

Forest and shrubland canopy carbon uptake in relation to foliage nitrogen concentration and leaf area index: a modelling analysis

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Abstract – A multi-layer canopy model was used to simulate the effects of changing foliage nitrogen concentration and leaf area index on annual net carbon uptake in two contrasting indigenous forest ecosystems in New Zealand, to reveal the mechanisms regulating differences in light use efficiency. In the mature conifer-broadleaved forest dominated by *Dacrydium cupressinum*, canopy photosynthesis is limited principally by the rate of carboxylation associated with low nutrient availability. Photosynthesis in the secondary successional *Leptospermum scoparium*/*Kunzea ericoides* shrubland is limited by electron transport. Maximum carbon uptake occurred in spring at both sites. Annual increases in canopy photosynthesis with simulated increases up to 50% in leaf area index, L , or foliage nitrogen concentration per unit foliage area, N_a , were largely offset by increases in night-time respiration. A realistic simulation where L was increased by 50% and N_a by 20% together (equivalent to an increase in total canopy nitrogen of 80%) led to decreases in net annual carbon uptake because the increase in photosynthesis was offset by the increase in respiration. Given the environmental constraints, both canopies in their natural states appear to be operating at the optimum conditions of leaf area index and nitrogen concentration for maximum net carbon uptake.

photosynthesis / respiration / leaf area index / nitrogen / light use efficiency

Résumé – Assimilation de carbone par une canopée forestière et une végétation buissonnante en relation avec l'indice foliaire et les teneurs en azote : un exercice de modélisation. Un modèle multi couche de canopée forestière a été utilisé pour simuler les effets de changements des teneurs en azote foliaire et d'indice foliaire sur le bilan net annuel d'assimilation de carbone dans deux écosystèmes forestiers contrastés de Nouvelle Zélande, afin de révéler les mécanismes de régulation et de contrôle d'efficacité d'utilisation de la lumière par les canopées. Dans la forêt primaire mixte conifère feuillue dominée par *Dacrydium cupressinum*, l'assimilation de carbone de la canopée est limitée par la carboxylation, essentiellement du fait d'une faible disponibilité en éléments minéraux. Cette assimilation est limitée par le transport d'électrons photosynthétiques dans le cas du peuplement buissonnant secondaire à base de *Leptospermum scoparium*/*Kunzea ericoides*. Le maximum d'assimilation de carbone se produit au printemps dans les deux cas. Au cours de l'année, les gains induits dans la photosynthèse par des augmentations simulées d'indice foliaire de 50 % ont été largement contrebalancés par les pertes dues à l'augmentation de respiration nocturne. Une simulation réaliste dans laquelle l'indice foliaire était augmenté de 50 % et l'azote foliaire de 20 % (ce qui correspond à une augmentation de 10 % de l'azote total de la canopée) a conduit à une baisse du gain de carbone cumulé sur l'année. Étant données les contraintes imposées par l'environnement, les deux couverts semblent fonctionner à l'optimum de leur indice foliaire et de leur concentration en N et maximisent ainsi le gain annuel de carbone.

photosynthèse / respiration / index foliaire / azote / efficacité d'utilisation de la lumière

1. INTRODUCTION

In New Zealand, indigenous forests occupy 59×10^3 km² (23%) of the land area and they comprise the largest national vegetation carbon reservoir (940 Mt C) [51]. There is increasing interest in shrublands, in particular, because of the potential for large areas of hill country that have become uneconomic for pastoral farming to revert to shrublands. The resulting uptake and storage of carbon could provide an important additional sink at the national scale [51]. However, most sites with poten-

tial for carbon storage are where soil fertility is low. To quantify the potential amount of carbon storage in forests and to predict future changes in relation to environmental factors or management, it is necessary to determine the rates of carbon uptake and storage by different forest types and to identify the factors regulating carbon uptake.

There are many examples where the addition of fertiliser to managed forests results in an increase in productivity [1, 15, 44, 46] and analysis using models has identified nutrient availability as a major source of variation in productivity [27, 39].

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Table I. Measured maximum values of the maximum rate of carboxylation, V_{cmax} , the apparent maximum rate of electron transport at saturating irradiance, J_{max} , rate of photosynthesis at saturating irradiance, A_{max} , and stomatal conductance, g_s , in relation to foliage nitrogen concentration on a mass basis, N_m , and specific leaf area, S , for forest species indigenous to New Zealand. All values are expressed on a half-total surface area basis.

Species	V_{cmax} $\mu\text{mol m}^{-2} \text{s}^{-1}$	J_{max} $\mu\text{mol E m}^{-2} \text{s}^{-1}$	$J_{\text{max}}:V_{\text{cmax}}$	A_{max} $\mu\text{mol m}^{-2} \text{s}^{-1}$	g_s $\text{mmol m}^{-2} \text{s}^{-1}$	N_m mmol kg^{-1}	S $\text{m}^2 \text{kg}^{-1}$	Source
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>	75	142	1.9	10.0	200	0.75	5.0	[4, 22, 41]
<i>Fuschsia exorticata</i>	54	128	2.4	14.5	300	1.78	14.3	[9]
<i>Aristotelia serrata</i>	52	115	2.2	14.6	250	1.51	11.1	[9]
<i>Leptospermum scoparium</i>	47	94	2.0	10.8	394	1.25	7.6	[59]
<i>Kunzea ericoides</i>								
<i>Meterosideros umbellata</i>	46	193	4.2	13.0	281	0.72	4.2	[51]
<i>Nothofagus fusca</i>	38	101	2.7	12.3	250	1.96	13.5	[20, 23]
<i>Quintinia acutifolia</i> ¹	17	50	2.9	5.7	107	0.82	8.4	[51]
<i>Weinmannia racemosa</i> ¹	13	49	3.8	2.9	44	0.75	6.1	[51]
<i>Dacrydium cupressinum</i>	12	32	3.3	2.7	46	1.06	8.3	[51]

¹ Growing as understorey species.

Physiologically, addition of fertiliser initiates processes that lead to larger pools of proteins in foliage that increase photosynthesis and promote nitrogen translocation for enhanced foliage growth [17]. The most pronounced result when nitrogen fertiliser is added is an increase in leaf area index, L , [1, 5, 15, 18, 54]. This is accompanied by an increase in the rate of photosynthesis, A , at the leaf and canopy scales, but the size of this response is usually much less than the effects on L [33, 48, 49]. Further, the combined effects of increases in self-shading, and rates of night-time respiration associated with increased foliage area [42], may result in only small increases in net carbon uptake at the canopy scale [7, 26, 36].

Much less work has been undertaken to investigate the potential for increasing productivity by adding fertiliser to unmanaged, indigenous canopies. However, evidence from modelling approaches shows that productivity in mature forests [57, 58] and shrublands [56] in New Zealand is limited principally by low nutrient availability.

An increase in photosynthetic capacity with increasing foliage nitrogen concentration is anticipated because of the high proportion of nitrogen in foliage in the carboxylating enzyme Rubisco [11, 14] and positive relationships between photosynthesis and foliage nitrogen concentration have been reported for a wide range of broadleaved evergreen species [19], broadleaved deciduous species [9, 52, 62] and conifers [55]. However, rates of respiration also increase with increasing foliage nitrogen concentration because of the greater need for maintenance and repair processes in cells [42, 43].

In this paper we use a modelling approach to investigate the effects of increasing L and foliage nitrogen concentration per unit area, N_a , on annual net canopy photosynthesis, integrating the effects on daily photosynthesis and night-time respiration, for two contrasting indigenous forest canopies in New Zealand. To allow comparison between the canopies, we present the results in terms of the effects on annual light use efficiency. We define gross light use efficiency as the ratio of annual daytime net canopy photosynthesis, A , and annual solar irradiance (400–700 nm) absorbed by the canopy, Q_a , ($\epsilon_{\text{gross}} = A/Q_a$), and net

light use efficiency as the ratio of the difference between annual net canopy photosynthesis and foliage night-time respiration, R_d , and annual absorbed irradiance ($\epsilon_{\text{net}} = [A - R_d]/Q_a$). Our objective was to explore the sensitivity of the response of canopy carbon uptake to changes in leaf area index and foliage nitrogen concentration for the two canopies. The conclusions are based on simulated results using a canopy model. While we are unable to validate the outputs from the model using experimental observations, we anticipated that the analysis would provide useful interpretation of the processes limiting canopy carbon uptake in the natural growing conditions. To provide perspective for the analysis, we begin by reviewing data on rates of photosynthesis at the leaf scale in relation to nitrogen concentration and light use efficiency at the canopy scale for woody species indigenous to New Zealand.

2. REVIEW OF DATA FOR NEW ZEALAND FORESTS

Few data are available for the photosynthetic properties of tree species indigenous to New Zealand, but those that have been measured show that there is a wide range in maximum rates of photosynthesis and stomatal conductance (Tab. I) [24, 57]. Consistent with this is the range in the values of the parameters describing the processes limiting photosynthesis: maximum rates of carboxylation, V_{cmax} , and the apparent maximum rate of electron transport at saturating irradiance, J_{max} . While values for broadleaved species on fertile sites are as high as those found in northern hemisphere deciduous forests, values for indigenous conifers and understorey species are lower than those for northern hemisphere coniferous species [25, 64]. For most of the species where measurements are available, values of the ratio $J_{\text{max}}:V_{\text{cmax}}$ are close to the average value at 20 °C of 2.7 reported for a wide range of species [31]. However, higher values of the ratio have been measured for some species and this is attributable to low values of V_{cmax} , consistent with low foliage nitrogen concentrations (Tab. I). These data suggest that rates of photosynthesis at the leaf scale in indigenous species in New Zealand are likely to be very variable, and that

Table II. Estimates of annual light use efficiency for indigenous forests in New Zealand using the multi-layer canopy model described in the text. The symbols refer to L , effective leaf area index (half-total surface area basis); Q_i annual incident irradiance (400–700 nm); Q_a irradiance absorbed by the canopy, ϵ_{gross} , gross and ϵ_{net} , net annual light use efficiency; A annual net canopy photosynthesis; and R_d , annual night-time respiration.

Species	Site	Latitude, longitude	L $\text{m}^2 \text{m}^{-2}$	Q_i kmol m^{-2}	Q_a/Q_i	$\epsilon_{\text{gross}}^1$ gC MJ^{-1}	ϵ_{net}^2 gC MJ^{-1}	Data source
<i>Nothofagus solandri</i>	Craigieburn Forest	43.2° S, 172.0° E	6.0	9.23	0.85	1.14	1.09	[41]
<i>Nothofagus fusca</i> ³	Maruia Forest	42.2° S, 172.3° E	7.3	10.15	0.91	0.99	0.83	
<i>Leptospermum scoparium</i> <i>Kunzea ericoides</i>	Tongariro National Park	39.5° S, 175.8° E	2.8	9.58	0.76	0.94	0.72	[59]
<i>Aristotelia serrata</i> <i>Fuchsia exorticata</i>	Taramakau River	42.8° S, 171.6° E	5.4	8.14	0.86	0.72	0.53	[10]
<i>Dacrydium cupressinum</i>	Okarito Forest	43.2° S, 170.3° E	3.5	10.74	0.78	0.46	0.27	[58]

¹ $\epsilon_{\text{gross}} = A / Q_a$.

² $\epsilon_{\text{net}} = (A - R_d) / Q_a$.

³ Unpublished data.

photosynthesis in some species is limited principally by low nutrient availability and low values of V_{cmax} [57].

For canopies, photosynthesis is regulated by both rates of photosynthesis at the leaf scale and canopy properties, principally leaf area index, L , and its effect on radiation interception. We have previously used the multi-layer canopy model described later in this paper to estimate annual light use efficiency for five forest canopies in New Zealand where meteorological data and values for parameters in the model are available. Leaf area index in these forests varied from 2.8 to 7.3, but the range in the fraction of incident irradiance absorbed by the canopies was smaller, from 0.76 to 0.91 (Tab. II). Rainfall at all these sites is sufficient such that root-zone water deficits sufficient to limit canopy photosynthesis are restricted to short periods in summer. Results from the model suggest that there is a wide range in light use efficiency of canopy photosynthesis (ϵ_{gross}) with the range increasing when foliage night-time respiration is included (ϵ_{net}) (Tab. II).

For the purposes of this paper we selected two contrasting canopies to simulate the effects of decreases and increases in N_a and L on light use efficiency. Leaf area index in the shrubland ecosystem dominated by the secondary successional species *Leptospermum scoparium* J.R. et G. Forst (mānuka) and *Kunzea ericoides* var. *ericoides* (A. Rich.) J. Thompson (kānuka) is low, but light use efficiency is relatively high (Tab. II). In contrast, leaf area index in the mature mixed conifer-broadleaved forest dominated by *Dacrydium cupressinum* Sol. ex Lamb. (rimu) is higher than the value at the shrubland site but low nutrient availability results in a very low light use efficiency.

3. METHODS

3.1. Field sites

The mixed podocarp-broadleaved forest was located at Okarito Forest, Westland (lat. 43.2° S, long. 170.3° E, elevation 50 m above sea level). This lowland terrace forest is dominated (72% of the basal area) by 400 to 600-year-old *Dacrydium* trees with a maximum height of 25 m and an average canopy depth of approximately 10 m. The

landform at the site is glacial in origin and the soil taxonomy is described as Entisols that have evolved to Inceptisols or Spodosols [47]. The loess is poorly preserved because of erosion and acid dissolution from extreme leaching resulting from high rainfall [2]. The soils have very low permeability and low porosity and are frequently waterlogged. The soils are extremely acid (pH 3.8–4.4) with medium levels of nitrogen (2.1 mol kg⁻¹) in the upper 150 mm, falling to very low values (0.14 mol kg⁻¹) at a depth of 150 mm, and low values of acid-extractable phosphorus and low phosphorus retention [37]. The mean annual biomass increment for the site was estimated to be 0.05 kg C m⁻² [58] and the effective leaf area index (half-total surface area basis) was 3.5. Average foliage nitrogen concentration was 128 mmol m⁻² [50].

Average daily values of air temperature and air saturation deficit were available from a station located 20 km south of the site and daily values of solar radiation were available from a station located 100 km north of the forest site. Mean annual temperature is 11.3°C with a small range between winter and summer of 8.6°C and annual rainfall is approximately 3400 mm. Further details of the site can be found in Whitehead et al. [58].

The shrubland site was located in the Tongariro National Park, central North Island, New Zealand (latitude 39.5° S, longitude 175.8° E, elevation 800 m above sea level), comprising dense shrubland vegetation dominated by *L. scoparium* and *K. ericoides* resulting from regrowth after burning approximately 39 years previously. The stand consisted of approximately 1.4 stems m⁻² of *Leptospermum* trees and 1.0 stems m⁻² of *Kunzea* trees. Average tree height (\pm standard error) was 5.0 \pm 0.1 m and average canopy depth was 1.7 \pm 0.3 m. The soil is classified as Podzolic Orthic Pumice soils of the Rangipo series [21], roughly similar to the Vitrand classification in the USDA soil taxonomy series [47] and low average nitrogen concentration to a depth of 300 mm of 0.17 mol kg⁻¹ [45]. The estimate of mean annual biomass increment for the site was 0.22 kg C m⁻² and the estimate of leaf area index (half-total surface area basis) was 2.8. Average foliage nitrogen concentration was 125 mmol m⁻² [59] and there were no significant differences between the species or with depth in the canopy.

Long-term mean annual temperature at the nearest weather station at Turangi (17 km away from the site) was 12.0°C and mean annual rainfall was 1586 mm [38]. The temperature data were extrapolated to the field site assuming a wet adiabatic lapse rate and rainfall was adjusted orographically based on comparisons of meteorological data from stations located at different elevations (J.D. White, personal communication). Further details of the site can be found in Whitehead et al. [59].

Table III. Values of parameters used in the model to estimate annual net carbon uptake at the two field sites. The parameters shown are maximum values for foliage in the upper canopies and are estimated from measurements made at a base temperature of 20 °C.

Parameter	Definition	<i>D. cupressinum</i>	<i>L. scoparium</i> <i>K. ericoides</i>	Units
V_{cmax}	Maximum rate of carboxylation	12	60	$\mu\text{mol m}^{-2} \text{s}^{-1}$
J_{max}	Apparent maximum rate of electron transport	32	120	$\mu\text{mol E m}^{-2} \text{s}^{-1}$
R_{l0}	Light-independent rate of respiration	0.7	1.5	$\mu\text{mol m}^{-2} \text{s}^{-1}$
α	Quantum yield of electron transport	0.22	0.24	$\text{mol E mol quanta}^{-1}$
β	Convexity of the light response curve	0.66	0.71	
a	Coupling parameter related to intercellular CO_2 concentration	4.0	4.2	
g_{sc0}	Residual stomatal conductance to CO_2 transfer	10	10	$\text{mmol m}^{-2} \text{s}^{-1}$
D_{s0}	Sensitivity of stomatal conductance to air saturation deficit D	8.9	11.6	mmol mol^{-1}
D_{smin}	Minimum value of D for decreasing g_{sc}	5.0	4.5	mmol mol^{-1}
l	Foliage dimension	1	3	mm
W_{max}	Root-zone water storage capacity	36	72	mm

3.2. The canopy model

A one-dimensional, multi-layer canopy model incorporating radiative transfer, energy balance, evaporation and canopy photosynthesis [32], and water balance [57] was used to explore the consequences of changing leaf area index and foliage nitrogen concentration on net annual carbon uptake for the canopy at the two sites. The model has been described fully elsewhere [58–61], so only brief details will be provided here. The canopy was divided into 20 layers based on the vertical distribution of cumulative canopy leaf area index. Leaf energy balance and the coupling of photosynthesis with stomatal conductance [30] are used to calculate photosynthesis for sunlit and shaded foliage separately in each layer [32]. Total photosynthesis is summed across layers within the canopy and daily values are obtained using Gaussian integration following Goudriaan and van Laar [16].

Photosynthesis, A , for sunlit and shaded foliage in each layer is calculated as the minimum of the rates limited by the carboxylation, A_c , and electron transport, A_q , such that

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

where R_l is the rate of light-independent respiration, A_c is dependent on the maximum rate of carboxylation, V_{cmax} , and A_q is dependent on the response of the rate of electron transport, J , to irradiance and its maximum value at saturating irradiance, J_{max} [12, 13]. Values for the parameters describing the dependence of V_{cmax} and J_{max} on temperature were taken from Benecke et al. [3] with the form of the response described by Walcroft et al. [55]. Photosynthesis is also coupled with stomatal conductance and the response of conductance to air saturation deficit following Leuning [30]. The response of foliage respiration to temperature is described by an Arrhenius function used previously by Turnbull et al. [52, 53]. Leaf temperature is estimated from air temperature using energy balance calculations and the characteristic foliage dimension following Leuning et al. [32].

The model incorporates water balance and the limiting effects of seasonal root-zone water deficit on canopy photosynthesis [57]. On wet days, the proportion of net rainfall penetrating the canopy is set at 0.8 (R.J. Jackson, personal communication) and transpiration and understorey and soil evaporation are reduced from their potential values by 25%. The root-zone water storage capacity of the soil was estimated from measurements of root-zone depth and soil texture at the two sites. Daily calculations of water balance, including components of transpiration from the tree canopy, evaporation from the wet tree canopy, and evaporation from the understorey vegetation and soil, are used to define a coefficient to reduce canopy photosynthesis when daily root-zone water storage fell below 50% of its maximum value.

Daily weather data required to drive the model are 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 [16]. The eleven parameters required for the model are defined in Table III.

3.3. Modelling procedure

Values for the parameters required for the model were taken from [58] for the *Dacrydium* site and [59] for the *Leptospermum/Kunzea* site and are listed in Table III. Daily weather data were used for 1 year with the model to estimate annual net canopy photosynthesis, A , and annual night-time respiration, R_d , for the actual conditions at both sites. Seasonal variability in A and R_d for the two sites has been reported previously [58–61] and will not be discussed in detail in this paper. Two types of simulations were then applied to the base conditions to simulate the effects of changing fertility. Leaf area index was decreased or increased by 25 and 50% uniformly with depth through the profile and the model was rerun with no changes in values for the parameters. Foliage nitrogen concentration per unit area, N_a , was then increased or decreased by 25 or 50%, resulting in changes to the values for the parameters V_{cmax} , J_{max} , and respiration at base temperature, R_{l0} . Values for the other parameters were held constant. Changes in annual canopy values of A and R_d were expressed as proportions of the values for the canopies in the actual conditions.

The relationships of V_{cmax} and J_{max} with changing foliage nitrogen concentration, N_a , for *Leptospermum/Kunzea* were taken from measurements made at the field site (Fig. 1) and described previously [59]. Foliage nitrogen concentrations for *Dacrydium* at the field site were low [50] and the range in values was small (Fig. 1), so it was not possible to use these to derive the response of photosynthetic parameters to N_a . Instead, slopes of the relationships (but not the actual values) for V_{cmax} and J_{max} and N_a for the conifer *Pinus radiata* D. Don from [55] were adopted (Fig. 1). Proportional changes in values for V_{cmax} and J_{max} at different foliage nitrogen concentrations used in the model were applied to the actual base value for *Dacrydium*. For all simulations, it was assumed that changes in the rate of respiration at base temperature, R_{l0} , were closely associated with changes in V_{cmax} [32]. Based on measurements at the field sites it was assumed that $R_{l0} = 0.06V_{cmax}$ for *Dacrydium* [50] and $R_{l0} = 0.025V_{cmax}$ for *Leptospermum/Kunzea* [59].

The final simulation was chosen to represent a realistic response of the canopy to an increase in nitrogen availability. Values for L and foliage nitrogen concentration per unit area, N_a were increased together by 50 and 20% respectively and the resulting values of V_{cmax}

and J_{\max} were used to simulate these effects on annual net canopy photosynthesis. For the canopy, this simulation was equivalent to increasing the total amount of nitrogen by 80%. Estimates of the vertical profiles of photosynthesis through the canopies from the model are presented to interpret the processes limiting canopy net carbon uptake.

4. RESULTS

4.1. Independent changes in N_a and L

Increasing or decreasing leaf area index, L , up to 50% from the actual value for each site resulted in a smaller than proportional effects on absorbed irradiance, Q_a (Fig. 2). Reductions in Q_a resulting from decreasing L by 50% were greater (maximum 27% for *Dacrydium*) than increases in Q_a resulting from an equivalent increase in L (maximum 10% for *Dacrydium*). The effects of changes in L on annual canopy net photosynthesis, A , were proportionately close to those resulting from similar changes in N_a with the effects of decreasing N_a and L being more pronounced (maximum 35% for *Dacrydium*) than equivalent increases (maximum 13% for *Dacrydium*). Canopy net photosynthesis with increasing N_a and L was increased more favourably for *Dacrydium* (maximum 13%) than for *Leptospermum/Kunzea* (maximum 9%). However, a 50% reduction in N_a resulted in a more pronounced effect on *Leptospermum/Kunzea* (34%) than on *Dacrydium* (29%), while a 50% reduction in L reduced A more in *Dacrydium* (35%) than in *Leptospermum/Kunzea* (31%). The effects of changing L on the ratio of A to Q_a to give gross light use efficiency, ϵ_{gross} , was very small, except when L was reduced by 50%, ϵ_{gross} decreased by 10% at the *Leptospermum/Kunzea* site and 12% at the *Dacrydium* site (Fig. 3). In contrast, ϵ_{gross} increased, but non-linearly, with increasing foliage nitrogen concentration.

Changing L resulted in a linear effect on integrated foliage respiration, R_d , for both species but the slope of the response was much steeper for *Leptospermum/Kunzea* than for *Dacrydium* (Fig. 2). A 50% change in N_a in *Leptospermum/Kunzea* resulted in a 50% change in R_d , but the change for

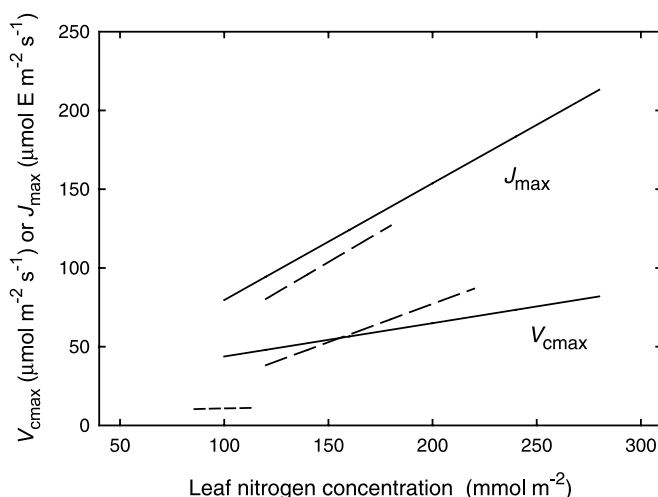


Figure 1. Relationships between the maximum rate of carboxylation, V_{cmax} , and the apparent maximum rate of electron transport at saturating irradiance, J_{max} , and foliage nitrogen concentration per unit area, N_a , for *Pinus radiata* (solid lines) [55] and *Leptospermum/Kunzea* seedlings (dashed lines) [59]. The data shown by the short dashed line are for *Dacrydium* [50]. The regression equations for the lines shown are $V_{\text{cmax}} = 0.212N_a + 11.26$ and $J_{\text{max}} = 0.742N_a + 2.668$ for *Pinus radiata* and $V_{\text{cmax}} = 0.487N_a - 20.29$ and $J_{\text{max}} = 0.777N_a - 12.96$ for *L. leptospermum/Kunzea*. The slopes of the lines for *Pinus radiata* were used to represent the proportional responses for *Dacrydium* as described in the text.

Dacrydium was only 25%. These resulting effects on R_d were more pronounced than the equivalent effects of changing N_a and L on A . The resulting effects of net light use efficiency, $\epsilon_{\text{net}} = (A - R_d)/Q_a$, were similar for the two canopies with changes in L , but the responses were different with changes in N_a (Fig. 3). Maximum values of ϵ_{net} at both sites occurred with a 25% reduction in L and, at high values of L , ϵ_{net} decreased below the actual value. For *Dacrydium*, ϵ_{net} increased with increasing N_a . In contrast, the maximum value of ϵ_{net} occurred for the actual conditions at the *Leptospermum/Kunzea* site.

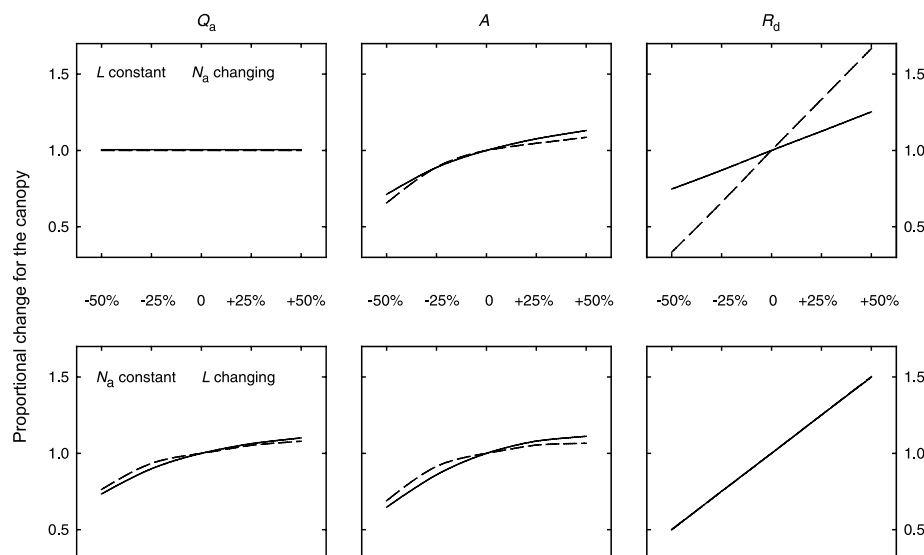


Figure 2. Proportional change in annual absorbed irradiance, Q_a , canopy photosynthesis, A , and night-time respiration, R_d , for the *Dacrydium* (solid lines) and *Leptospermum/Kunzea* (dashed lines) canopies in response to changes in foliage nitrogen concentration, N_a , with constant leaf area index, L , (upper panels) and changes in L with N_a constant (lower panels). Changes in N_a and L are indicated as $\pm 50\%$ and $\pm 25\%$ from the actual values shown as zero change.

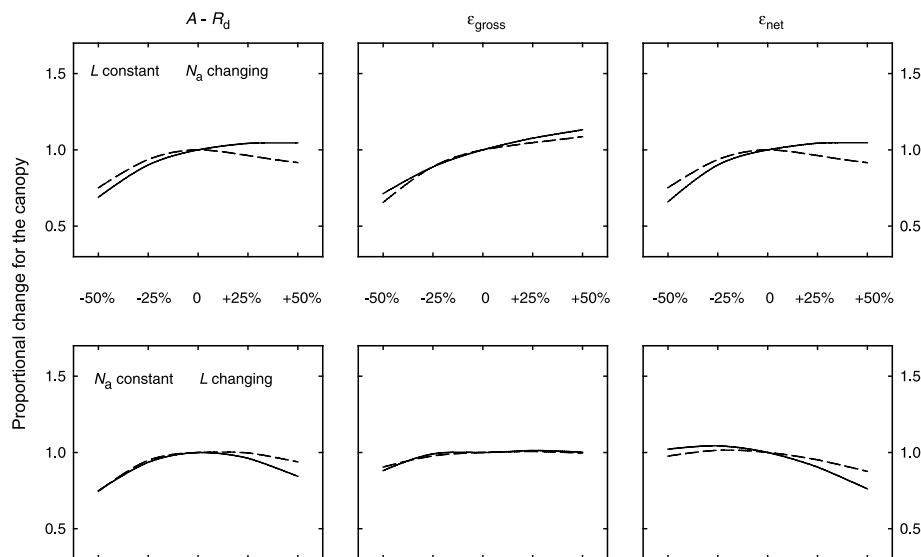


Figure 3. Proportional change in the annual difference between canopy photosynthesis, A , and night-time respiration, R_d , gross light use efficiency, ϵ_{gross} ($= A/Q_a$) and net light use efficiency, ϵ_{net} ($= [A - R_d]/Q_a$), where Q_a is the annual irradiance absorbed by the canopy for *Dacrydium* (solid lines) and *Leptospermum/Kunzea* (dashed lines) in response to changes in foliage nitrogen concentration, N_a , with constant leaf area index, L , (upper panels) and changes in L with N_a constant (lower panels). Changes in N_a and L are indicated as $\pm 50\%$ and $\pm 25\%$ from the actual values shown as zero change.

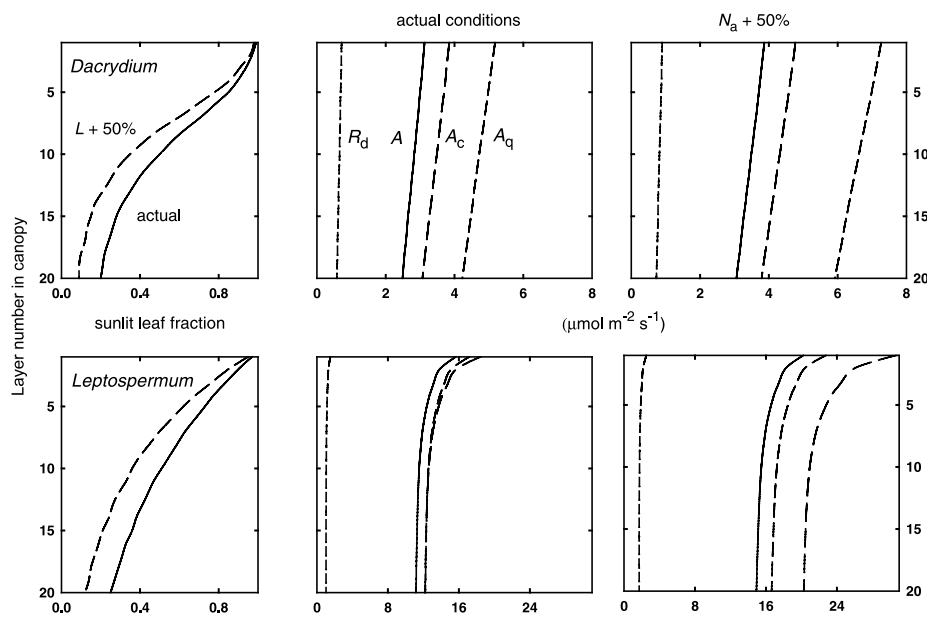


Figure 4. Vertical distribution through 20 canopy layers of the sunlit leaf fraction and components of photosynthesis for sunlit foliage for *Dacrydium* (upper panels) and *Leptospermum/Kunzea* (lower panels). The panels on the left show the changes in sunlit leaf fraction for the actual conditions (solid lines) and with an increase in leaf area index, L , of 50% (dashed lines). The panels in the centre show the actual conditions for the canopies and the panels on the right show the effects of an increase in foliage nitrogen concentration, N_a , of 50%. The components of photosynthesis shown are the rate limited by carboxylation (long dashed lines), A_c , the rate limited by electron transport (medium dashed lines), A_q , and the rate of light-independent respiration (short dashed lines), R_d . A is the actual rate of photosynthesis (solid lines) as given by equation (1). The conditions used in the calculations are typical for a bright day in summer with incident irradiance (400–700 nm) 1000 W m^{-2} , diffuse fraction 0.2, solar elevation 75° , air temperature 20°C , and air saturation deficit 1 kPa .

4.2. Vertical profiles of photosynthesis through the canopies

The sunlit leaf fraction decreased at all depths through the canopies at both sites when L was increased by 50% in the model, although the decrease was less pronounced in the top half of the *Dacrydium* canopy compared with the *Leptospermum/Kunzea* canopy (Fig. 4). For typical midday conditions in summer, rates of photosynthesis, A , for sunlit foliage were higher at all depths in the *Leptospermum/Kunzea* canopy when compared with values at equivalent depths in the *Dacrydium* canopy. For *Dacrydium*, rates of photosynthesis for sunlit foliage decreased linearly with depth. But, for *Leptospermum/*

Kunzea, photosynthesis was high for sunlit foliage in the upper canopy layers and lower, but constant, in layers lower in the canopy. At all depths, photosynthesis for sunlit *Dacrydium* foliage in the actual canopy conditions was strongly limited by the rate of carboxylation, A_c . Although A_q , A_c and A were increased at all canopy depths in the simulation when N_a was increased by 50%, photosynthesis remained strongly limited by the rate of carboxylation. In the actual *Leptospermum/Kunzea* canopy, photosynthesis was co-limited by the rates of carboxylation and electron transport, except in the top five layers that were limited marginally by electron transport. An increase in N_a by 50% resulted in increased rates of A_c and A_q and a clear limitation to photosynthesis by electron transport.

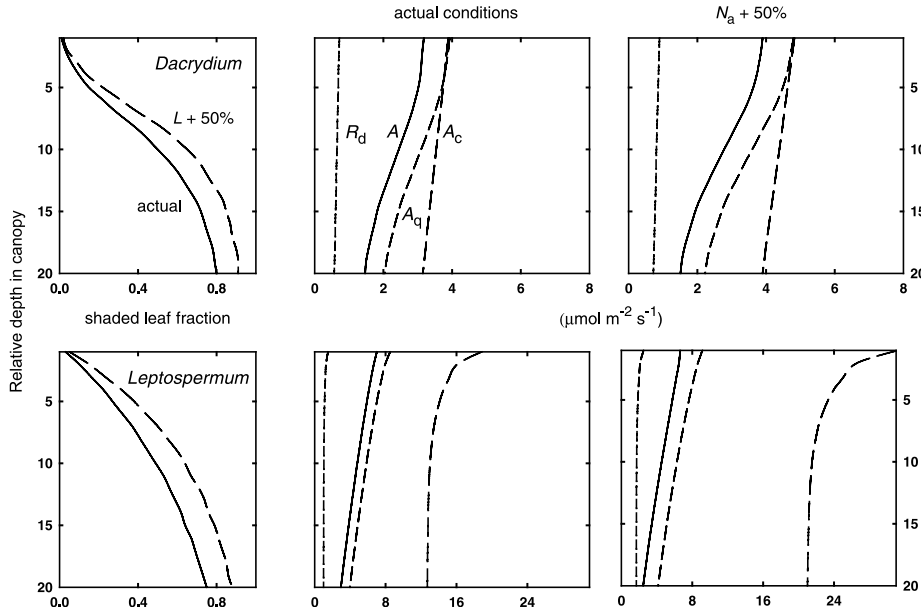


Figure 5. Vertical distribution through 20 canopy layers of the shaded leaf fraction (1 – sunlit leaf fraction) and components of photosynthesis for shaded foliage for *Dacrydium* (upper panels) and *Leptospermum* / *Kunzea* (lower panels). The panels on the left show the changes in shaded leaf fraction for the actual conditions (solid lines) and with an increase in leaf area index, L , of 50% (dashed lines). The panels in the centre show the actual conditions for the canopies and the panels on the right show the effects of an increase in foliage nitrogen concentration, N_a , of 50%. The symbols shown and the conditions used in the calculations are the same as those in Figure 4.

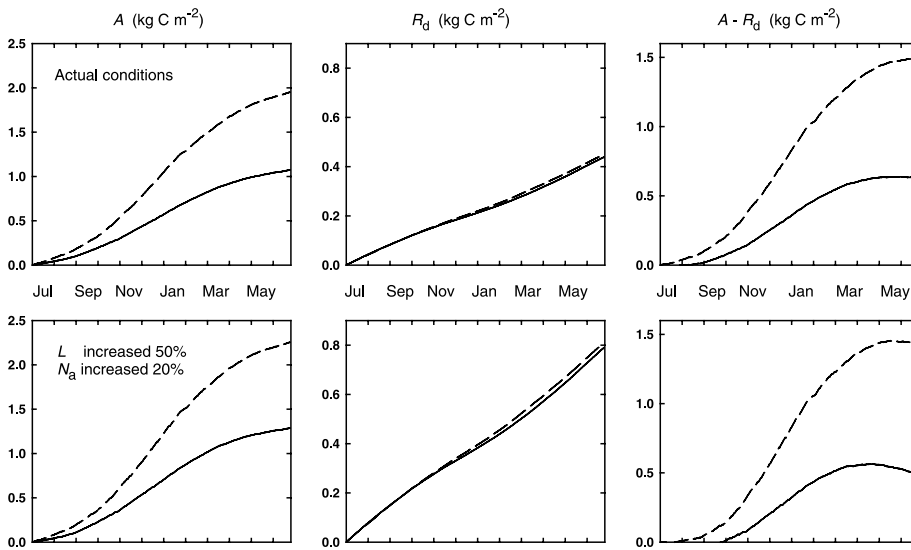


Figure 6. Seasonal cumulative canopy photosynthesis, A , night-time respiration, R_d , and the difference $A - R_d$ for the *Dacrydium* (solid lines) and *Leptospermum*/*Kunzea* (dashed lines) canopies. The upper panels show the actual conditions for the canopies and the lower panels show the results of a simulation where leaf area index, L , is increased by 50% and foliage nitrogen concentration, N_a , is increased by 20%.

Photosynthesis in shaded foliage in the *Dacrydium* canopy was limited by carboxylation rate in the top five layers, then by electron transport in lower layers (Fig. 5). In the *Leptospermum*/*Kunzea* canopy, foliage was strongly limited by electron transport in all layers. When L was increased by 50% in the model, this increased the shaded leaf fraction in all layers in both canopies. Increasing N_a by 50% increased A in the top layers of the *Dacrydium* canopy but did not affect rates of photosynthesis at lower layers, or throughout the *Leptospermum*/*Kunzea* canopy, as photosynthesis remained limited by the rate of electron transport.

4.3. Realistic simulation

For both canopies, maximum rates of canopy net photosynthesis occurred in early spring (October) to midsummer (February)

with no periods of pronounced limitation during this time [58, 59]. Cumulative daily values of canopy photosynthesis showed higher rates throughout the year for the *Leptospermum*/*Kunzea* canopy compared with the *Dacrydium* canopy (Fig. 6). Following seasonal changes in temperature and day length, maximum respiration rates occurred in spring (September) and autumn (April) with slightly lower rates in late spring (November). Rates were only slightly greater for *Leptospermum*/*Kunzea* than for *Dacrydium* from summer onwards. The rate of net carbon uptake ($A - R_d$) for both canopies was at maximum in late spring and summer (November to January), then decreased during autumn (March to June).

The effects of increasing L by 50% and foliage nitrogen concentration per unit area, N_a by 20% resulted in small increases in annual net canopy photosynthesis (16% for *Leptospermum*/*Kunzea*, 20% for *Dacrydium*) but more marked

increases in respiration (80% for both *Leptospermum/Kunzea* and *Dacrydium*) compared with the actual conditions for the two canopies. This resulted in slight decreases in the rates of net carbon uptake for both canopies in spring and summer and more marked decreases in autumn (April to June) compared with actual conditions for the two canopies. At the end of the year, annual net carbon uptake for the simulation was lower by 4% and 22% for *Leptospermum/Kunzea* and the *Dacrydium* canopies, respectively, compared with net uptake for the actual conditions.

5. DISCUSSION

The most significant result from the analysis simulating the effects of increasing L by 50% and foliage nitrogen concentration per unit area, N_a by 20% is that this led to decreases in net annual carbon uptake, with the decrease larger for the *Dacrydium* canopy than for the shrubland species (Fig. 6). At both sites, the simulated conditions enhanced canopy photosynthesis substantially, but this was offset by much larger increases in respiration associated with increased foliage area and increased foliage nitrogen concentration. We suggest that this simulation is a realistic possibility for both sites. Our simulated results are dependent on the assumption that there is a constant relationship between the parameters R_{f0} and V_{cmax} with changing foliage nitrogen concentration [32]. While there is evidence that the slope of increasing foliage respiration rate with increasing N_a is greater than the slope of the relationship between V_{cmax} and N_a [42, 43, 59], an alternative approach would be to change the base rate of respiration in relation to carbon uptake. Support for this approach is provided from the demonstration at the leaf scale of a clear relationship between cumulative night-time respiration and cumulative photosynthesis during the previous day in a *Quercus rubra* canopy [60]. However, our analysis does serve to highlight the importance of respiration to the annual carbon balance and confirms earlier conclusions using models for conifers elsewhere. Net carbon gain in response to fertiliser application was less than 5% for *Pinus radiata* [36] or not detectable for *Pinus elliottii* [7]. When L in young *Pinus taeda* was doubled following application of fertiliser, canopy A increased by only 50% and canopy R_d was increased by 100% [26].

While the use of multi-layer models for scaling CO_2 exchange from leaves to canopies has been well tested in forests [8, 28, 63], there has generally been much more emphasis on measurements for obtaining parameter values of photosynthesis than those needed for respiration [29]. Our results highlight the need for careful determination of parameter values for respiration in models. Rates of respiration are low compared with photosynthesis but, when integrated over night periods, total respiration becomes large and canopy carbon balance is very sensitive to this [29]. Based on available data, in our model we held the base value of respiration as a constant proportion of V_{cmax} . From the relationships shown in Figure 1, a change in N_a of 50% led to a change in the base rate of respiration, R_{f0} , of about 25% for *Dacrydium* and 50% for *Leptospermum/Kunzea* (Fig. 2). Slopes of the linear response of respiration to foliage nitrogen concentration per unit foliage mass reported for boreal species [42] and *Pinus radiata* [43] showed that a

change in foliage nitrogen concentration of 50% led to a change in the base rate of respiration, R_{f0} , close to 50%. Our proportional changes in R_{f0} with N_a were consistent with this. The response of respiration to N_a for *Dacrydium* was less than that for *Leptospermum/Kunzea* because of lower values for V_{cmax} . Tissue et al. [50] argue that the low rate of canopy photosynthesis in *Dacrydium* is, in part, attributable to a high ratio of R_f to A .

The effects of changes in N_a and L on annual A are smaller than the changes in R_d (Fig. 2) because of the non-linear processes of radiative transfer and the response of photosynthesis to irradiance at the leaf scale. Interpretation of the vertical profiles of the components of photosynthesis with changes in N_a and L is useful to explain the simulated responses in canopy photosynthesis and light use efficiency. For typical midday conditions on a summer day, low values of V_{cmax} in the *Dacrydium* canopy resulted in photosynthesis for sunlit foliage being limited strongly by the rate of carboxylation in all layers, even when N_a was increased by 50% (Fig. 4). In contrast, photosynthesis for sunlit foliage in the *Leptospermum/Kunzea* canopy was limited almost equally in all layers by the rates of carboxylation and electron transport. When N_a was increased, the dominant limitation to photosynthesis was the rate of electron transport. The consequence of the relationships between V_{cmax} , J_{max} , and N_a for the *Leptospermum/Kunzea* canopy (Fig. 1) is that the ratio $J_{max}:V_{cmax}$ increases with increasing N_a . Since we assume that R_{f0} is a constant fraction of V_{cmax} , then with increasing N_a , the ratio $R_{f0}:J_{max}$ increases. The result is that the increase in the ratio $A:R_d$ is greater when L is increased and N_a held constant than when L is held constant and N_a is increased. Thus, for the *Leptospermum/Kunzea* canopy, net carbon uptake is enhanced more by an increase in L than by an increase in N_a (Fig. 3). The opposite is true for the *Dacrydium* canopy because photosynthesis is limited dominantly by the rate of carboxylation, rather than the rate of electron transport.

Strong limitation of photosynthesis by electron transport in the *Leptospermum/Kunzea* canopy also suggests that photosynthesis would respond more to fluctuations in irradiance than in the *Dacrydium* canopy. Evidence supporting this conclusion is provided by an analysis of the effects of the fraction of diffuse irradiance on canopy photosynthesis. Canopy photosynthesis in the *Dacrydium* canopy was much less sensitive to increases in the fraction of diffuse irradiance than a *Quercus* canopy with photosynthetic properties similar to the *Leptospermum/Kunzea* canopy [61]. However, it is important to note that the analysis in Figures 4 and 5 is confined to midday conditions in summer, and integration of the dynamic effects of changing sun angle, weather variables, and the fractions of sunlit and shaded foliage on photosynthesis is encapsulated in the overall results in Figure 6.

Canopy net photosynthesis started in late winter (August) but reached maximum rates in late spring (November and December, Fig. 6). The smooth increase in cumulative A throughout the year at both sites confirms the lack of marked seasonal limitations to canopy photosynthesis resulting from, for example, temperature extremes or drought. From late summer (March) onwards, net carbon uptake was reduced because of decreases in photosynthesis associated with lower irradiance but continued rates of respiration. This emphasises the important

contribution of net carbon uptake in spring and early summer for tree growth [26]. There may be less carbon available for growth in summer and winter when canopy photosynthesis is more offset by respiration or, at sites elsewhere, when other environmental influences, for example drought, limit photosynthesis [34, 49].

In our analysis, net canopy carbon uptake was greater for *Leptospermum/Kunzea* than for *Dacrydium*. This is consistent with the difference in rates of biomass accumulation at the sites [56, 59]. Because of the limited data available, we have concentrated on the relationships of photosynthesis and respiration to changes in foliage nitrogen concentration, rather than other nutrients. However, there is strong evidence that productivity in most indigenous ecosystems in New Zealand is limited by phosphorus, rather than nitrogen supply [40]. It is known that photosynthesis is reduced in young trees growing at low phosphorus supply [6], possibly because of reduced carboxylation activity [35], but more experimental work is required to quantify the interactive effects of nitrogen and phosphorus supply on photosynthesis and respiration at the canopy scale.

6. CONCLUSION

Our analysis suggests that annual $(A - R_d)$ did not increase with increasing leaf area index at either site, despite a small increase in ϵ_{net} with decreasing L for *Dacrydium* (Fig. 3). Annual $(A - R_d)$ with changes in foliage nitrogen concentration per unit area, N_a were also highest for the actual conditions for *Leptospermum/Kunzea* and would be increased only slightly at higher values of N_a for *Dacrydium*. From this we conclude that there is considerable uncertainty that adding fertiliser to these unmanaged ecosystems will result in increased foliage nitrogen concentration, annual net carbon uptake and thus productivity. This is clearly attributable to the pronounced offset of increased photosynthesis by respiration resulting from increases in leaf area index and foliage nitrogen concentration. The *Leptospermum/Kunzea* canopy appears to be adjusted to operate at the optimum conditions of L and N_a for maximum net carbon uptake, given the environmental constraints. Despite differences in the processes limiting photosynthesis in the *Dacrydium* canopy, this is also operating close to its optimum conditions for L and N_a , although net carbon uptake would be weakly enhanced if foliage nitrogen concentration were increased or leaf area index reduced. The model we have adopted to scale measurements of photosynthesis and respiration from leaves to canopies is useful to explain differences in the components of net carbon uptake and light use efficiency for canopies. Further, the approach increases confidence in making predictions of productivity for forests and shrublands at a range of site fertilities at the national scale.

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