MODELLING CANOPY PHOTOSYNTHESIS IN PINUS RADIATA STANDS

J. C. GRACE, D. A. ROOK, and P. M. LANE
Ministry of Forestry, Forest Research Institute, Private Bag, Rotorua,
New Zealand

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ABSTRACT

A model for simulating canopy net photosynthesis in stands of **Pinus radiata** D. Don has been developed from measurements of rates of net photosynthesis on individual shoots and a radiative transfer model. It has been shown that estimates of net photosynthesis for a tree crown can be in error by up to 40% if the model assumptions do not agree with the method of measuring rates of net photosynthesis. Specific leaf area has been used to account for the variation in rates of net photosynthesis due to the physiological and morphological state of individual shoots throughout the canopy. Comparing estimates of canopy net photosynthesis for three different stands of **Pinus radiata** with above-ground dry matter production indicates that the model realistically estimates canopy net photosynthesis.

Keywords: photosynthesis; modelling; **Pinus radiata**.

INTRODUCTION

The use of models which simulate the processes affecting tree growth has been advocated for predicting forest growth under new management practices, or on previously unforested sites, or due to changing climatic conditions (Rook *et al.* 1985; Landsberg 1986). Such models simulate the interception of solar radiant energy, canopy photosynthesis, respiration, and allocation of carbon to above- and below-ground biomass. The objective of this paper is to present a model for estimating canopy net photosynthesis in stands of *Pinus radiata.*

Photosynthetically active radiant energy (PAR) (400–700 nm) is essential for photosynthesis, and the rate of net photosynthesis is related to the quantum flux density (Q) incident on the foliage. Hence, in developing a model of canopy net photosynthesis it is usual to use a radiative transfer model to provide an estimate of Q incident on foliage in different parts of the canopy, and to use an equation relating rate of net photosynthesis to Q to provide an estimate of net photosynthesis in that part of the canopy. Summing the estimates of net photosynthesis for all the foliage within the canopy provides an estimate of canopy net photosynthesis.. However, for a given value of incident Q there are differences in the rate of net photosynthesis for conifer shoots of different ages and in different positions within the canopy (Jarvis & Sandford 1986). Hence, in developing a model of canopy net photosynthesis it will be necessary to measure rates of net photosynthesis on different types of foliage and account for such differences within the model.

We have chosen to use the radiative transfer model of Grace *et al.* (1987) in developing a model of canopy net photosynthesis because location of individual trees within a stand must be specified and so it is particularly suitable for the widely spaced *P. radiata* grown in New Zealand. The size of each tree is specified and the crown of each tree is assumed to be represented by an ellipsoid which may be truncated at the base. Within this ellipsoid three other ellipsoids are specified, dividing the crown into four shells. To enable net photosynthesis for a tree to be predicted, we have divided the tree crown into six horizontal layers, which together with the four shells divide the tree crown into a maximum of 52 segments (Fig. 1). To estimate net photosynthesis for a tree crown, we estimate Q and the rate of net photosynthesis at one point within each segment using one of the two methods given below and assume this rate applies to all foliage within that segment (see later for more details). Summing the estimates of net photosynthesis for each segment provides an estimate of net photosynthesis for a tree crown. Canopy net photosynthesis is obtained by summing the estimates of net photosynthesis for all trees within the stand.

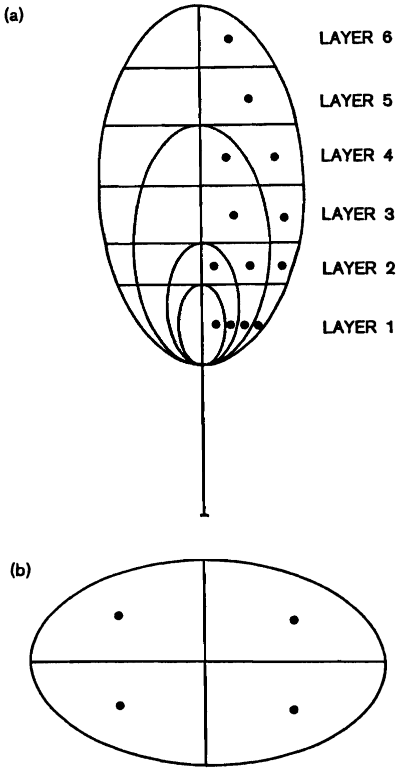

FIG. 1—Location of segments within crown used in estimating net photosynthesis.
(a) vertical cross-section
(b) horizontal cross-section at Layer 6.

The probability that a beam of sunlight passes unintercepted to a particular point within the canopy is given by:

$$p = \exp(-k \rho S)$$

where: p is the probability that a beam of sunlight is not intercepted

k is the fraction of the "one-sided" foliage area projected on a plane normal to the beam

S is the distance that a ray passes through the tree crowns

ρ is the "one-sided" foliage area density.

The probability that diffuse radiant energy is unintercepted is obtained by numerically averaging the result of the above equation over the hemisphere. Further details have been given by Grace *et al.* (1987) and Norman & Welles (1983).

The foliage is assumed to be randomly distributed within each shell, with no preferred azimuthal direction. Any distribution of leaf inclination angles may be assumed but in this paper we have assumed that the foliage inclination angles are distributed according to the spherical leaf angle distribution. This assumption appears realistic (Grace *et al.* 1987).

To obtain realistic estimates of canopy photosynthesis, it is necessary that assumptions linking the radiative transfer model to equations predicting rates of net photosynthesis match the way incident Q and rates of net photosynthesis are measured in the field. Norman (1980) discussed methods of linking the interception of solar radiant energy and rates of net photosynthesis together in continuous canopies. The most accurate method for estimating canopy net photosynthesis from measurements of rate of net photosynthesis on individual leaves is:

(a) Firstly, calculate the beam and diffuse quantum flux density at different levels within the forest canopy; secondly, calculate the incident quantum flux density for shaded leaves and for classes of leaves that are exposed at various angles to the sun's beam; thirdly, calculate rate of net photosynthesis for each of these classes. The net photosynthesis for that layer is obtained by summing over these leaf classes weighted by their respective areas. Net canopy photosynthesis is obtained by summing over all the layers.

A less accurate method of estimating canopy net photosynthesis from measurements of rate of net photosynthesis on individual leaves (Norman 1980) is:

(b) Divide the canopy into layers and calculate the average quantum flux density on a horizontal plane for each layer by calculating the transmittance of beam and diffuse visible radiant energy separately. This average quantum flux density is then used to estimate net photosynthesis for that layer.

This latter method does not take into account the orientation of foliage within the canopy and also neglects sunflecks. Net canopy photosynthesis can be over-estimated by about 50% (Norman 1980).

Both these methods assume that the rate of net photosynthesis has been measured on a planar leaf. However, if the rate of net photosynthesis is measured on a shoot where the natural arrangement of needles is not disturbed, method (b) should provide realistic estimates of canopy net photosynthesis since needle orientation is taken into account when measuring the rate of net photosynthesis. Method (a) is not appropriate since needle orientation will be accounted for twice.

Methods (a) and (b) have been incorporated into the radiative transfer model of Grace *et al.* (1987) to link the radiative transfer model with equations predicting rates of net photosynthesis.

In the first section of this paper, needle arrangement study, we examine the differences in net photosynthesis for a *P. radiata* tree crown obtained from measuring the rate of net photosynthesis with the needles in their natural arrangement or in a plane, and using the above two methods (a and b) of linking equations predicting the rate of net photosynthesis with radiative transfer models.

In order to account for the differences in rates of net photosynthesis due to position in the crown and age, crowns have been divided into layers, either subjectively (e.g., Beadle *et al.* 1985) or by defining the boundary between "sun" and "shade" foliage (Benecke & Nordmeyer 1982), and rates of net photosynthesis have been measured on foliage of different ages in the different zones within the crown. Separate equations predicting the rate of net photosynthesis have been derived for each class of foliage.

In the second section of this paper we examine the possibility of including a variable in equations predicting rates of net photosynthesis which will objectively account for the variability due to the morphological and physiological state of the shoot. The variable considered is specific leaf area (l_s) since studies have shown that l_s varies with incident radiant energy (e.g., Kellomäki & Oker-Blom 1981) and with age of foliage (Hager & Sterba 1984) and that specific leaf weight (inverse of l_s) is related to photosynthetic performance (Oren *et al.* 1986).

Finally, we present estimates of annual net photosynthesis for three stands of *P. radiata* growing at Puruki (Beets & Brownlie 1987), but differing in age and stocking. Annual canopy net photosynthesis has been estimated by running the radiative transfer-photosynthesis model for representative days throughout the year, deriving an equation relating daily canopy net photosynthesis to daily incoming visible radiant energy, and then using this equation with daily meteorological data to estimate canopy net photosynthesis for each day of the year (cf. Grace *et al.* 1987).

NEEDLE ARRANGEMENT STUDY

Methods

This study was carried out in the Long Mile experimental area at the Forest Research Institute, Rotorua (38° 10′ S, 176° 16′ E) from 8 to 15 October 1986. During this period there was a mixture of sunny and overcast days. Measurements of rates of net photosynthesis were made on nine trees approximately 2.5 m tall. There were three trees from each of three clones, namely J100/64, 266.345, and 850.451. Clone J100/64 originated as a tissue culture plantlet from an embryo which was germinated 6 years previously. Clones 266.345 and 850.451 were propagated from scions of hedged trees and had been set as cuttings 6 years previously; both clones were coning and had the appearance of mature trees. Three similar adjacent shoots on second- or third-order branches, approximately 1 m from ground level, were selected on each tree. The expanding apical buds were removed and the shoots assigned at random to one of two needle arrangements:

(i) Shoot and needle fascicles left in their natural position;

(ii) Needle fascicles arranged to form a plane of non-overlapping needles. This required the removal of some fascicles. The attached needles were held in a plane by taping the needles together at their tips and close to where they were attached to the twig.

The measurements of rate of net photosynthesis were made using the Licor 6000 Portable Photosynthesis System (Licor Inc. Nebraska, USA) with a 4-*l* assimilation chamber held horizontal. Each recorded value of rate of net photosynthesis was the mean of nine readings taken at 5-s intervals over 45 s. When the quantum flux density was low, the time steps were increased to 10 s. As the relationship between rate of net photosynthesis and incident quantum flux density is non-linear, measurements were discarded if the quantum flux density fluctuated by more than 10% while the nine readings were being taken.

To examine how needle arrangement affected rates of net photosynthesis, the projected area of the shoots (twig plus needles) on a horizontal plane was measured using an image analyser (Optomax System III). The shoots were held under the image analyser as they would have been positioned on the tree. The total surface area of the fascicles was determined by the volume displacement technique (Beets 1977). The fascicles were oven-dried at 80°C until a constant weight was reached; they were then weighed and specific leaf area (total surface area/oven-dry weight) was calculated.

While rates of net photosynthesis can be modelled at many levels, e.g., the single chloroplast, the whole leaf, and the whole plant or crop, Thornley (1976) contended that a simple, probably empirical, model of leaf photosynthesis would be suitable for modelling whole plant photosynthesis. Two equations which have been used to predict the rate of net photosynthesis of leaves from incident quantum flux density are the rectangular hyperbola (Eqn 1) and the non-rectangular hyperbola (Eqn 2) (Thornley 1976). Both these equations have been fitted to the data collected for each needle arrangement.

$$P_n = \frac{a\,b\,Q}{a + b\,Q} - R \qquad (1)$$

$$P_n = \frac{b\,Q + a - \sqrt{(b\,Q + a)^2 - 4\,\theta\,a\,b\,Q}}{2\,\theta} - R \qquad (2)$$

where: P_n is the rate of net photosynthesis

Q is the quantum flux density

a, b, and θ are parameters.

R is the rate of respiration occurring concurrently with photosynthesis.

According to Thornley (1976) the non-rectangular hyperbola can be deduced from a mechanistic model of photosynthesis for a planar leaf. However, when the rate of net photosynthesis is measured on a coniferous shoot where there is mutual shading between the individual needles, a non-rectangular hyperbola will not be a mechanistic model of shoot photosynthesis and may not necessarily be more appropriate than a rectangular hyperbola for predicting rates of net photosynthesis.

Daily crown net photosynthesis was estimated on a sunny day for a tree within an 11-year-old stand of *P. radiata* at Puruki with 170 stems/ha using the more appropriate of Eqn 1 and 2 for both needle arrangements (i) and (ii), and using both methods (a) and (b) to link equations predicting the rate of net photosynthesis with the radiative transfer model. Each tree was assumed to be the same size (17.5 m tall). The tree crown was assumed to be a truncated ellipsoid. The maximum width of the crown in both horizontal directions was 6.8 m and the length of the crown was 14.8 m. The leaf area index was 2.6.

Results

The values of the parameters from fitting both Eqn 1 and 2 to data from arrangements (i) and (ii) separately are shown in Table 1. There was no obvious pattern when the residuals (actual – predicted value) were plotted against predicted values. For arrangement (i), the residuals for Clone 266.345 tended to be negative while those from Clone J100/64 tended to be positive and those from Clone 850.451 were in between. The above pattern could be explained by the fact that the ratio of shoot projected area to surface area of foliage in shoot (l_r) varied between shoots and that the residuals increased as l_r increased. For arrangement (ii) there was no obvious pattern when the residuals were plotted against both fitted values and l_r. There were no obvious differences between the three clones.

TABLE 1—Estimated values for the parameters of the rectangular hyperbola (Eqn 1) and non-rectangular hyperbola (Eqn 2) and their standard errors for shoots which have been left in their natural arrangement or arranged as a plane

Parameter	Needle arrangement	
	(i) Natural	(ii) Plane
Rectangular hyperbola (Eqn 1)		
a (µmol/m²/s)	8.14 ± 0.49	9.69 ± 1.43
b (dimensionless)	0.0189 ± 0.0060	0.0286 ± 0.017
R (µmol/m²/s)	1.02 ± 0.70	1.47 ± 1.80
Residual mean square	0.243	0.459
Non-rectangular hyperbola (Eqn 2)		
a (µmol/m²/s)	7.63 ± 1.88	9.06 ± 4.98
b (dimensionless)	0.015 ± 0.013	0.022 ± 0.046
θ (dimensionless)	0.28 ± 0.88	0.22 ± 1.61
R (µmol/m²/s)	0.71 ± 1.21	0.94 ± 4.17
Residual mean square	0.247	0.466

The value of θ (Eqn 2) was not significantly different from zero. Also the residual mean square from fitting Eqn 1 was smaller than that from fitting Eqn 2, indicating that the rectangular hyperbola is more appropriate than the non-rectangular hyperbola for describing the relationship between rate of net photosynthesis and incident quantum flux density for *P. radiata* shoots. The shapes of the two rectangular hyperbolae, together with the field data, are shown in Fig. 2.

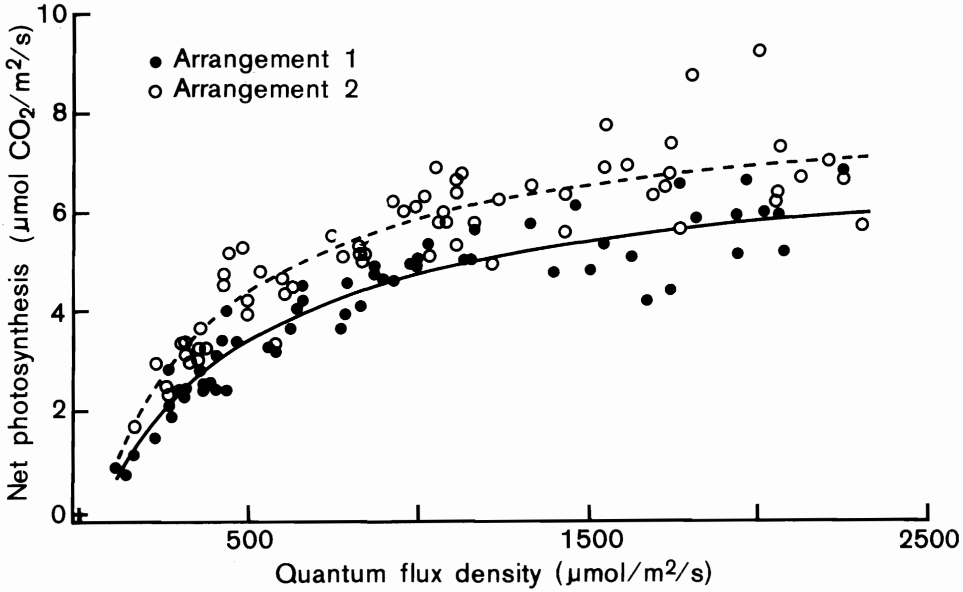

FIG. 2—Shapes of rectangular hyperbolae fitted to data collected in needle arrangement study.

Net photosynthesis for a tree crown was estimated for a sunny day using both methods of linking equations predicting rates of net photosynthesis with radiative transfer models and both sets of coefficients for the rectangular hyperbola (Table 1). The results (Table 2) show that the estimate of net photosynthesis for a tree is highly

TABLE 2—Estimated daily net photosynthesis (mol CO_2) for one tree crown within a stand with 170 stems/ha on a sunny summer day. Values have been estimated using the two methods of linking radiative transfer models to rates of net photosynthesis, and the two methods of arranging needles (see text for details)

	Needle arrangement	
	(i) Natural	(ii) Plane
Method (a)	35	44
Method (b)	48	61

dependent on the linkage method used. Using linkage method (b) rather than method (a) increases the estimate of net photosynthesis for a tree by about 40%. Theoretically, linkage method (a) with shoot arrangement (ii) and linkage method (b) with shoot arrangement (i) should provide realistic estimates of canopy photosynthesis. These two methods do give similar estimates of net photosynthesis for a tree crown (Table 2), 44 or 48 mols CO_2 per tree per day. If the incorrect linkage is used then net photosynthesis is either over-estimated by about 40% or under-estimated by about 30%.

VARIATION IN RATES OF NET PHOTOSYNTHESIS WITHIN TREE CROWNS

Methods

In 1984 measurements of rates of net photosynthesis were collected on shoots (containing only one age-class of foliage) throughout the crowns of 11-year-old *P. radiata* in sub-catchment Toru at Puruki (38° 26′ S, 176° 13′ E). These data have been used to examine the effect of including specific leaf area, l_s, in equations predicting the rate of net photosynthesis to represent the variation in rates of net photosynthesis within tree crowns due to morphology and physiology of individual shoots.

Within sub-catchment Toru, there were approximately 540 stems/ha. The mean tree height, during winter 1984, was 14.8 m with a crown length of 11.9 m. For further details of the stand structure *see* Beets & Brownlie (1987). Ten trees growing adjacent to a narrow track were sampled using a mobile elevated platform which gave access to the tree crowns up to a height of about 12 m. The crowns were subjectively divided into "sun" and "shade" portions with the latter being approximately the lower third of the crown. Rates of net photosynthesis were measured on fully expanded 0- to 1-, 1- to 2-, and 2+-year-old needles on second-order branches. Rates of net photosynthesis were also measured on first-, second-, and third-order branches with fully expanded 0- to 1-year-old foliage. There were three replicates of each sample type from both "sun" and "shade" portions of the crown.

Rates of net photosynthesis were measured with the needle fascicles in their natural position using the Licor 6000 Portable Photosynthesis System with a 4-*l* chamber held horizontal. The measurements were made during the first week of each month between January and June inclusive. Each month the shoots used were harvested, and the total surface area of the needles was determined using the volume displacement technique (Beets 1977). The fascicles were then oven-dried at 80°C until a constant weight was reached; they were then weighed, and their specific leaf areas were calculated. There were 616 observations of rates of net photosynthesis.

The data collected on 0- to 1-year-old foliage on different branch orders were first examined to see if there was any significant effect of branch order. Since an analysis of variance on the rates of net photosynthesis for which the incident quantum flux density was over 1000 μmol/m/s (i.e., above saturation level for photosynthesis) indicated that there was no significant difference between rates of net photosynthesis of foliage on branches of different orders, all observations were considered together.

To investigate how rates of net photosynthesis varied with specific leaf area, l_s, the parameters of Eqn 1 were calculated with the data split into the following classes of l_s in square centimetres per gram:

$100 < l_s \leq 125$
$125 < l_s \leq 140$
$140 < l_s \leq 160$
$160 < l_s \leq 180$
$180 < l_s \leq 220$
$220 < l_s \leq 300$.

The values of a, b, and R (Eqn 1) were plotted against the mid-point l_s for the different classes to determine an appropriate form for an equation containing l_s. An equation, including l_s, was then fitted to all the data, and residuals were plotted against fitted values, l_s, vapour pressure deficit, stomatal conductance, temperature, quantum flux density, needle age, sun/shade foliage, and month number to determine whether the equation could be improved by including any other variables.

Results

When the estimated values of a, b, and R (Eqn 1) were plotted against the mid-point l_s for each respective class (Fig. 3), both a and b were found to decrease approximately exponentially with increasing l_s, while there was no obvious relationship between R and l_s. Equation 3 was then fitted to all the data:

$$P_n = \frac{a \exp(-y_1 l_s) \; b \exp(-y_2 l_s) \; Q}{a \exp(-y_1 l_s) + b \exp(-y_2 l_s) \; Q} - R \qquad (3)$$

where: P_n is the rate of net photosynthesis
Q is the incident quantum flux density
l_s is the specific leaf area
R is the rate of respiration occurring concurrently with photosynthesis
a, b, y_1 and y_2 are parameters.

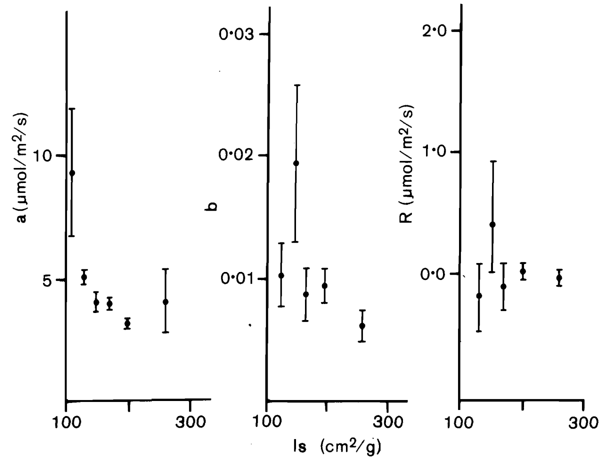

FIG. 3—Parameter estimates and their standard error when the rectangular hyperbola (Eqn 1) was fitted to data on rates of net photosynthesis.

Since the estimated values of y_1 and y_2 (Table 3) were not significantly different, Eqn 3 could be simplified to:

$$P_n = \frac{\exp(-y\, l_s)\, a\, b\, Q}{a + b\, Q} - R \quad (4)$$

where: P_n is the rate of net photosynthesis
Q is the incident quantum flux density
R is the rate of respiration occurring concurrently with photosynthesis
a, b, and y are parameters.

TABLE 3—Estimated values of the parameters of Eqn 3 and their standard errors

a (μmol/m²/s)	10.39 ± 1.75
b (dimensionless)	0.0281 ± 0.0070
y_1 (g/cm²)	0.00595 ± 0.00113
y_2 (g/cm²)	0.00566 ± 0.00164
R (μmol/m²/s)	0.00405 (no standard error estimated due to singularity)
Residual mean square	0.318

When Eqn 4 was fitted to the data, the estimated value of R was negative which is theoretically impossible. Hence, the values of a, b, and y were recalculated with R equal to 0.004, the estimated value of R in Eqn 3. The parameter values for Eqn 4 are shown in Table 4. When the residuals from fitting Eqn 4 with R=0.004 were plotted against fitted values, l_s, vapour pressure deficit, stomatal conductance, temperature, quantum flux density, needle age, sun/shade foliage, and month, the only variable for which there was any pattern in the residual plot was vapour pressure deficit. Since there was no pattern when the residuals were plotted against needle age or sun/shade foliage, using l_s overcomes the need to have separate light response curves for both sun and shade foliage. It also takes into account any change in light response curves with increasing needle age.

TABLE 4—Estimated values of the parameters of Eqn 4 and their standard errors

	R estimated	R = 0.004
a (μmol/m²/s)	10.25 ± 0.85	10.24 ± 0.85
b (dimensionless)	0.0288 ± 0.0026	0.029 ± 0.003
y (g/cm²)	0.00585 ± 0.00058	0.0058 ± 0.0005
R (μmol/m²/s)	−0.0005 ± 0.0634	
Residual mean square	0.317	0.316

To examine the effect of vapour pressure deficit (D) on rates of net photosynthesis, the data were split into the following classes according to D in kilopascals:

$D \leq 0.2$
$0.2 < D \leq 0.4$
$0.4 < D \leq 0.6$
$0.6 < D \leq 0.8$

and Eqn 4 was fitted to the data in each class. The results (Fig. 4) indicate that D affects only the parameter "a". The relationship between a and D appears to be linear; however, the range of D in the data set is narrow, and published data (e.g., Bennett & Rook 1978) have shown an exponential relationship. For these reasons both Eqn 5 and 6 were fitted to the data.

$$P_n = \frac{\exp(-y\, l_s)\, a\,(1 - z\,D)\, b\,Q}{a\,(1 - z\,D) + b\,Q} - R \qquad (5)$$

$$P_n = \frac{\exp(-y\, l_s)\, a \exp(-z\,D)\, b\,Q}{a \exp(-z\,D) + b\,Q} - R \qquad (6)$$

where: P_n is the rate of net photosynthesis
Q is the incident quantum flux density
l_s is the specific leaf area
R is the rate of respiration occurring concurrently with photosynthesis
D is the vapour pressure deficit
a, b, y, and z are parameters.

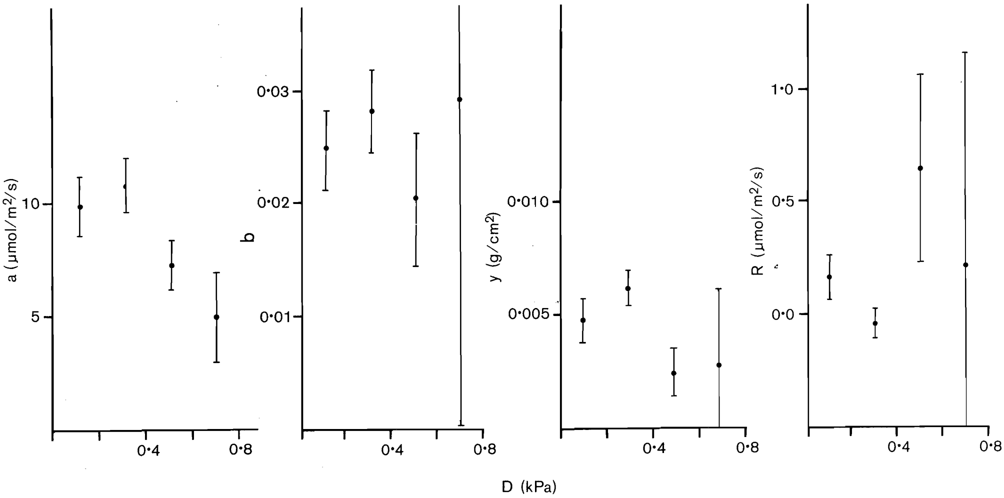

FIG. 4—Parameter estimates and their standard error when Eqn 4 was fitted to data on rates of net photosynthesis.

The parameter estimates for Eqn 5 and 6 are shown in Table 5. There was no obvious pattern when the residuals were plotted against fitted values, l_s, D, stomatal conductance, temperature, quantum flux density, needle age, sun/shade foliage, or month. This indicates that either Eqn 5 (linear function of D) or Eqn 6 (exponential function of D) is suitable for predicting rates of net photosynthesis at any point within a tree canopy. We have chosen to use Eqn 6 in preference to Eqn 5 for estimating canopy net photosynthesis as Eqn 6 can accommodate all values of D whereas Eqn 5 can only accommodate D values of 2 or less (Table 5).

TABLE 5—Estimated values of the coefficients of Eqn 5 and 6

	Equation 5	Equation 6
a (μmol/m²/s)	11.30 ± 0.82	11.47 ± 0.84
b (dimensionless)	0.0232 ± 0.0020	0.0232 ± 0.0020
y (g/cm²)	0.00497 ± 0.00049	0.00496 ± 0.00049
z (1/kPa)	0.488 ± 0.049	0.604 ± 0.078
Residual mean square	0.291	0.292

CANOPY PHOTOSYNTHESIS

Methods

To use any of Eqn 3 to 6 in a model predicting canopy net photosynthesis, the variation in specific leaf area, l_s, within tree crowns needs to be known. Data on the variation in l_s within tree crowns at Puruki are available from 1983 to 1985 (Beets & Lane 1987), and these data were used to derive equations predicting the variability of l_s within tree crowns. These equations form part of the model predicting rates of net photosynthesis. Using the radiative transfer model of Grace *et al.* (1987) with linkage method (b) and Eqn 6, annual canopy net photosynthesis was then calculated for three stands. The stands represent a 5-year-old stand at Puruki with 1960 stems/ha, a 9-year-old stand at Puruki with 495 stems/ha, and an 11-year-old stand with 160 stems/ha (Table 6). In running the model it was assumed that all trees were the same

TABLE 6—Details of stand structure and estimates of annual net photosynthetic production for three stands of *Pinus radiata* at Puruki

	Stand 1	Stand 2	Stand 3
Age (years)	5–6	9–10	11–12
Stems/ha	1950	495	160
Mean tree height (m)			
Initial	5.3	13.4	18.1
Final	6.2	14.3	19.4
Crown shape (breadth x width x height) (m)			
Initial	2.4 x 2.4 x 4.8	4.8 x 4.8 x 10.9	6.8 x 6.8 x 15.4
Final	2.4 x 2.4 x 5.7	4.8 x 4.8 x 11.6	7.3 x 7.3 x 16.4
Leaf area index (one-sided)			
Initial	6.4	5.6	2.0
Final	10.5	5.7	3.3
Net photosynthesis (t C/ha/yr)	23.2	27.6	20.5
Above-ground dry matter production (t dry matter/ha/yr)	28.4	28.2	20.9

Note: Values of above-ground dry matter production from Beets & Pollock (1987).

size, regularly spaced, with the foliage randomly distributed throughout ellipsoidal crowns .The leaf areas and crown lengths were obtained from annual biomass measurements (Beets & Pollock 1987), and crown widths were interpolated from field data. To account for the growth of trees during the year, the initial tree size was used for the first 6 months, and the final tree size for the rest of the year. Meteorological data collected in the actual years (R. Brownlie, unpubl. data) were used to drive the model.

To investigate the importance of l_s and D on the estimate of annual canopy net photosynthesis, Eqn 1 was fitted to all the data collected at Puruki and annual canopy net photosynthesis for Stand 3 (Table 6) was estimated using this equation as well.

Sensitivity analysis was used to investigate the variability in the estimate of annual canopy net photosynthesis due to the uncertainty in the values of the parameters in Eqn 6. One hundred sets of random numbers from a 4-variate normal distribution were derived using the mean and variance of the parameter estimates, and the correlation matrix between the parameter estimates. For Stands 1 and 3 (Table 6), estimates of annual canopy net photosynthesis were obtained for each set of random numbers and compared with the estimate obtained using the actual parameter estimates (cf. Huson 1984).

Results

When the data on l_s within tree crowns at Puruki were analysed, the most obvious trend was for l_s to decrease with increasing height from the ground. There was no consistent effect of thinning and stocking between sub-catchments. Hence, it was decided to combine all data for a given-aged foliage and derive one equation to predict the change in l_s within a tree crown. The equations derived were:
for 1-year-old foliage

$$l_{s1} = 230.85 - 9.65\ H + 0.1720\ H^2 \qquad (7)$$

for 2-year-old foliage

$$l_{s2} = 198.66 - 6.77\ H + 0.0695\ H^2 \qquad (8)$$

where: H is the height of the shoot above ground level
l_{s1} is the specific leaf area of 1-year-old foliage
l_{s2} is the specific leaf area of 2-year-old foliage.

These equations have been included in the model predicting rates of net photosynthesis. As there were few data points for foliage older than 2 years, the equation for 2-year-old foliage has been assumed to apply for foliage older than 2 years.

Annual canopy net photosynthesis for the three stands ranged from 20.5 to 27.6 t C/ha while annual dry matter production (Beets & Pollock 1987) varied between 20.9 and 28.4 t dry matter/ha.

The parameter estimates when Eqn 1 was fitted to all the data collected at Puruki are shown in Table 7. By comparing the residual mean square with those in Tables 4 and 5, it can be seen that including both l_s and D has improved the fit of the equation. Using the initial size for Stand 3 (Table 6) and meteorological data for 1985 (R. Brownlie, unpubl. data), the difference in annual canopy net photosynthesis using

TABLE 7—Estimated values for the parameters for the rectangular hyperbola (Eqn 1) and their standard errors when fitted to data on rates of net photosynthesis on *Pinus radiata* shoots at Puruki

a (μmol/m^2/s)	4.55 ± 0.10
b (dimensionless)	0.0136 ± 0.0012
R (μmol/m^2/s)	0.197 ± 0.077
Residual mean square	0.391

Eqn 1 or Eqn 6 was less than 1%. Also there was little change in the distribution of photosynthesis within the crown (Fig. 5) and within the year (Fig. 6).

The effect of the uncertainty in the values of the parameters in Eqn 6 on the estimate of annual canopy net photosynthesis was evaluated by calculating the percentage of the 100 estimates of annual canopy net photosynthesis which differed by more than 5%, 10%, and 20% from the estimated value obtained using the actual parameter estimates. For the 5-year-old stand only 10 out of the 100 estimates of annual canopy net photosynthesis differed by more than 5% from the original estimate and none by

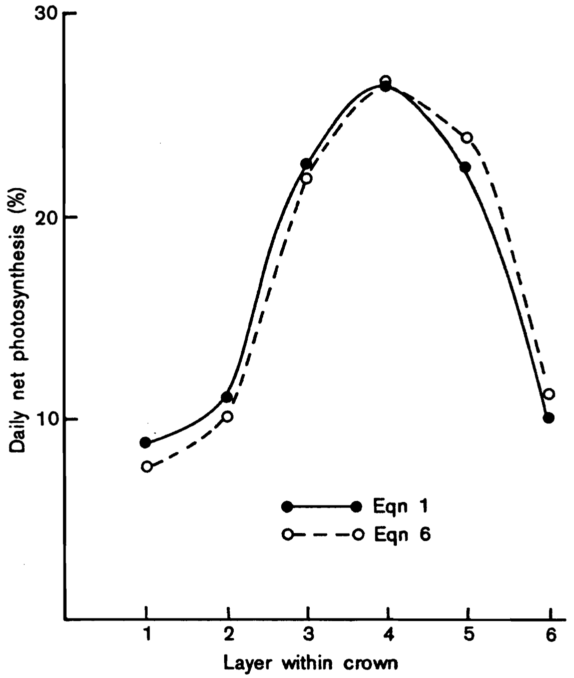

FIG. 5—Distribution of daily net photosynthesis within the tree crown for Stand 3 on a sunny summer day using Eqn 6 or Eqn 1 to estimate shoot net photosynthesis.

more than 10%. For the 11-year-old stand only one of the estimates differed by more than 5%. These results indicate that the uncertainty in the parameter estimates will not cause large variations in the estimate of annual canopy net photosynthesis.

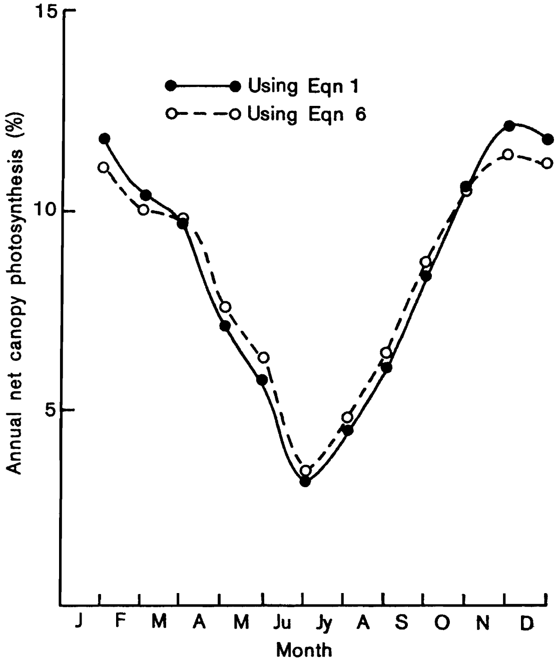

FIG. 6—Distribution of annual canopy net photosynthesis by month using Eqn 6 or Eqn 1 to estimate shoot net photosynthesis.

DISCUSSION

In simulating forest growth using process-based models it is essential to have a sound model for estimating canopy net photosynthesis since it provides the estimate of the amount of carbon available for respiration and growth. Currently it is not possible to validate such models by measuring canopy photosynthesis directly; hence, they must be evaluated on whether the assumptions are realistic, and whether the amount of carbon produced is sufficient for respiration and dry matter production. In this paper we have presented a model for estimating canopy net photosynthesis from rates of shoot net photosynthesis and a radiative transfer model. In evaluating this model the assumptions in linking equations predicting the rate of net photosynthesis with the radiative transfer model, and the assumptions in the equations predicting rates of net photosynthesis must be examined, as well as whether it provides realistic estimates of canopy net photosynthesis. An alternative approach which can be used to provide an estimate of canopy net photosynthesis, without measuring shoot net photosynthesis, is the eddy correlation method. Although both methods give similar estimates of canopy net photosynthesis (Baldocchi *et al.* 1987), the advantage of the first approach is that the distribution of net photosynthesis within the canopy can be estimated and hence the model can be used to simulate the effect of different management practices, e.g., thinning or pruning, on canopy net photosynthesis.

Results of the needle arrangement study emphasise the importance of ensuring that the way rates of net photosynthesis are measured matches the assumptions used to link the radiative transfer model with equations predicting rates of net photosynthesis. Similar estimates of canopy net photosynthesis (Table 2) can be obtained from

(a) Measuring rates of net photosynthesis on a plane of non-overlapping needles, and accounting for the different needle orientations in the radiative transfer model;

or

(b) Measuring rates of net photosynthesis on shoots with the needles in their natural arrangement and estimating the average quantum flux density at different points within the canopy.

Canopy photosynthesis can be over- or under-estimated by about 40% or 30% respectively, if incorrect assumptions are made.

Consideration needs to be given to whether method (a) or (b) is more appropriate for measuring rates of photosynthesis and estimating canopy net photosynthesis. Both methods have merit. The planar arrangement of needles is more suitable where the effect of some factor (e.g., nutrition or defoliation) on the photosynthetic process *per se* is being examined, while the natural arrangement of needles is preferable where morphological factors are important, e.g., density of foliage per unit shoot length. Since nutrition affects both the process of photosynthesis and shoot morphology, these individual effects could be quantified using the two shoot arrangements.

Although there is a considerable body of information on rates of net photosynthesis for individual shoots of *P. radiata* under different environmental conditions (e.g., Rook 1969; Bennett & Rook 1978; Benecke 1980; Attiwill & Cromer 1982) and of different ages (e.g., Rook & Corson 1978), such studies have of necessity considered only a limited range of shoot types and environmental conditions. The availability of portable photosynthesis systems allowing a wide range of shoot types to be sampled facilitates the development of realistic models of canopy net photosynthesis. However, to be able to use such data in developing a model of canopy net photosynthesis, one needs to know objectively how rates of net photosynthesis will vary throughout the crown.

Although the current study indicates that l_g can account for the variation in rates of net photosynthesis due to needle age and position within the crown, l_g should not be regarded as directly causing changes in the rates of net photosynthesis; l_g is, however, correlated with variables which directly affect the rate of net photosynthesis. For example, Lewandowska *et al.* 1977 have related photosystem I and II activity to l_g.

To evaluate whether the estimates of net photosynthesis (Table 6) are realistic, one needs to be able to convert from dry matter to carbon. Mohren (1987, p. 72) indicated that the carbon content of dry matter in Douglas fir is on average 0.52 kg C/kg dry matter while Landsberg (1986, p. 89) suggested that assimilated CO_2 may be converted to dry matter by multiplying by 28.5 g/mol, giving a carbon content of

0.42 kg C/kg dry matter. Although the latter conversion factor is a general average (Landsberg 1986), there is a 20% difference between these two conversion factors, indicating a need for the carbon content of dry matter to be investigated for the different components of *P. radiata*. Using the conversion factor of 0.52, between 35% and 46% of the carbon produced by photosynthesis will be available for below-ground growth and respiration. If the conversion factor of 0.42 is used, between 48% and 56% of the carbon will be available (Table 6).

Rook *et al.* (1985) suggested that respiration can account for 30–50% of the carbon produced, while root growth can account for 23–78% of annual dry matter production. At Puruki, total root production was estimated to be between 22% and 31% of total production in 11- to 12-year-old stands with 570 stems/ha and 170 stems/ha respectively (D. Santantonio, pers. comm.).. Assuming that root production accounted for 31% of total production in Stand 3, then total dry matter production would be 30.3 t. In terms of carbon this would be 12.7 or 15.8 t C depending on the conversion factor used, leaving 38% or 23% of the carbon for respiration. These estimates of carbon available for respiration do not appear to be unrealistic, particularly as Puruki has cool night temperatures (R. Brownlie, unpubl. data).. The sensitivity analysis indicates that the uncertainty associated with the parameter estimates will not unduly affect the estimate of net photosynthesis. Taken together these results suggest that the model presented in this paper is realistically predicting canopy net photosynthesis.

Since the ratio of above-ground dry matter production to carbon produced is similar in all three stands (Table 6) it is reasonable to assume that the estimates of canopy net photosynthesis are realistic for all three stands.

Including l_s and D in Eqn 6 alters the distribution of photosynthesis both within the tree crown (Fig. 5) and within the year (Fig. 6) compared with Eqn 1. The small difference in Fig. 6 will be due to the fact that high vapour pressure deficits rarely occur at Puruki (R. Brownlie, unpubl. data). On other sites with a greater range of vapour pressure deficits larger differences in the estimate of monthly net photosynthesis from Eqn 1 and from Eqn 6 can be expected.

Whether this model for predicting shoot net photosynthesis is equally applicable to all stands of *P. radiata* needs to be evaluated further. Firstly, it is not known whether the relationship between l_s and rates of net photosynthesis will be generally applicable, or whether other factors will be needed to account for the physiological and morphological state of the shoot in stands differing in age, genotype, or nutritional status. It is possible that l_s will account for such differences in *P. radiata* stands since l_s is known to vary with stand age (Beets & Lane 1987) and with site (M. Bollmann, unpubl data). The needle orientation study indicates that the variation in rates of net photosynthesis due to genotype can be explained by l_r which was correlated with l_s ($r=0.77$).

Secondly, environmental factors other than quantum flux density are known to influence the rate of net photosynthesis. In this study, the only environmental factor which was found to significantly affect rates of net photosynthesis once incident quantum flux density and l_s had been accounted for was vapour pressure deficit. Mechanistically the main effect of vapour pressure deficit on rates of net photosynthesis is through its effect on stomatal conductance (Bennett & Rook 1978); in this study, however, stomatal conductance was not found to be significantly correlated with rates of net photosynthesis once incident quantum flux density and l_s had been accounted for.

Rates of net photosynthesis have been found to be correlated with temperature (e.g., Jarvis & Sandford 1986). In this study measurements were taken only between January and June and the range in temperature was small (4.4°C to 18.8°C). Although frosts reduce rates of net photosynthesis (Neilson *et al.* 1972), during the period of measurement at Puruki there were no days when the minimum air temperature 2 m above the canopy was below 0°C. Generally such air temperatures are recorded only on about 5 days a year (R. Brownlie, unpubl. data). This is unlikely to significantly affect estimates of canopy net photosynthesis for a year at Puruki.

In conclusion, the model presented in this paper realistically estimates canopy net photosynthesis at Puruki, but further data need to be collected on shoot photosynthesis to evaluate whether the model will be applicable for trees of different ages and genotype, and for different sites.

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