.71	
D_{s0}	Sensitivity of stomatal conductance to D	11.6	mmol mol^{-1}
D_{smin}	Minimum value of D for decreasing g_{sc}	4.5	mmol mol^{-1}
a	Parameter in Equation 6 related to intercellular CO_2 partial pressure (c_i)	4.2	mol mol^{-1}
$g_{\text{sc}0}$	Residual stomatal conductance to CO_2 transfer	10	$\text{mmol m}^{-2} \text{s}^{-1}$
W_{max}	Root-zone water storage capacity	72	mm
l	Leaf dimension	3	mm

leaf area between the species (mean values of 7.26 ± 0.25 and $7.92 \pm 0.39 \text{ m}^2 \text{ kg}^{-1}$ for mānuka and kānuka, respectively). Similarly, there were no significant differences in leaf nitrogen concentration per unit leaf area (N_a) between the species (mean values of 144.1 ± 5.8 and $132.5 \pm 4.0 \text{ mmol m}^{-2}$ for mānuka and kānuka, respectively). There were strong positive relationships between both V_{cmax} and J_{max} and N_a for the measurements from the field trees and the young trees grown at various nitrogen availabilities (Figure 1). For V_{cmax} , analyses of covariance showed that there were no significant differences in the slopes or intercepts of the linear relationship between species or between the measurements made on the young trees and trees at the field site. Thus, a single relationship was used to describe the response. Similarly, for J_{max} , there were no significant differences between the slopes of the linear relationship with N_a for the measurements made on the young trees and on trees at the field site, but the intercept was significantly higher ($P < 0.01$) for the young trees than that for

the trees at the field site. Therefore, the relationship between J_{max} and N_a was described by two lines with the same slope but different intercepts (Figure 1).

Analysis of the response of the rate of electron transport (J) to irradiance (Q) (Equation 4) for leaves at the field site showed that there were no significant differences in the values of the parameters α and β between the species. Mean α and β values for both species combined were $0.24 \pm 0.02 \text{ mol electron mol}^{-1} \text{ photon}$ and 0.71 ± 0.06 , respectively.

Stomatal conductance was high (between 0.25 and 0.45 $\text{mol m}^{-2} \text{ s}^{-1}$) at low values of air saturation deficit, then decreased with increasing D_s (Figure 2). Values for the parameters D_{s0} and g_{smax} did not differ significantly between species with D_{smin} set at 4.5 mmol mol^{-1} . Therefore, one set of parameters was used to describe the relationship for both species with values for maximal stomatal conductance (g_{smax}) of 0.34 $\text{mol m}^{-2} \text{ s}^{-1}$ and D_{s0} of 11.6 mmol mol^{-1} .

Neither the slopes nor the intercepts of the linear relation be-

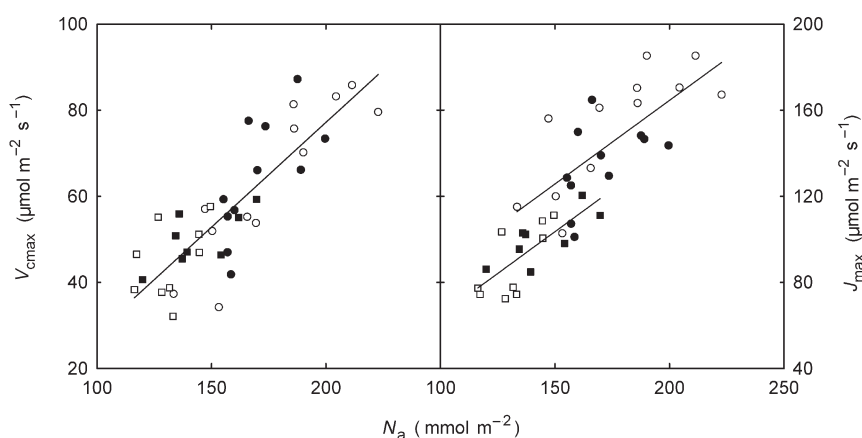


Figure 1. Relationships between maximum rate of carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}) with leaf nitrogen concentration on an area basis (N_a) for kānuka (○) and mānuka (●) trees grown in the nursery at three nitrogen supply rates and for kānuka (□) and mānuka (■) trees at the field site. Data for one mānuka tree grown in the nursery and one mānuka tree at the field site were omitted from the analysis and are not shown. Results for the two species were combined and the data fit by linear regression: $V_{\text{cmax}} = 0.487N_a - 20.29$, $r^2 = 0.71$, $t = 9.59$, $P < 0.001$ (nursery- and field-grown trees combined), $J_{\text{max}} = 0.777N_a + 9.19$ (nursery-grown trees only) and $J_{\text{max}} = 0.777N_a - 12.96$ (field-grown trees only), $r^2 = 0.81$, $t = 5.86$, $P < 0.001$.

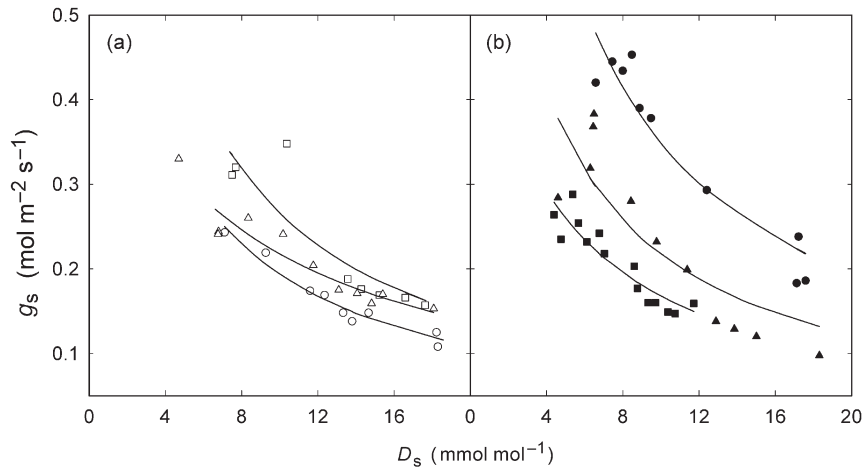


Figure 2. Sensitivity of stomatal conductance (g_s) to air saturation deficit at the leaf surface (D_s) for three shoots of (a) kānuka and (b) mānuka trees grown with high nitrogen supply. The lines are fitted to the data based on the function $g_s = g_{s\max} (1 + (D_s - D_{s\min})/D_{s0})^{-1}$. There were no significant differences between the species for the parameters D_{s0} and $g_{s\max}$, with $D_{s\min}$ set at $4.5 \text{ mmol mol}^{-1}$ and $g_{s\max}$ at $0.34 \text{ mol m}^{-2} \text{ s}^{-1}$. For definition of symbols, see Equation 6.

tween g_{sc} and $A/((c_s - \Gamma)(1 + (D_s - D_{s\min})/D_{s0}))$, known as the “stomatal index” (Equation 6), were significantly different for mānuka and kānuka (Figure 3).

Annual estimates of canopy photosynthesis

For the year in which canopy photosynthesis was modeled, maximum solar irradiance occurred in midsummer, reaching 34 MJ m^{-2} (76 mol m^{-2}) in late December. Daily maximum air temperature and daily mean air saturation deficit were highest in late summer (late February) at $26.5 \text{ }^\circ\text{C}$ and $9.3 \text{ mmol mol}^{-1}$, respectively. Annual rainfall of 1371 mm was evenly distributed throughout the year. Rain occurred on 150 days, with the largest event being 48 mm on one day in autumn (May). The

longest continuous periods without rain were 16 days in spring (November) with only 1.9 mm rain falling on one day in the middle of this period, 14 days in summer (January), 13 days starting in late summer (March) and 16 days starting in late April.

Maximum modeled transpiration rates from the forest canopy occurred in early summer, reaching values of 2.7 mm day^{-1} (Figure 4). High canopy transpiration rates also occurred in spring during a dry period from mid-October to mid-November when air saturation deficits were low and root-zone water storage was high (Figure 4). Root-zone water storage remained high during the winter months, then decreased rapidly in spring (November) and summer (January), reaching a minimum in early February. Less pronounced decreases in root-zone water storage occurred later in the year (March and May). Photosynthesis continued throughout the year, except for the period in summer (starting in mid-January) when root-zone water storage fell to a minimum. The minimum was accompanied by a marked decrease in canopy conductance, transpiration rate and intercellular CO_2 partial pressure (Figure 4).

Annual incident irradiance (400–700 nm) was $12.81 \text{ kmol m}^{-2}$, of which 76% was absorbed by the canopy. Annual daytime net photosynthesis on a ground area basis was 164.5 mol m^{-2} (equivalent to 1.97 kg C m^{-2}). Annual respiration loss from leaves at night was 37.5 mol m^{-2} (equivalent to 0.45 kg C m^{-2}), or 23% of net carbon uptake. The initial slope of the response of modeled daily photosynthesis to absorbed irradiance (data not shown) gave a value for potential canopy light-use efficiency of $25.8 \text{ mmol mol}^{-1}$ (equivalent to $1.42 \text{ kg C GJ}^{-1}$). When respiration at night is subtracted from net photosynthesis, the mean value of light-use efficiency was $13.0 \text{ mmol mol}^{-1}$ (equivalent to $0.72 \text{ kg C GJ}^{-1}$) and absorbed irradiance was $16.9 \text{ mmol mol}^{-1}$ (equivalent to $0.94 \text{ kg C GJ}^{-1}$).

Transpiration from the tree canopy (352 mm , 26% of annual rainfall) was a large component in the water balance with evaporation from the wet tree set at 274 mm (20%) and evaporation from the understory and soil accounting for a further 239 mm (18%). Drainage accounted for 37% of annual rain-

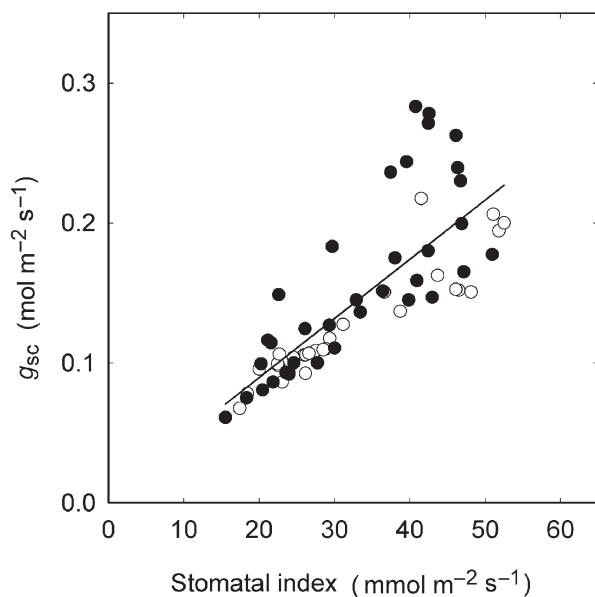


Figure 3. Relationship between stomatal conductance to CO_2 transfer (g_{sc}) and the stomatal index (Equation 6) from measurements of stomatal conductance and photosynthesis made at high irradiance but variable air saturation (Figure 2) for three replicate kānuka (○) and mānuka (●) trees. The slope of the line, a , is $4.2 \text{ mmol mol}^{-1}$.

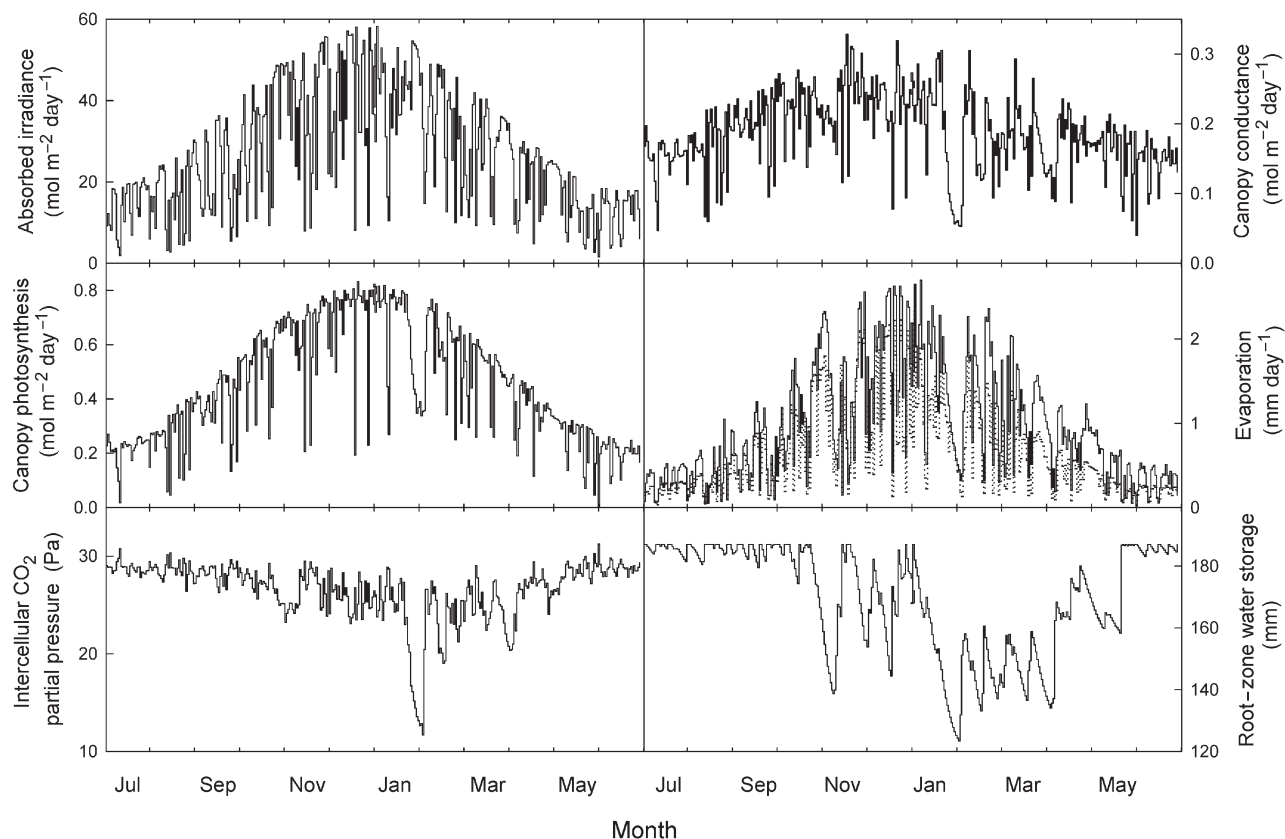


Figure 4. Daily absorbed irradiance, canopy net photosynthesis, intercellular CO₂ partial pressure, canopy conductance, transpiration rate (solid line), evaporation rate from the understory and soil (dotted line) and root-zone water storage at the field site estimated with the model described in the text. Daily canopy photosynthesis is calculated from the hourly values of photosynthesis at the leaf scale weighted by sunlit and shaded leaf areas and integrated over the daylight period. Daily canopy conductance is the mean of hourly values of stomatal conductance weighted for sun and shade leaves and integrated over the daylight period. Canopy intercellular CO₂ partial pressure is the hourly mean of leaf scale values of c_i weighted by photosynthesis, excluding respiring leaves, integrated over the daylight period.

fall. The annual mean value of water-use efficiency (ratio of photosynthesis to transpiration) for the tree canopy was $3.34 \text{ g C (kg water)}^{-1}$.

Discussion

The overall mean (\pm standard error) values of V_{cmax} and J_{max} for mānuka and kānuka at the field site were $47.3 \pm 1.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $94.2 \pm 3.7 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively. These values are only slightly higher than the mean maximum values of $V_{cmax} = 36 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $J_{max} = 72 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for temperate forest species reported by Wullschleger (1993). However, comparison of values for these parameters from the literature is difficult because of differences in measurement temperature and in the parameters used to describe their dependence on temperature (Leuning 2000, Medlyn et al. 2002b). There are few published values of these parameters for other woody species native to New Zealand. However, the values for mānuka and kānuka are similar to those reported for two fast-growing broad-leaved seral species, *Fuchsia excorticata* J.R. Forst. & G. Forst. and *Aristotelia serrata* J. R. Forst. & G. Forst. (Dungan et al. 2003), higher than those for the broad-leaved ever-

green tree *Nothofagus fusca* (Hook. f.) Ørst. (Hollinger 1996), and much higher than that for the rainforest conifer *Dacrydium cupressinum* Soland. ex Lamb. (Whitehead et al. 2002). Our data for the young trees grown with additional nutrient supply demonstrate that values of V_{cmax} and J_{max} increase, and thus photosynthetic capacity is enhanced, in leaves with increased nitrogen concentration (Figure 1). Linear increases in V_{cmax} and J_{max} with increased leaf nitrogen concentration on a leaf area basis (N_a) are consistent with results for a wide range of broad-leaved evergreen species (Grassi et al. 2002), broad-leaved deciduous species (Wilson et al. 2001, Turnbull et al. 2002, Dungan et al. 2003) and conifers (Walcroft et al. 1997). The strong correlation between photosynthetic capacity and leaf nitrogen concentration (Field and Mooney 1986) is explained by the high proportion of nitrogen in leaves that is stored in the carboxylating enzyme Rubisco (Evans 1989). However, the relationship may be nonlinear because of changes in the state of activation of Rubisco with leaf nitrogen concentration (Cheng and Fuchigami 2000), or change with seasonal acclimation processes (Kull et al. 1998, Warren and Adams 2001). But, for modeling, the strong relationships between V_{cmax} and J_{max} and leaf N_a support the use of leaf N_a as an

index for scaling photosynthesis from leaves to canopies (Leuning et al. 1995). The lack of a difference in the slope of the relationships of V_{cmax} and J_{max} with N_a (Figure 1) suggest that differences in productivity between the species in relation to nutrient availability are associated with differences in nitrogen-use efficiency and carbon allocation, rather than cumulative photosynthesis. Values of V_{cmax} and J_{max} are also sensitive to leaf phosphorus concentrations in species growing at sites with low phosphorus supply (Carswell et al. 2003), but the mechanism of the response is uncertain.

Tight coupling between V_{cmax} and J_{max} has been demonstrated for a wide range of species by Medlyn et al. (2002b), giving a value for the slope of the linear relationship between J_{max} and V_{cmax} , standardized to a temperature of 25 °C, of 1.67. The J_{max}/V_{cmax} ratio is dependent on temperature, because V_{cmax} has a higher temperature sensitivity than J_{max} (Walcroft et al. 1997, Medlyn et al. 2002b, Dungan et al. 2003). Based on the data reported by Medlyn et al. (2002b), the slope of the relationship between J_{max} and V_{cmax} at 20 °C is approximately 2.2. From our data (Figure 2), mean J_{max}/V_{cmax} for the measurements made at 20 °C in the field were very close to this value (mean of 2.00 ± 0.05). However, the value of J_{max}/V_{cmax} was significantly higher ($P < 0.01$) for young trees in the nursery with the same leaf nitrogen concentration (2.32 ± 0.08). This difference in J_{max}/V_{cmax} was attributable to the higher values of J_{max} in the young trees compared with the field trees and may be associated with differences in partitioning of nitrogen between carboxylation and electron transport processes, but we cannot confirm this without further data.

Results from the model showed that measured light-use efficiency for the year was about half the potential value. The difference is caused by seasonal limitations to photosynthesis as a result of temperature, air saturation deficit and short periods of marked rootzone water deficit. Although these combined effects resulted in a decrease in potential productivity at the site, the relationships between cumulative canopy photosynthesis and transpiration with cumulative absorbed radiation were nearly linear (data not shown). Marked departure from linearity would have indicated strong seasonal limitations such as those found on sites with low rainfall and shallow stony soils (e.g., Cromer et al. 1983, Arneth et al. 1998). The value for potential light-use efficiency was lower than the maximum value of 1.8 kg C GJ^{-1} used by Landsberg and Waring (1997) and 2.2 kg C GJ^{-1} used by White et al. (2000a). This suggests that low leaf nitrogen concentration and associated low leaf area index were the major limitations to canopy photosynthetic capacity at our field site. Some confirmation was provided by the higher rates of photosynthesis in the young nursery-grown trees with higher leaf nitrogen concentration. Studies with both *Pinus radiata* D. Don in eastern Australia (Raison and Myers 1992) and *Pinus elliottii* var. *elliottii* Engelm. in Florida, USA (Gholz et al. 1991) have demonstrated that light-use efficiency is reduced in stands deficient in nitrogen.

Low nutrient status is not unusual in mānuka, although kānuka is generally restricted to more fertile sites (Wardle 1991). Low leaf nitrogen concentrations are typical for other forest trees native to New Zealand (White et al. 2000b, Whitehead et al. 2001) and it is likely that annual photosynthesis and

leaf area index in many of the native forest ecosystems is limited by nitrogen supply. This is consistent with the wider global perspective of the factors limiting productivity in forest ecosystems (Schulze and Hall 1982). Simulation using the model gave an indication of the potential effects of increasing leaf nitrogen concentration on photosynthesis. In the model, the nitrogen concentration of the leaves at the top of the canopy was set at $165 \text{ mmol mol}^{-1}$. From the slopes of the relationships in Figure 1, an increase in leaf nitrogen concentration of 20% to $198 \text{ mmol mol}^{-1}$ would lead to increases in V_{cmax} (a similar increase in R_d was also assumed to occur) and J_{max} of 28 and 22%, respectively. Using these values in the model resulted in an increase in annual canopy net photosynthesis of 6.1%. An increase in nitrogen concentration of 40% to $231 \text{ mmol mol}^{-1}$ would raise leaf nitrogen concentrations to values similar to the maximum values in the young nursery-grown trees fertilized with nitrogen (Figure 1). This resulted in an increase in annual canopy net photosynthesis of 9.6%. Similarly, a decrease in leaf nitrogen concentration by 30% to $115 \text{ mmol mol}^{-1}$ would give values similar to the minimum values we measured in the trees at the field site. Such a decrease would lead to a reduction in annual canopy net photosynthesis of 15%. These effects are not large because the potential changes in photosynthesis are offset by changes in respiration from the leaves at night. However, the effects on net primary productivity are likely to be greater because of anticipated changes in leaf area index associated with nitrogen availability.

Seasonal variability in photosynthetic parameters has been shown to occur in both deciduous (Wilson et al. 2001, Kotsugi et al. 2003) and coniferous (Medlyn et al. 2002a) canopies. Such data were unavailable at our site. However, the effects of leaf age on photosynthetic parameters is likely to be small at our site because phenological observations (C.M. Trotter, unpublished data) suggest that a high proportion of leaves are replaced each year.

The estimate of mean net biomass increment from allometric relationships (Scott et al. 2000) and mensurational measurements at the field site when the trees were about 39 years old was $0.22 \pm 0.03 \text{ kg C m}^{-2} \text{ year}^{-1}$. This includes carbon in the aboveground, coarse root and standing dead stem components. If we assume no net change in soil carbon and that respiration from the stems and branches is negligible, we can make an approximate estimate of net biomass increment for the site from the difference between modeled net carbon uptake and respiration losses from the leaves and soil surface (Landsberg and Gower 1997). Fitting measurements of soil respiration (N.A. Scott, unpublished data) to temperature using an Arrhenius-type relationship (Lloyd and Taylor 1994) and applying this for the year at our site gave an annual estimate for soil respiration of $1.21 \text{ kg C m}^{-2} \text{ year}^{-1}$ (heterotrophic and autotrophic processes combined). This is lower than the estimate of $1.4 \text{ kg C m}^{-2} \text{ year}^{-1}$ given as the national average for shrubland, but respiration rates are known to vary widely, especially in relation to temperature (Tate et al. 2000). When the value for soil respiration at our site is subtracted from our estimate of net carbon uptake ($1.97 \text{ kg C m}^{-2} \text{ year}^{-1}$ net day-

light carbon uptake minus $0.45 \text{ kg C m}^{-2} \text{ year}^{-1}$ respiration from leaves at night), then the difference of $0.31 \text{ kg C m}^{-2} \text{ year}^{-1}$ is reasonably close to, and as expected slightly larger than, the estimate of net biomass increment obtained by mensuration, providing confidence in the capability of the model. Our modeled estimate would be further reduced toward the value derived from mensuration if respiration losses from stems and branches were included in the calculation, but respiration data were unavailable for our site.

In conclusion, we have demonstrated the sensitivity of photosynthesis to leaf nitrogen concentration in the shrubland species mānuka and kānuka. Similarity of the slopes of the relationships between the photosynthetic parameters V_{cmax} and J_{max} and leaf nitrogen concentration for trees growing in field conditions and for young trees growing in a nursery suggest that measurements of leaf nitrogen concentration will provide a helpful approach to predicting carbon uptake across a wide range of nutritional conditions. The modeling approach to scaling measurements of photosynthesis and respiration from leaves to canopies, incorporating limitations associated with climate variables and the seasonal development of root-zone water deficit, can provide robust values for canopy light-use efficiency that are commonly used to model forest productivity at large spatial scales (Landsberg and Coops 1999).

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