Modelling environmental limits to light use efficiency for a canopy of two broad-leaved tree species with contrasting leaf habit

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Abstract: We used outputs from a model of canopy carbon uptake [Dungan *et al*. (2004) *Functional Ecology 18*: 34–42] and measurements of irradiance (PAR, 400–700 nm) intercepted by the canopy to investigate the effect of daily changes in environmental conditions on daily light use efficiency, ε, for a canopy comprising two broadleaved New Zealand tree species with contrasting leaf habit. Irradiance absorbed by the canopy was 93% of the incident irradiance, and seasonal changes in the proportion of this absorbed by leaves of each species was estimated with a detailed model of leaf area phenology. Over the year, ε for semi-deciduous wineberry (*Aristotelia serrata*) was 0.43 g C MJ^{-1} PAR, with maximum and minimum values of 0.80 g C MJ^{-1} PAR and 0.07 g C MJ^{-1} PAR in summer and winter respectively. In contrast annual ε was 0.60 g C MJ^{-1} PAR for winter deciduous fuchsia, with a maximum value of 0.92 g C MJ^{-1} PAR in spring. The most important environmental regulator of ε for both species was τ, atmospheric transmissivity. Maximum values for ε were estimated on days when τ ≈0.2, on cloudy days in mid-summer. Limits to photosynthesis from restricted root-zone water availability were also important, showing that drought limitations can restrict ε even at a field site with annual rainfall of 4800 mm. Environmental limits to photosynthesis and ε have been investigated for only a few canopy tree species. Uncertainty in models of the national carbon budget required for reporting purposes would be reduced by considering the environmental regulation of ε for a wider range of tree species.

Keywords: radiation use efficiency; *Aristotelia serrata*; *Fuchsia excorticata*; simulation models

Introduction

The productivity of terrestrial ecosystems depends on the interception of irradiance and its conversion to biomass via photosynthesis. Accurate quantification of changes in the carbon stored in terrestrial biomass required by the United Nations Framework Convention on Climate Change and the Kyoto Protocol requires a robust understanding of the processes determining the conversion of irradiance to biomass. There is a large number of modelling approaches available to investigate forest carbon uptake, and a national estimate of carbon uptake by native New Zealand forests has recently been generated with an environmentally driven process-based model (Whitehead *et al*. 2001; Whitehead *et al*. 2004).

For a variety of reasons (e.g. computational convenience, lack of species-specific model input parameters, etc.) large-scale models of forest carbon uptake depend on a range of simplifying assumptions. For example it is often assumed that the gross primary productivity of a forest is a constant fraction of the absorbed photosynthetically active irradiance (PAR, 400–700 nm). This relationship is expressed as light use efficiency, ε, and can be calculated as

$$\varepsilon = A/Q_{abs}, \qquad (1)$$

where A is photosynthetic carbon uptake, and Q_{abs} is the PAR intercepted by the canopy (Monteith 1977; Landsberg *et al*. 1996). This provides a simple method for estimating forest ecosystem productivity over wide spatial scales, because satellite data can be used to estimate solar radiation absorbed by forest canopies (Hall *et al*. 1990). At time scales of weeks to months, this is a robust assumption that yields accurate estimates of ecosystem productivity (Lansdberg *et al*. 1996). Recent work (Medlyn 1998; Turner *et al*. 2003) has questioned the validity of this assumption at finer timescales and has shown that daily values of ε can be highly variable. This variability may be due to seasonal changes in photosynthetic capacity, or environmental factors (e.g. temperature, root-zone water availability) that reduce photosynthesis, and investigating this variability provides insights into factors determining

forest productivity.

The amount of solar radiation absorbed by a forest is a function of the amount and distribution of leaf area in the canopy. New Zealand forest tree species are predominantly evergreen (Wardle 1991, McGlone *et al*. 2004) and on this basis Whitehead *et al*. (2001) held leaf area constant in their nationwide carbon uptake model. While this assumption is appropriate at large spatial scales, this is not always the case, such as when considering carbon uptake by native deciduous or semi-deciduous trees (e.g. Dungan *et al*. 2004) or by seral vegetation dominated by introduced deciduous tree species.

We examine the effects of environmental variables on modelled values of light use efficiency for a canopy of two tree species that differ in the phenology of canopy leaf area. Wineberry (*Aristotelia serrata*) and fuchsia (*Fuchsia excorticata*) commonly co-occur in early successional vegetation in New Zealand, but differ in leaf habit. Wineberry is semi-deciduous and produces a single annual cohort of leaves which is replaced each year, whereas fuchsia is only one of 10 tree or shrub species in the native New Zealand flora that is winter deciduous (Dungan *et al*. 2003a, McGlone *et al*. 2004). Annual carbon uptake by these species at a site in New Zealand has been estimated previously, using an environmentally driven process-based model (Dungan *et al*. 2004). The forest canopy we describe offers useful insights into factors that determine limits to daily estimates of ε for forest canopies. Although photosynthetically active leaves are present in the canopy year round, canopy leaf area index (*L*) varies by a factor of ten from summer to winter. Furthermore, the seasonal pattern of leaf area phenology differs markedly for these two species. We begin by describing a model of seasonal changes in *L* for each species in the canopy, based on detailed measurements of leaf emergence and mortality at the shoot level. Using the model we are able to estimate the proportion of measured irradiance intercepted by leaves of each species in the canopy. The estimates of Q_{abs} are combined with estimated of daily canopy carbon uptake determined previously (Dungan *et al*. 2004), to derive estimates of daily ε. We then use these estimates to investigate the environmental limits to ε for a mixed wineberry and fuchsia canopy.

Methods

Field site

Data were collected from a forest in the Taramakau Valley, Westland, New Zealand (lat. 42° 46' S, long. 171° 33' E, elevation 200 m a.s.l.) during 1999–2000. Wineberry and fuchsia dominated the site with tree numbers of 18 225 and 2500 stems ha^{-1} and basal areas

of 38.7 and 3.3 m^2 ha^{-1} respectively. The forest canopy was very uniform in height, and averaged 7 m tall. The trees were growing on a recently disturbed debris-flow fan, and had regenerated following clearance for agriculture about 20 years prior to sampling. Soil at the site was a Fluvial Recent Soil (Hewitt 1998) on poorly sorted colluvium [≈Fluventi Dystrudept; Soil Survey Staff (1996)].

Daily weather data were collected at the site with an automatic weather station. Average daily T_{max} at the site was 21 °C in January, the warmest month, and average daily T_{min} was 4.5 °C in July, the coldest month. Daily average PAR was 18.07 MJ m^{-2} day^{-1} in December and 3.01 MJ m^{-2} day^{-1} in June. Rainfall at the site was 4830 mm for the year. Rain was recorded on 146 days in the year, and the longest period with no rainfall recorded was 12 days.

Seasonal changes in canopy leaf area

Although leaves are retained in the canopy year round, wineberry and fuchsia have markedly different seasonal leaf area index (*L*). The area of leaves per shoot was measured from a population of 15 fuchsia shoots and 53 wineberry shoots, selected at random from five mature fuchsia and fourteen mature wineberry trees that could be safely reached from a tower walkway built to access the canopy. The length and width of individual leaves on each shoot was recorded, and a record was kept of the presence or absence of every leaf. Leaves were counted at weekly intervals during the time of maximum leaf and shoot expansion, with frequency of visits reduced to fortnightly, and then to monthly once leaves had stopped expanding (for additional detail, see Dungan *et al*. 2003a). Leaf area emergence and mortality for each shoot were calculated by multiplying the number of leaves that emerged or died at each measurement period by the average area of leaves present at the time. The area (*a*, m^2) of each leaf was estimated from empirical relationships derived from measurements of the length (*l*), width, (*w*) and area of a random sample of 50–100 leaves for each species (wineberry $a = 0.625 \times l \times w$, $r^2 = 0.98$, $P < 0.001$; fuchsia $a = 0.0172 \times l$, $r^2 = 0.92$, $P < 0.001$).

Maximum canopy *L* was estimated from destructive measurement of leaf area on six trees per species that encompassed the range of tree diameters present in the forest, harvested at the time of maximum leaf area. All the leaves were removed from each tree and the fresh weight of the total tree foliage measured. A well-mixed sub-sample of leaves (the percentage of total foliage in the sample ranged from 25% for large trees, to 100% for small trees) was weighed and the total leaf area of the sample measured with a leaf area meter (LI3000, LiCor, Lincoln, NE). The total tree leaf area was thus estimated from the ratio of sample area to fresh mass, and canopy *L* estimated from
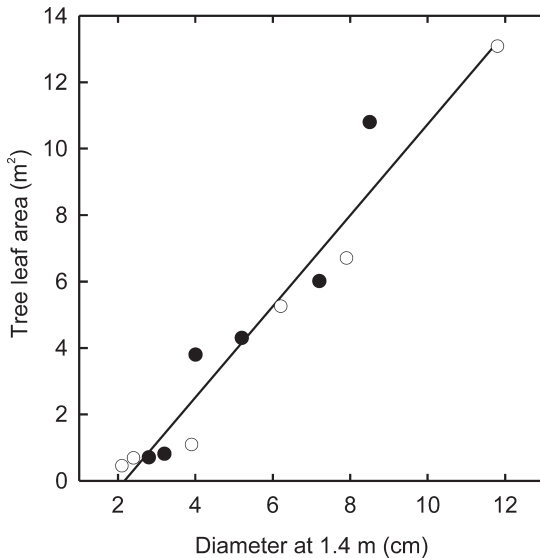
Figure 1. The relationship between stem diameter and total tree leaf area for wineberry ($\bullet$) and fuchsia (o) used to estimate stand leaf area index from measurements of stem diameter in a 400 m^2 forest plot. There was no significant difference in this relationship between the species (ANCOVA; $P = 0.31$), so a single relationship was calculated (leaf area = diameter $\times$ 1.37 -2.97, $R^2 = 0.94$, $P <0.001$).

measurements of tree diameter in a 400 m^2 quadrat and the linear relationship between tree diameter and total leaf area for each species (Figure 1). Maximum L was 5.4 m^2 m^{-2}, of which wineberry was 4.9 m^2 m^{-2} and fuchsia was 0.5 m^2 m^{-2}. Daily changes in L were estimated as the numerical difference between average leaf area emergence and mortality per shoot, described by growth equations (Dungan *et al*. 2003a), multiplied

by a factor to scale maximum shoot leaf area to the maximum canopy L.

Measurement of Q_{abs}

PAR at the top of the canopy (Q_i) was measured with a quantum sensor (Li190SA, LiCor, Lincoln, Nebraska) and total shortwave irradiance (S, 298–1100 nm) at the forest floor was measured with an array of four thermopile solarimeters (TSL, Delta-T, Cambridge, UK) placed on the corners of a 5×5 m grid square. Solarimeter data were corrected to account for the differential absorption of irradiance in the blue and red wavebands by chlorophyll in the canopy leaves following Chen *et al*. (1997), and these corrected values used to estimate irradiance in the photosynthetically active waveband at the forest floor following Gaudriaan and van Laar (1994). Half-hourly average values were integrated to give daily totals, and Q_{abs} was estimated as the difference in daily totals above and below the canopy. Although this approximation ignores the effect of canopy reflectance, modelling simulations using the formulation of Spitters *et al*. (1986) for our canopy indicate that reflectance in the photosynthetically active waveband is only a small proportion of Q_i (<4%; data not shown).

Estimating ε from model outputs

Daily values of ε were estimated using values of daily photosynthesis (A) for wineberry and fuchsia obtained from an environmentally driven process-based model (Whitehead *et al*. 2004, Dungan *et al*. 2004), using daily weather data collected at the site. The canopy model scales leaf-level photosynthesis to the whole canopy by accounting for the interception of irradiance by leaves, and day-to-day limits to photosynthesis regulated by changes in environmental conditions. The canopy is divided into homogenous layers based

Table 1. Values for parameters used in the canopy photosynthesis model. Parameters are V_{cmax}, the maximum rate of rubisco carboxylation when RuBP and CO_2 are at saturating concentrations; J_{max}, the maximum rate of electron transport when irradiance (Q) is saturating; and R_d, the rate of respiration from processes other than photosynthesis; g_{s0}, the minimum stomatal conductance; D_{smin}, the minimum value of D below which g_s is at its maximum value, and D_{s0}, a parameter describing the sensitivity of g_s to D.

Parameter		Value		Units
		wineberry	fuchsia	
L	summer	4.9	0.5	m^2 m^{-2}
	winter	0.5	0.0	m^2 m^{-2}
V_{cmax}	summer	47.8	58.7	μmol CO_2 m^{-2} s^{-1}
	winter	21.4	40.7	μmol CO_2 m^{-2} s^{-1}
J_{max}	summer	108.3	143.31	μmol electrons m^{-2} s^{-1}
	winter	52.5	100.04	μmol electrons m^{-2} s^{-1}
R_d		0.97	0.97	μmol CO_2 m^{-2} s^{-1}
D_{smin}		1001	1001	Pa
D_{s0}		480	480	Pa

on an assumed vertical distribution of canopy L. Direct and diffuse beam irradiance in the visible and near infra-red wavebands is estimated for sunlit and shaded leaves in each layer following Leuning (1997; after Spitters et al. 1986).

Photosynthesis in leaves is described by the model of Farquhar et al. (1980). The rate of photosynthesis in a leaf is determined by the minimum of the rates of carboxylation and regeneration of ribulose-1,5-bisphosphate (RuBP) catalysed by the enzyme rubisco (ribulose-1,5-bisphosphate carboxylase-oxygenase). Parameters for the model describing this relationship were derived from seasonal measurements of leaf gas exchange at the field site (described by Dungan et al. 2003b), and are listed in Table 1. The parameters include V_{cmax}, maximum rate of rubisco carboxylation when RuBP and CO_2 are at saturating concentrations; J_{max}, the maximum rate of electron transport when irradiance (Q) is saturating; and R_d, the rate of respiration from processes other than photosynthesis. The canopy model accounts for the coupling between photosynthesis and stomatal conductance following Leuning et al. (1997). Parameters describing the relationship of decreasing stomatal conductance to increasing air saturation deficit (D) are g_{s0}, the minimum stomatal conductance; D_{smin}, the minimum value of D below which g_s is at its maximum value, and D_{s0}, a parameter describing the sensitivity of g_s to D. The vertical distribution of foliage was very similar for each species and, on this basis, daily values for Q_{abs} were as estimated by assuming that each species absorbed sunlight in direct proportion to its relative contribution to canopy L, calculated as described above.

Data analysis

The effect of environmental variables on daily ε, together with their interactions, was investigated for each species with a multiple regression model. The environmental factors investigated were daily average air temperature (T_{avg}); total daily above-canopy irradiance (Q_i); τ, the atmospheric transmissivity, the fraction of irradiance reaching the top of the canopy after absorption and scattering by clouds and atmospheric turbidity (estimated from Gaudriaan and van Laar 1994); f, a factor derived from field measurements that simulates the down-regulation of photosysnthesis resulting from cold-induced photoihnibition (Dungan et al. 2003c), and a factor, φ, that simulates the effect of root-zone water availability by reducing modelled photosynthesis once the daily root-zone water storage falls below 20% of its maximum value (Walcroft et al. 1997). This analysis was conducted in three steps. First, the environmental factors were included in an initial regression model, and the least predictive factors eliminated with automated backward selection, using the minimum value for Akaike's Information Criterion (AIC) as the selection statistic (Venables and Ripley 1995). Once the best model (i.e. the model with the minimum AIC) was selected, the effect of each of the remaining input variables on daily values of ε was estimated by calculating the change in scaled values of AIC ($Δ_i$) when each variable was removed from the model. This indicates the degree of regulation of ε by each variable, and similar analytical methods were used to examine the degree of regulation by model variables on the annual carbon uptake (Whitehead et al. 2001) and spatial distribution of species in indigenous New Zealand forests (Leathwick et al. 1998). Finally, to determine the nature of the relationship of each variable to ε, coefficients for each variable were calculated from a generalised linear model that included only the variables retained in the second step. We used the statistical package R version 2.1.1 (the R Development Core Team 2004) to fit the models to the data and to obtain AIC values, and estimates of model parameters.
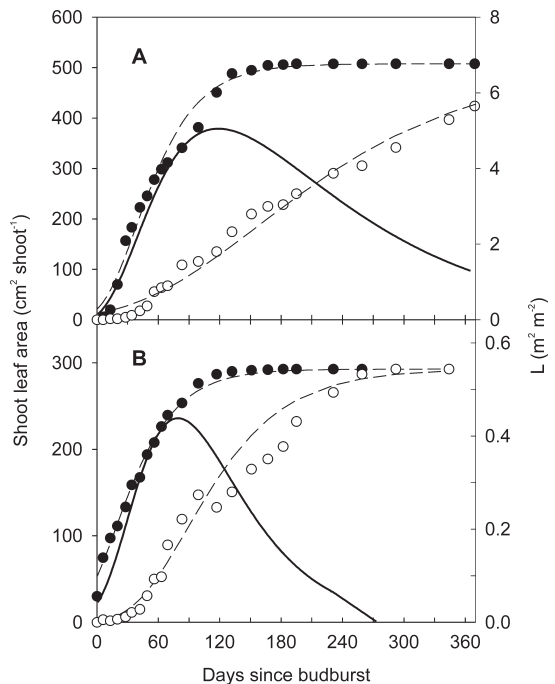

Figure 2. The seasonal pattern of leaf area index (L, heavy line, right-hand axis) for wineberry (A) and fushcia (B) was described as the numerical difference between cumulative leaf area emergence (●) and mortality (○) for a sample of shoots (left-hand axis), described by growth equations, multiplied by a factor to scale leaf area per shoot to canopy L.

Results

Seasonal changes in canopy leaf area index

For wineberry, the maximum leaf area per shoot was 33.7×10^{-3} m^2 shoot^{-1} (Figure 2). This value was observed 119 days after bud burst. In contrast, the maximum leaf area per shoot for fuchsia was 16.7×10^{-3} m^2 shoot^{-1}, observed 67 days after bud burst. The scaling factor to convert per-shoot leaf area (m^2 shoot^{-1}) to L (m^2 m^{-2}) was 1.45×10^{-2} and 2.99×10^{-3} shoots m^{-2} for wineberry and fuchsia respectively. Canopy L declined more rapidly for fuchsia than for wineberry; L was within 25% of the maximum value for only 80 days for fuchsia, but for 140 days for wineberry.

Estimating environmental effects on daily ε

Total photosynthetically active irradiance (PAR) measured at the site over the year was 3463 MJ PAR m^{-2}. During this time irradiance below the canopy was 247 MJ PAR m^{-2}. Irradiance absorbed by the canopy was thus 3216 MJ PAR m^{-2}, or 93% of the total solar radiation.

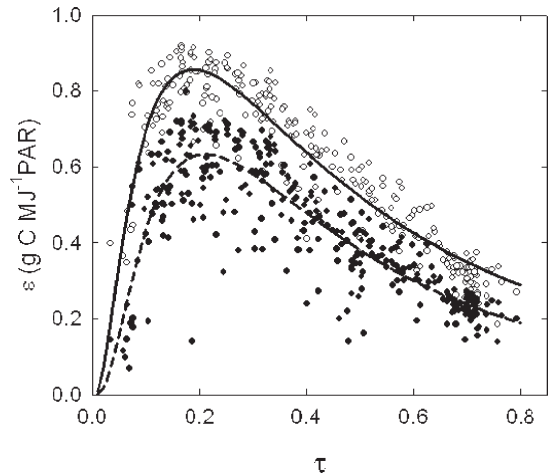Over the year, Equation 1 predicted average values for daily ε (±1 s.e.) of 0.60 (0.012) g C MJ^{-1} PAR for

Figure 3. The relationship between daily values of ε and atmospheric transmissivity (τ) for fuchsia (•) and wineberry (o). The relationship between ε and τ was described by an equation of the form $\varepsilon = y_0 + a \times \exp(-0.5 \times (ln(\tau/x_0)/b)^2)$, (where y_0, a, x_0, and b are parameters estimated from the data) and had adjusted R^2 values of 0.88 and 0.73 for fuchsia and wineberry, respectively.

Table 2. Effect of model input variables on calculated values for daily ε for wineberry and fuchsia. Variables are Q_i, PAR reaching the top of the canopy; τ, atmospheric transmissivity; φ, a factor that reduces phosotynthesis when root-zone water storage falls >20% below its maximum value; and f, a parameter describing the effect of frost-induced photoinhibition of photosynthesis. The effect of each variable is determined from Δ_i, the scaled change in AIC values, and variables are ranked from most to least important. See text for details.

Variable	d.f.	Deviance	Δ_i	Coefficient
Fuchsia				
$Q_i \times \tau$	1	0.154	112.67	-0.017
φ	1	0.030	13.08	0.172
T_{avg}	1	0.001	8.66	-0.003
f	1	0.002	5.65	0.367
Q_i	1	1.092	0	0.012
τ	1	0.376	0	-0.260
Intercept	1			-0.185
Null	272	1.950		
Wineberry				
f	1	0.319	175.68	0.225
$Q_i \times \tau$	1	0.262	164.31	-0.020
T_{avg}	1	0.001	17.78	-0.004
φ	1	0.015	0.03	0.066
Q_i	1	0.354	0	0.014
τ	1	0.494	0	-0.140
Intercept	1			-0.043
Null	355	1.886		

fuchsia, and 0.43 (0.009) g C MJ^{-1} PAR for wineberry. Maximum and minimum values were 0.80 and 0.07 g C MJ^{-1} PAR, and 0.92 and 0.18 g C MJ^{-1} PAR for wineberry and fuchsia respectively. During the 274-day period when fuchsia leaves were present, values of ε estimated for wineberry were 27% lower than those estimated for fuchsia ($t_{273,0.05} = 44.0$, $P < 0.001$).

For both fuchsia and wineberry, the automatic model selection process retained all five single-term environmental variables (T_{avg}, Q_i, τ, f, and φ), but removed all the two-way interactions except for the interaction between Q_i and τ (Table 2). The interaction between Q_i and τ had the largest effect on daily values of ε for fuchsia, and was one of the two most important variables for wineberry. The parameter describing frost-induced photoinhibition had an important effect on ε for wineberry, as f reduced canopy photosynthesis on 49 days over the year. In contrast, because fuchsia was leafless during the coldest winter months, f reduced modelled photosynthesis on only three days over the year.

By itself, atmospheric transmissivity (τ) explained 90% and 75% of the variability in daily ε for fuchsia and wineberry respectively (Figure 3). For both species the relationship between τ and ε was negative, indicating that as transmissivity increases canopy ε decreases. For both species, the effect of restricted root-zone water availability (φ) had an important effect on ε,

showing that root-zone water storage can be an important limit to canopy photosynthesis even at relatively wet sites.

Discussion

Determination of values for ε

Our estimates of average daily ε were 0.60 g C MJ^{-1} PAR for fuchsia, and 0.43 g C MJ^{-1} PAR for wineberry. Reasons for the differences in values for wineberry and fuchsia relate to differences in their photosynthetic physiology, and the relationship between the phenology of leaf area and environmental limits to photosynthesis. As Dungan *et al.* (2003b) showed, values for the parameters V_{cmax} and J_{max} are 30% higher in fuchsia than they are for wineberry, showing that fuchsia would have greater photosynthesis for an equivalent Q_{abs} than wineberry. Although wineberry and fuchsia coexist in the canopy at the field site, and are exposed to the same environmental conditions, Table 1 shows that the implications of these conditions for ε are different for each species. For example, because annual carbon uptake for fuchsia is concentrated in the summer months, environmental limitations to ε associated with restricted root-zone water (φ in Table 1) exert proportionally more influence on daily ε than they do for wineberry. Conversely, because wineberry retains photosynthetically active leaves during the time that fuchsia is leafless the effect of frost-induced photoinhibition is much more important for wineberry than fuchsia. Clearly, the seasonal phenology of these species, and the timing of this relative to changes in weather conditions over the year, determines the environmental variables that exert the strongest effect on the efficiency of canopy photosynthesis.

The annual average values of ε that we estimate for wineberry and fuchsia are similar to values estimated for other broadleaved forest types. Landsberg *et al.* (1996) suggest that global average values for ε should lie between 1–2 g dry mass MJ^{-1} for most forest types. Assuming that the carbon content of forest dry matter is around 50% would place a global average value in the range 0.5–1.0 g C MJ^{-1}. Measured values of ε vary widely between forest types. Gower *et al.* (1999) present a summary of a variety of studies, with values of ε ranging from 0.1 g C MJ^{-1} for a *Pinus ponderosa* forest in Montana, to 0.79 g C MJ^{-1} for coppiced *Salix vimnalis* (Cannell *et al.* 1987). Values for temperate deciduous forest average 0.54 g C MJ^{-1} (Gower *et al.* 1999).

For both species, atmospheric transmissivity (τ) had a significant effect on daily values of ε. Low values of τ correspond with high scattering of solar irradiance, mainly by clouds (Roderick *et al.* 2001), increasing diffuse and scatted direct beam irradiance. As light is more scattered, relatively more penetrates to lower levels in the canopy, increasing the net photosynthesis of leaves lower in the canopy. Although canopy light use is more efficient on days with low τ (maximum values for ε for wineberry and fuchsia were estimated for days with τ equal to 0.19 and 0.21 respectively; Figure 3), it does not correspond that canopy carbon uptake is necessarily higher on these days. Indeed, the canopy carbon uptake for days when τ <0.4 was c.42% of the annual total, although τ was <0.4 on 52% of the days during the year.

Although rainfall at our study site is high (4800 mm year^{-1}) and relatively evenly dispersed, periods of restricted root-zone water availability had a strong effect on reducing light use efficiency for the canopy for two reasons. First, soil at the site is relatively shallow and free-draining. Although tree roots were found to depths greater than 0.5 m, most were concentrated in the top 0.1 m (Dungan *et al.* 2003b). Mineral soil at the site has a high proportion of gravel and sand, typical of colluvial soils that form on alluvial fans. As such, water drains quickly from the root zone and unless more rain falls, root-zone water availability can quickly become limiting to photosynthesis. Second, periods of restricted rainfall occurred during the warmer summer months (Dungan *et al.* 2004), increasing evaporative demand and intensifying the effect of restricted root-zone water storage. Casual observations at the field site during this dry period showed clear effects of water stress, such as wilting leaves, particularly for fuchsia. However this did not result in increased leaf mortality (Dungan *et al.* 2003a), and leaves appeared to recover rapidly after new rain. Other modelling approaches have demonstrated the importance of considering the response of plants to soils and atmospheric water deficits. For example, it has been shown that the distribution of New Zealand's indigenous tree species is determined by species' responses to root-zone water deficit and air saturation deficit (Leathwick and Whitehead 2001). Similarly, it has been shown that considering the coupling between root-zone water, xylem hydraulic conductivity, and transpiration in models of CO_2 and water fluxes, particularly in environments with restricted root-zone water storage, can strongly determine the accuracy of ecosystem-scale predictive models (Tuzet *et al.* 2003). However, despite the importance of hydraulic effects for determining forest productivity, the response of stomatal conductance to root-zone water and air saturation deficit has been quantified for only a small number of New Zealand's native tree species.

Implications for models of forest productivity and carbon uptake

Our results show that a relatively simple model of the seasonal phenology of canopy leaf area, derived from

shoot-level measurements of the emergence and mortality of individual leaves, can be used to model light use efficiency in forest canopies with highly variable seasonal leaf area. Because leaf emergence and mortality can be related to environmental variables this simple approach lends itself to models that investigate the response of vegetation to global climate change. Our observation that ε is strongly related to atmospheric transmissivity supports Turner et al's (2003) suggestion to include parameters describing sky conditions such as cloudiness or transmissivity in large scale models of light use efficiency and primary productivity. Although canopy photosynthesis is fundamentally related to Q_i, the quality of light received exerts a strong influence on the efficiency of canopy photosynthesis. This becomes clear when considering that while high values of Q_i can only be obtained when the sky is clear (and τ is large), intermediate values of Q_i can be experienced under a range of conditions; on clear days when the sun is low in the sky (i.e. in winter, or in the early morning/late afternoon) or on cloudy days when τ is low, and diffuse irradiance is increased by clouds or atmospheric aerosols. Under these conditions diffuse irradiance penetrates further into the canopy, increasing photosynthesis of shaded leaves that are not directly illuminated. The interaction between Q_i and τ we observed (Table 2) shows that values for ε can be higher on days with low ε than Q_i would suggest. Direct measurements have shown that τ can have a strong effect on net ecosystem exchange (a measure of total flux of carbon between vegetation and the atmosphere that includes more than just canopy photosynthesis) (Hollinger et al 1994; Gu *et al*. 2003). Although this effect can be variable, related in part to differences in the canopy architecture of the vegetation studied (e.g. Letts *et al*. 2005), it has been shown that changes in the direct and diffuse irradiance resulting from decreased atmospheric transmissivity associated with increased cloud cover and atmospheric particles can alter carbon uptake at regional (Roderick *et al*. 2001, Misson *et al*. 2005) and global (Gu *et al*. 2003) scales.

While the simplifying assumption of constant ε (Landsberg *et al*. 1996; Rosati *et al*. 2004) has compelling advantages in global-scale carbon balance models, it is probably only strictly valid in systems with few environmental constraints to carbon uptake. For natural systems, like the native forest of New Zealand, future modelling efforts should consider the environmental regulation of ε, particularly by factors regulating hydraulic conductance along the soil-plant-atmosphere continuum and the effect of nutrient availability on photosynthesis.

Acknowledgements

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