

Corrigendum

Conversion of canopy intercepted radiation to photosynthate: a review of modelling approaches for regional scales

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The equation in Figure 1 as published was incorrect. The correct figure appears below.

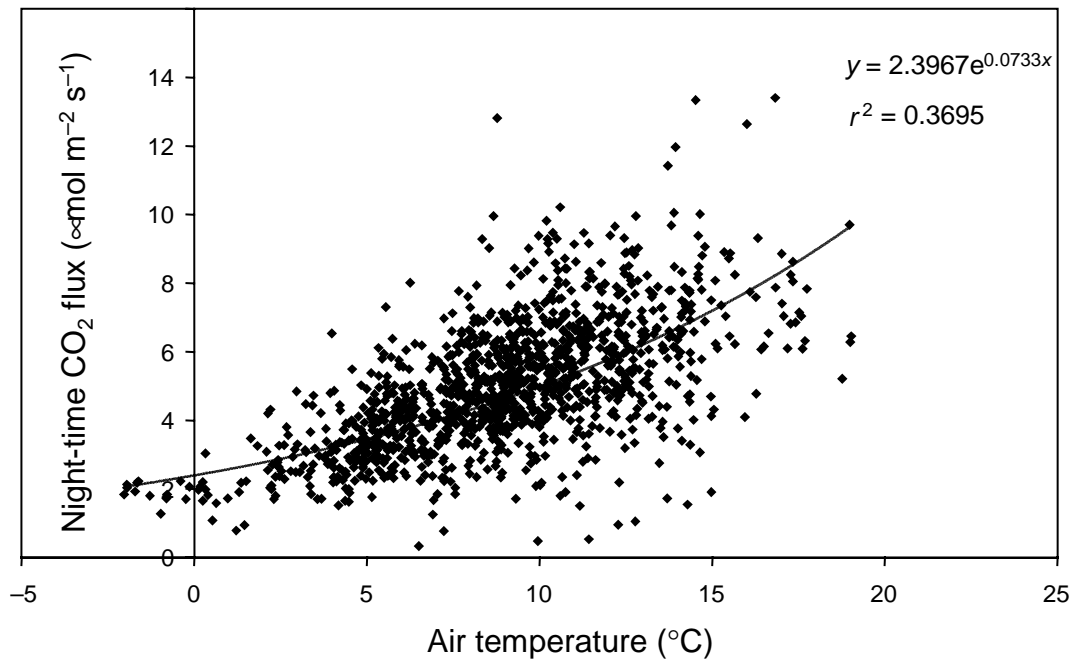


Fig. 1. Half-hourly night-time CO₂ flux data measured at Griffin forest, Scotland, plotted against air temperature. Summertime (May–August) values for periods when wind speed >3 m s⁻¹. The regression line shown was used to estimate daytime whole-ecosystem respiration.

Conversion of canopy intercepted radiation to photosynthate: review of modelling approaches for regional scales

Belinda Medlyn^A, Damian Barrett^B, Joe Landsberg^C, Peter Sands^D and Robert Clement^E

^ASchool of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia. Corresponding author; email: B.Medlyn@unsw.edu.au

^BCSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia.

^C22 Mirning Crescent, Aranda, Canberra, ACT 2614, Australia.

^DCooperative Research Centre for Sustainable Production Forestry and CSIRO Forestry and Forest Products, GPO Box 252–12, Hobart, Tas. 7001, Australia.

^EIERM, University of Edinburgh, King's Buildings, Mayfield Road, Edinburgh EH9 3JU, UK.

Abstract. A fundamental component of most models of terrestrial carbon balance is an estimate of plant canopy photosynthetic uptake driven by radiation interception by the canopy. In this article, we review approaches used to model the conversion of radiation into photosynthate. As this process is well understood at the leaf-scale, the modelling problem is essentially one of up-scaling, to canopy, regional or global scale. Our review therefore focuses on issues of scaling, including model identification, parameterisation and validation at large scales.

Four different approaches are commonly taken to modelling photosynthate production at large scales: the maximum productivity, resource-use efficiency, big-leaf, and sun-shade models. Models representing each of these approaches are discussed and model predictions compared with estimates of gross primary productivity derived from eddy covariance data measured above a Sitka spruce forest. The sun-shade model was found to perform best at all time scales considered. However, other models had significant advantages including simplicity of implementation and the ability to combine the model with remotely-sensed information on vegetation radiation interception. We conclude that all four approaches can be successfully used to model photosynthetic uptake and that the best approach in a given situation will depend on model objectives and data availability.

Keywords: canopy photosynthesis, model comparison, modelling, radiation, scaling.

Introduction

Physiologically-based models of plant production were developed only gradually over the 1960s and 1970s (Boote and Loomis 1991), but since the advent of fast, affordable and user-friendly computers in the early 1980s, their use has expanded dramatically. Plant production models are now applied in almost every area of whole-plant physiology. While early models were generally applied at the scale of individual plants or stands, advances in computer processing speeds and storage capacity now allow such models to be run at regional, continental, or even global scales. This advance has been driven by growing concern about global environmental problems such as the enhanced greenhouse effect. Models of net primary production (NPP) and net ecosystem exchange (NEE) at regional and continental

scales are key tools in summarising current theoretical understanding of the role of terrestrial vegetation in the global carbon (C) cycle and predicting future responses by the C cycle to climate change.

Of the large number of diverse models of plant production that have been developed in recent years, a number are suitable for studies at large spatial scales (e.g. Cramer *et al.* 1999). These models differ in many aspects, but have generally converged on a similar basic structure with two major steps: calculating how much photosynthate is available to the plant, and determining how it should be distributed between growth of various organs and other plant functions. The aim of this review is to discuss how the first step is modelled. In many models, the amount of photosynthate is largely determined by the amount of photosynthetically-active

Abbreviations used: APAR, canopy absorbed photosynthetically active radiation; AVHRR, advanced very high resolution radiometer; GCM, global climate model; GPP, gross primary production; LAI, leaf area index; NDVI, normalised difference vegetation index; NPP or P_n , net primary production; P_{max} , potential net primary production; PAR, photosynthetically-active radiation; RUE, radiation use efficiency; WUE, water use efficiency.

radiation (PAR) intercepted by the plant canopy. It has been argued that, particularly for regions such as Australia, water availability is a much stronger driver of photosynthate production than radiation. Models driven by water availability have been developed (Tanner and Sinclair 1983) but have, to date, rarely been applied at regional scale (but see Raupach *et al.* 2001). It is more common for the influence of water availability to be modelled as a factor modifying the rate of radiation-driven production (Eamus 2003). In this review, we therefore focus on the process of conversion of radiation to photosynthate.

The calculation of available photosynthate in plant production models is essentially a scaling problem. The underlying process, the leaf photosynthetic response to light, has been studied in great detail and is generally well understood (Farquhar *et al.* 1980). The major outstanding issue is how to scale the short-term leaf-level response of photosynthesis to plant canopies, and thence to regions, from subdiurnal to annual time scales. This scaling up is not straightforward for two major reasons. Firstly, the leaf-level photosynthetic response is strongly non-linear: at low light levels photosynthesis responds almost linearly to increasing light, but it saturates as light levels approach full sunlight. Secondly, vegetation is inherently heterogeneous and so model parameters and forcing variables vary considerably within and between plant canopies. The interaction between non-linearity and heterogeneity makes scaling up photosynthesis from leaf to region a difficult task in practice. Our review focuses on the question of scaling, and associated issues such as model parameterisation and validation at large scales.

We begin by using a theoretical statistical framework developed previously (Raupach *et al.* 2002) to systematically examine the issues confronted when attempting to scale up a photosynthesis model developed at the leaf scale to make predictions at the regional scale. We then describe several different approaches commonly used to model plant photosynthetic uptake at large scales, and discuss how each approach tackles the challenge of scaling. Finally, we attempt to compare the performance and utility of the different approaches.

The scaling problem

The leaf-level response of photosynthesis to incident radiation can be expressed in a model of the form:

$$A = A(\mathbf{M}, \mathbf{P}), \quad (1)$$

where \mathbf{M} is a vector of forcing variables (light, temperature, etc.) and \mathbf{P} a vector of model parameters (maximum electron transport capacity, etc.), both measured at the same scale as A . To obtain large scale estimates of photosynthesis for a canopy, it is theoretically possible to apply this model repeatedly to all individual leaves, but two practical problems prevent this: there are insufficient data available

for parameterisation of the model for each leaf, and for large canopies it is computationally too expensive. Instead, the leaf-level model may be applied directly at the canopy scale as follows:

$$\bar{A} = A(\bar{\mathbf{M}}, \bar{\mathbf{P}}), \quad (2)$$

where the overbars signify means taken across the population of leaves. To investigate the conditions under which the equality in Equation 2 holds, we relate leaf and canopy scale photosynthesis using a Taylor expansion of A about the mean of \mathbf{M} and \mathbf{P} , and group terms into the statistical moments to get (Raupach *et al.* 2002):

$$\bar{A} \approx A(\bar{\mathbf{X}}) + 0.5 \sum_{i=1}^n \frac{\partial^2 A}{\partial \mathbf{X}_i^2} \sigma_i^2 + \sum_{i=1}^{n-1} \sum_{j=i+1}^n \frac{\partial^2 A}{\partial \mathbf{X}_i \partial \mathbf{X}_j} \sigma_i \sigma_j \rho_{ij}, \quad (3)$$

where $\mathbf{X} = (\mathbf{M}, \mathbf{P})$, and σ_i and ρ_{ij} quantify standard deviation of and correlation among the i^{th} and j^{th} forcing variables and parameters \mathbf{M} and \mathbf{P} . Equation 3 shows that the equality in Equation 2 is exact only when the second and third terms on the RHS of Equation 3 equal zero. These two terms, referred to as the ‘bias terms’ (Raupach *et al.* 2002), describe how the presence of non-linearity in the leaf scale photosynthesis model interacts with the covariance among parameters and forcing variables to introduce error into estimates of canopy photosynthesis based on the mean values of \mathbf{M} and \mathbf{P} .

From Equation 3 we can state four general conditions for the bias terms to approach zero. Firstly, if the model is linear, there is no bias because the partial differentials in each term are zero. Secondly, where variation in \mathbf{M} and \mathbf{P} is small, the standard deviations σ_i are small and so the bias terms are insignificant. Thirdly, if the \mathbf{M} and \mathbf{P} are independent, then the correlation coefficients ρ_{ij} are zero and the third term on the RHS of Equation 3 disappears. Fourthly, the second and third terms on the RHS may (depending on the model or covariance or both) approximately cancel one another such that model predictions at the large scale are unbiased. None of these four conditions is met in the case of canopy photosynthesis on short timescales (e.g. hours). The fine scale model of leaf photosynthesis is non-linear, so the partial differentials are not equal to zero. Under natural conditions, variation in \mathbf{M} and \mathbf{P} through the canopy is likely to be large. Also, parameters and variables are known to be correlated through the canopy (e.g. average irradiance and nitrogen concentration of leaves in a canopy are correlated with light-saturated photosynthesis — see below) and so the bias terms will be significant. Thus, a canopy treated as a single ‘big leaf’ having average properties for \mathbf{M} and \mathbf{P} will generate erroneous estimates of canopy photosynthesis because the bias terms cannot be ignored.

This statistical approach summarises some of the problems faced when attempting to upscale photosynthesis from leaf to canopy. In addition to model identification (finding an appropriate functional form of the model), characterising means, variances and co-variances of param-

eter values across the model domain is a key problem. A further question is that of validation, or verification that our scaled estimates are correct. Below, we discuss several common approaches to modelling canopy photosynthetic uptake at large scales, and examine how each approach tackles these problems of up-scaling.

Approaches to modelling canopy photosynthesis

We have identified four major modelling approaches used at large scales; these are the ‘maximum productivity’ approach, the ‘radiation-use efficiency’ (RUE) approach, the ‘big-leaf’ approach, and the ‘sun-shade’ approach. The development, theory and implementation of each of these models is described below. Many, but not all, models use one of these four approaches. Table 1 gives examples of models that fall into each these four classes. Some of the models explicitly calculate both gross primary production (GPP) and respiration, whereas others only calculate NPP. The distinction between models calculating GPP and those calculating NPP lies with the treatment of respiration, not the underpinning theory of light interception and photosynthesis. Variations on the four major approaches considered here are also possible, and we briefly discuss the variations used by three other well-known models of regional-scale plant production.

The maximum productivity model

The maximum productivity model is the simplest of the four approaches. It does not directly use radiation interception to calculate photosynthate production. Instead, the maximum productivity is specified for each crop or tree species. Actual production is calculated by reducing this maximum for adverse environmental factors, such as non-optimal temperature, inadequate water availability or nutrition and self-shading of canopy leaves.

The widely-used CENTURY model (Parton *et al.* 1987; 1993) illustrates this approach. In CENTURY, potential net primary production (P_{\max}) is specified for each species or functional type. Actual NPP is calculated by reducing P_{\max} by scalars that depend on soil temperature, moisture status, self-shading and nutrient availability. The effect of self-shading is represented for grasses as a linearly increasing function of the live:dead ratio of foliage (Parton *et al.* 1993). For trees, this effect is represented as a saturating function of leaf area index (LAI) (Hilinski 2001), which is similar to the Beer’s Law approach used to calculate the fraction of radiation intercepted in several other models (see Equation 8, below).

The maximum productivity approach is used in CENTURY because it was originally developed as a model of soil organic matter dynamics. The model’s monthly time-step is dictated by the timescale of humification processes governing soil organic matter formation. With this focus on soil C turnover processes, it is argued that an elaborate plant production model is unnecessary (Parton *et al.* 1993). However, the omission of incident radiation means that the model will not simulate differences between sites caused by different incoming radiation, or responses to future changes in radiation such as variation in the ratio of direct to diffuse radiation (Roderick *et al.* 2001).

Differences between sites can to some extent be captured by calibration of the potential net primary production, P_{\max} . Since production in the field rarely reaches its maximum value, values of P_{\max} are generally obtained by model calibration against observations of net primary productivity. Values given in the literature include P_{\max} of 250 g C m⁻² month⁻¹ for grasses (Parton *et al.* 1996) and 300 g C m⁻² month⁻¹ for forests (Peng *et al.* 1998). For crops, values range from 200 g C m⁻² month⁻¹ for sorghum and up to 650 g C m⁻² month⁻¹ for high-yielding corn (S. Del Grosso, pers. comm.). An alternative method to

Table 1. Examples of large scale models using different approaches to modelling radiation conversion
Ecosystem column lists the type of ecosystems for which the model was originally developed. ‘All’ in parentheses means that the model has now been applied to all ecosystem types

Model	Approach	Output	Time-step	Ecosystem
CENTURY	Maximum productivity	NPP	Monthly	Grasslands (All)
3-PG	RUE	GPP	Monthly	Forests
VAST	RUE	NPP	Monthly	All
CASA	RUE	NPP	Monthly	All
PROMOD	Big-leaf	GPP + WUE	Daily	Forests
HYBRID	Big-leaf	GPP	Daily	All
SIB2	Big-leaf	GPP	Minutes	All
CBM	Sun-shade	GPP	Hourly	All
G'DAY	Sun-shade	GPP	Daily	Forests (All)
TEM	Hyperbolic	GPP	Monthly	All
PnET	Numerical integration	GPP	Monthly	Forests
IBIS	Simple sun-shade	GPP	Hourly	All

calibration would be to assume that the maximum net production is given by the upper values recorded in very large databases of production. The pros and cons of this methodology are discussed by Bragg (2001), who used this method to estimate maximum yearly diameter growth of woody species.

The CENTURY model has been tested at site scale using data from a wide range of sites, including grasslands (Parton *et al.* 1996; Gilmanov *et al.* 1997) and forests (Peng *et al.* 1998). The types of data used to test the model include above-ground biomass, above-ground plant production, soil carbon and nitrogen contents, and net N mineralisation. The tests showed that the model performed adequately, with error terms generally less than $\pm 25\%$ of observations (Parton *et al.* 1996). However, the data used for parameterisation and those used for validation were not, in general, independent (Gilmanov *et al.* 1997), so these tests cannot be regarded as rigorous evaluations of the model's performance.

The radiation use efficiency model

The radiation use efficiency model is based on work by Monteith (1977), who found a linear relationship between absorbed photosynthetically-active radiation (APAR) and annual above-ground crop productivity. This study suggested that productivity could be modelled by multiplying APAR by a constant parameter, known as the radiation use efficiency (RUE) and denoted ϵ . This approach greatly simplified data requirements of plant production models and Monteith's work was quickly followed by data showing its general applicability to both crops (Gallagher and Biscoe 1978; Legg *et al.* 1979) and forests (Jarvis and Leverenz 1983; Linder 1985).

While modelling productivity as a linear function of radiation interception is a simple concept, variation among studies on the units for ϵ has led to confusion (Landsberg *et al.* 1997; Gower *et al.* 1999). The RUE is generally calculated as the ratio of some measure of plant productivity to a measure of intercepted radiation. Plant productivity may be above-ground production, total net primary production, or GPP, expressed in terms of g C or g dry matter, while radiation may be intercepted or absorbed and may be solar radiation or PAR. We define the following terms for use in this paper:

$$\begin{aligned}\epsilon_g &= G_p/I_p \text{ (g C MJ}^{-1} \text{ PAR)}, \\ \epsilon_n &= P_n/I_p \text{ (g C MJ}^{-1} \text{ PAR)}, \\ \epsilon_a &= P_{n,a-g}/I_p \text{ (g C MJ}^{-1} \text{ PAR)},\end{aligned}\quad (4)$$

where G_p is gross primary productivity (total canopy photosynthetic uptake), P_n is net primary productivity, $P_{n,a-g}$ is above-ground net primary production, and I_p is absorbed PAR, all estimated over a time interval Δt . A relatively simple interconversion between the different forms of ϵ is

possible, as shown below, but it is important that a clear definition accompany each usage of the term to avoid confusion.

The terms ϵ_g and ϵ_n can be related as follows. Net primary production (P_n) is $G_p - R$, where R is autotrophic respiration. If we assume that P_n/G_p is a constant, c (Gifford, 2003), then $\epsilon_n = c\epsilon_g$. Also, net primary production (NPP) must be allocated to above-ground and below-ground growth, so above-ground NPP is

$$P_{n,a-g} = cG_p(1 - \eta_r), \quad (5)$$

where η_r is the allocation coefficient that determines the proportion of P_n going below-ground. Thus, $\epsilon_a = (1 - \eta_r)\epsilon_n = c(1 - \eta_r)\epsilon_g$.

An interesting question raised by the RUE model is how a non-linear process such as the leaf photosynthetic response to light can be successfully scaled-up to a linear model. It is important to note that the linear model is applicable only on time-scales of two weeks or more; both modelling studies and empirical data show that the relationship between productivity and radiation absorbed is non-linear on shorter time scales (Spitters 1990; McMurtrie and Wang 1993; Ruimy *et al.* 1995; Medlyn 1998). Two alternative hypotheses have been advanced to explain the observed linearity. The first is the simple argument that the process of integration over time tends to linearise the response curve, such that a proportional relationship is observed on an annual time scale (McMurtrie and Wang 1993; Sands 1996; Medlyn 1998). A second, more intriguing argument is the 'functional convergence' hypothesis, which postulates that interactions with other resource limitations determine a long-term linearity in the effects of light limitation on canopy photosynthesis (Goetz and Prince 1999). The hypothesis is quantified in models by Dewar (1996) and Haxeltine and Prentice (1996), who show that optimisation of LAI with respect to nitrogen availability results in a proportional relationship between canopy photosynthesis and absorbed radiation. This argument is supported by data from Runyon *et al.* (1994), who found that values of RUE were remarkably constant across a transect with a large gradient in both LAI and nitrogen availability.

The parameter ϵ must be estimated from relatively laborious experimental studies of stand-scale radiation interception and net primary productivity. Gower *et al.* (1999) have recently published a new table of values, corrected to provide standard estimates of ϵ_n (total NPP in g dry mass MJ⁻¹ APAR). In general, the reported values for C₃ crops are in the range 2–3 g dry mass MJ⁻¹ APAR; the values for grasslands and deserts are much lower, ranging from 0.04–2 g dry mass MJ⁻¹ APAR; and the values for forests are intermediate, with most temperate and boreal forests having values of less than 1 g dry mass MJ⁻¹ APAR. These values can be converted to the units used here,

g C MJ⁻¹ APAR, by dividing by two, since the C content of biomass approximates 50%.

One reason for the range in values of ϵ given by Gower *et al.* (1999) is that these empirical values reflect the constraints imposed on growth by insufficient water availability, nutrition and suboptimal temperature. Landsberg (1986) suggested that the relationship between absorbed PAR and photosynthate production should be modified by factors that describe the effect of environmental constraints, so that

$$P_n = \epsilon_n f_w f_N f_T I_p, \quad (6)$$

where f_w , f_N and f_T denote modifiers ranging from 0 to 1 that constrain the effective value of ϵ_n by soil water status, nutrition and temperature, respectively. In this model, ϵ_n represents the maximum value of RUE, a value that might be expected from vegetation with optimum canopy structure and no limitations to photosynthesis. Goetz and Prince (1999) provide evidence that unstressed values of ϵ_g should converge towards the quantum yield of photosynthesis. Jarvis and Leverenz (1983) and Russell *et al.* (1989) indicate a maximum value of ϵ_g of 4.5–5 g C MJ⁻¹ PAR. This value is seldom achieved, although it is of interest to note that Sands and Landsberg (2002) and Landsberg *et al.* (2002) find a value of 3.8 g C MJ⁻¹ PAR necessary to simulate the growth of short-rotation eucalyptus plantations supplied with ample water and nutrients.

Given the simplicity, ease of use, and availability of parameters of the RUE model, it is unsurprising that it has been incorporated into many regional-scale plant productivity models. Here we examine in detail three examples of such models, 3-PG, VAST, and CASA. Each of these three models was developed with a distinctly different objective, but the RUE approach is appropriate for all three objectives.

The 3-PG model, developed by Landsberg and Waring (1997), is a generalised forest stand model with a monthly time step, applicable to plantations or even-aged, relatively homogeneous forests. The objective of this model was to predict forest growth, in a manner suitable for forest management, based on physiological principles. Intercepted radiation is calculated using Beer's Law (Equation 8 below), and biomass production is determined by applying an effective canopy quantum efficiency (denoted α_c by Landsberg and Waring; ϵ_g in the notation used here) to I_p . ϵ_g is determined from a maximum value, constrained by atmospheric vapour pressure deficit through the effects of vapour pressure deficiency (VPD) on stomatal conductance and hence canopy conductance, and limited by air temperature, frost, water balance and nutrition. The maximum value of ϵ_g is taken to be 3.8 g C MJ⁻¹ for broad-leaf forests and 3 g C MJ⁻¹ for conifers. Some calibration of ϵ_g to a particular site is possible through the fertility index, which is an input multiplier assumed to reflect the site fertility. 3-PG has been extensively tested both as a stand model

(Landsberg *et al.* 2000; Sands and Landsberg 2002) and as a satellite driven-model providing estimates of forest productivity over large areas (Coops and Waring 2001a, b; Coops *et al.* 2001b). Used in this way, the model is driven by radiation measurements derived from ground stations and relationships with topography, latitude and time of year (Coops *et al.* 2000), radiation interception being calculated from the relationship between normalised difference vegetation index (NDVI), derived from satellite measurements, and LAI. Validation tests generally confirm that the model performs well (e.g. Coops *et al.* 1998), although the study by Tickle *et al.* (2001) demonstrates that model performance may be affected by bias in parameter values.

VAST (Barrett 2002) is a linear model of production, growth, mortality and decomposition of vegetation for the Australian continent at a resolution of 0.05° (~ 5 km). It uses a multi-objective optimisation approach coupled with a genetic algorithm search method to estimate model parameters based on available data of plant production, biomass, litter and soil carbon. The optimisation method fits production, partitioning and turnover parameters for three biomes (productive forests, open woodlands and arid shrublands) by minimising model-data deviations while maximising consistency between model prediction, all observations and prior information on parameters. Thus, predictions by VAST at the continental scale are constrained globally by the extensive and representative distribution of observations in all datasets (Barrett 2001; Barrett *et al.* 2001). NPP is predicted on monthly time steps using simple water balance and canopy light absorption sub-models. Relative soil moisture content is calculated as a function of rainfall, temperature and net radiation and is used to scale NPP linearly with water limitation. APAR is calculated monthly using NASA Pathfinder AVHRR data and short-wave radiation data. The parameterisation method yields estimates of unstressed (maximum) ϵ_n for the three biomes well supplied with water were 1.06, 1.00 and 0.55 g C MJ⁻¹ APAR for forests, woodlands and arid shrublands. Differences in maximum ϵ_n between biomes are due to nutrient limitations of the soil and any intrinsic differences in the physiology of photosynthesis between biomes.

The CASA model, developed by Potter *et al.* (1993), aimed to simulate the productivity of global ecosystems, making use of remotely-sensed information on intercepted radiation. The approach is based on Equation 6, with I_p calculated as a linear function of the simple ratio $(1 + \text{NDVI})/(1 - \text{NDVI})$, derived from satellite measurements. The value of ϵ_n was estimated by calibrating the model against NPP data from 17 locations throughout North and South America. After accounting for the effects of temperature and water stress, the unstressed value for ϵ_n was estimated to be 0.405 g C MJ⁻¹ PAR. Thompson and Randerson (1999) have tested CASA by comparing predictions of global atmospheric $\delta^{13}\text{C}$ composition against

measurements from the atmospheric NOAA–CMDL CO₂ concentration network. The isotopic disequilibrium of atmospheric ¹³C predicted by the model agreed well with observations from the network, increasing confidence that global predictions are constrained by atmospheric measurements. Local predictions require comparison with net ecosystem flux measurements made at instrumented towers.

The calculation of P_n by 3-PG, VAST and CASA is simple, being based on a linear relationship. They all have the advantage that they can be used to predict P_n over large areas, using satellite data to estimate I_p , and coarse resolution climate data to resolve water and nutrient budgets at week to month timescales. However, they do not perform well at shorter time and space scales and more complex models are required to resolve non-linearities between light, water and canopy photosynthesis at timescales of less than one month.

The big-leaf model

The big-leaf model is based on the assumption that the distribution of leaf photosynthetic capacity within the plant canopy is proportional to the distribution of time-averaged irradiance. This assumption allows the leaf photosynthetic response to radiation to be readily scaled to the canopy. The derivation of the big-leaf model is given by Sands (1995b) and Sellers *et al.* (1992). Briefly, this derivation runs as follows. Leaf photosynthetic rate, A , is assumed to be a hyperbolic function of incident radiation, I :

$$\theta A^2 - (A_{\max} + \alpha I)A + A_{\max} \alpha I = 0, \quad (7)$$

where A_{\max} is the photosynthetic capacity, α is the quantum yield, and θ describes the curvature of the response. Radiation flux density is assumed to decline through the canopy according to Beer's Law:

$$I(L) = I_0 \exp(-kL), \quad (8)$$

where $I(L)$ is the radiation flux density incident at cumulative LAI L , I_0 is the radiation incident at the top of the canopy, and k is the light extinction coefficient. Instantaneous canopy photosynthesis, A_{can} , is given by the integral of A over the canopy, i.e.

$$A_{\text{can}} = \int_0^{L_i} A(L) dL. \quad (9)$$

If the photosynthetic capacity is assumed to decline exponentially through the canopy, in proportion to the incident radiation estimated by Beer's Law, i.e.:

$$A_{\max}(L) \propto I(L), \quad (10)$$

then the integral (9) can be solved analytically to give:

$$A_{\text{can}} = A_0 [1 - \exp(-kL)] / k, \quad (11)$$

where A_0 is the photosynthetic rate of foliage at the top of the canopy.

This line of reasoning was first used by Farquhar (1989), who showed that since the distribution of photosynthetic capacity within a leaf paralleled the distribution of radiation, it was possible to scale photosynthesis from individual cells to leaves. The argument was rapidly extended to develop canopy-scale models (Thornley and Johnson 1990; Sellers *et al.* 1992).

A large number of studies have examined the assumption that photosynthetic capacity declines exponentially through the canopy in proportion to incident radiation (Equation 10). As photosynthetic capacity is linearly related to leaf nitrogen content (Field and Mooney 1986), such studies have also generally examined the distribution of leaf nitrogen through the canopy. Optimisation arguments have shown that the distribution given in Equation 10 represents an optimal allocation of nitrogen in the plant canopy (Field 1983; Sellers *et al.* 1992; Sands 1995a). Most studies find that there is a significant decrease in both leaf nitrogen content and photosynthetic capacity through the canopy (DeJong and Doyle 1985; Hirose and Werger 1987; Hirose *et al.* 1988; Hollinger 1989; Evans 1993). However, it is commonly found that this distribution is not exponential, as optimisation arguments predict, but is more uniform (Dang *et al.* 1997; Meir *et al.* 2002). This finding does not necessarily invalidate the model: simulations comparing canopy photosynthesis obtained with the observed distribution of nitrogen to that obtained with the optimal distribution generally find that the optimal distribution provides a good approximation, provided that the total amount of canopy nitrogen is held constant (Field 1983; Hirose and Werger 1987; Friend 2001).

An example of a model using the big-leaf approach is HYBRID (Friend *et al.* 1997), a model of terrestrial ecosystem dynamics. HYBRID simulates the cycling of carbon, nitrogen and water within the biosphere, using a daily time-step, and also predicts the relative dominance of different plant functional types. In HYBRID, mean daily canopy photosynthesis is modelled using Equation 11, with A_0 taken to be the mean daytime rate of net photosynthesis of the uppermost leaf. This photosynthetic rate is calculated using a mechanistic model of leaf photosynthesis (Friend 1995). The main parameters required are leaf photosynthetic parameters, namely leaf nitrogen content, the fractions of leaf nitrogen bound in Rubisco and in chlorophyll, and the light-saturated electron transport rate per unit chlorophyll. Leaf nitrogen content is calculated within the model, as a result of carbon and nitrogen dynamics, while the electron transport rate is assumed constant for all plant functional types. Only the fractions of leaf nitrogen bound in Rubisco and in chlorophyll vary; these values are estimated from experimental studies of leaf nitrogen distribution (Friend *et al.* 1997).

Concerning validation of the model, Friend *et al.* (1997) argue that adjusting parameters of the model to fit global

datasets of net primary productivity, LAI or evapotranspiration (i.e. 'model tuning') is a meaningless exercise, and that it is necessary to test the model without altering the internal parameterisation. To this end, Friend and White (2000) evaluated the model by comparing outputs with global patterns of pre-industrial vegetation, primary productivity, biomass carbon and soil carbon. In general the model performed well, but several areas of disagreement between the model and observations highlighted areas requiring further development.

Although the assumption of proportionality between photosynthetic capacity and incident radiation allows photosynthesis to be readily integrated over the canopy, it does not simplify integration over time. Models such as HYBRID ignore variation over the day and simply use mean daily values of radiation and photosynthesis. However, this approach overlooks the interaction between model non-linearity and variability in absorbed radiation by the canopy throughout the day. Sands (1995*b*) shows how the big-leaf model can be generalised to include daily variation in incident radiation. This version of the big-leaf model is used in the models PROMOD (Battaglia and Sands 1997) and CENW (Kirschbaum 1999*a*). PROMOD is a simple process-based model of plantation productivity, designed as a tool for forest managers (Sands *et al.* 2000), and has been used on large scales to screen for potential plantation establishment sites (Mummery and Battaglia 2001). CENW is a more detailed forest growth model describing flows of carbon, nutrients and water in trees and soil organic matter, and has been used to examine sensitivity of Australian forests to changes in atmospheric [CO₂] and climate (Kirschbaum 1999*b*) at the stand scale. PROMOD has been parameterised from ecophysiological studies of *Eucalyptus globulus*, *E. nitens* and *Pinus radiata*, and CENW for *P. radiata*. Both models have been validated at the plot scale. For example, PROMOD was validated by comparing predicted values of mean annual increment (MAI) to values observed at the nine plots used to develop the model, plus an additional nineteen validation plots (Battaglia and Sands 1997), while CENW was validated against data on foliar nitrogen content, soil water content, stem diameter, and foliar and stem biomass, obtained from a forest fertilisation and irrigation experiment (Kirschbaum 1999*a*).

In the discussion of the RUE model, we noted that one advantage of the model was the ability to use remotely-sensed estimates of intercepted radiation to drive the model, thus eliminating the need to model intercepted radiation. The big-leaf model also shares this advantage: the term $[1 - \exp(-kL)]$ in Equation 11 can be derived from satellite observations. This advantage is exploited in the SiB2 model (Sellers *et al.* 1996). The SiB2 model forms the land-surface component of the Colorado State University Global Climate Model (GCM). As such, it is required to be run on very short time scales (minutes) for the whole globe.

At this time scale, it is important to account for the non-linearity of the response of canopy photosynthesis to intercepted radiation, so the big-leaf model is an appropriate model choice. Biome-specific model parameters are derived from the literature and validation is carried out using the GCM model as a whole (Randall *et al.* 1996).

The major advantage of the big-leaf model over the simpler RUE, water use efficiency (WUE) and maximum productivity models is that it uses fine scale information on leaf photosynthesis from laboratory and field studies as its basis for up-scaling to the canopy scale. For expediency, the simpler models disregard fine scale information in their aggregated representation of processes at the canopy scale. Parameter values for the big-leaf model are thus simpler to obtain, as they can be estimated directly from leaf-level studies rather than the laborious and time-consuming stand-scale studies required to obtain values of potential productivity or RUE. Additionally, effects of other environmental constraints such as water, nutrition and temperature are simpler to incorporate into the model, since all that is required is an understanding of their effects at the leaf-scale.

However, there are also drawbacks to the big-leaf model. It is more complex to implement and hence slower to run than the simpler RUE and WUE models because it resolves production on time-steps of hours or days rather than weeks or months. As noted above, the model relies on the assumption that photosynthetic capacity decreases exponentially through the canopy with average irradiance, an assumption which is generally known to be incorrect; however, this assumption is unlikely to lead to serious errors. Potentially more serious are the two problems highlighted by de Pury and Farquhar (1997) and Gu *et al.* (2002). De Pury and Farquhar (1997) note that, although the mean level of irradiance decreases exponentially through the canopy, this mean includes sunlit and shaded foliage, which are experiencing very different levels of irradiance. The foliage that is sunlit changes on a minute-by-minute basis, and hence it is impossible for photosynthetic capacity to be proportional to actual irradiance. They argue that it is necessary to calculate photosynthesis by sunlit and shaded foliage separately. Gu *et al.* (2002) use eddy covariance data to demonstrate that canopy photosynthetic response to diffuse radiation is different from that to direct radiation, and argue that the two types of radiation must be treated separately. These two arguments are addressed in the fourth model approach we consider, the sun-shade model.

The sun-shade model

Detailed models of canopy radiation interception and photosynthesis generally divide the canopy into several layers or subvolumes and perform calculations for each section, assuming that radiation interception and hence photosynthesis are homogeneous within each section. Studies using such models have consistently shown that a sufficient

subdivision of the canopy is that between sunlit and shaded foliage (de Pury and Farquhar 1997; Norman 1980; Reynolds *et al.* 1992; Stockle 1992). Recently, several authors have proposed that a simple but accurate model of canopy photosynthesis could be obtained by combining the description of sun and shade foliage with the assumption of an optimal distribution of canopy nitrogen (de Pury and Farquhar 1997; Medlyn *et al.* 2000; Thornley 2002; Wang and Leuning 1998). Based on these assumptions, it is possible to derive an analytic expression for canopy photosynthesis. The derivation of this expression presented by Medlyn *et al.* (2000) is summarised here.

The response of photosynthesis to light is assumed to be a rectangular hyperbola:

$$A = (A_{\max}\alpha I)/(A_{\max} + \alpha I). \quad (12)$$

This is a special case of Equation 7, with $\theta = 0$. Thornley (2002) shows how to generalise the following derivation to the general non-rectangular hyperbola given by Equation 7. The distributions of direct and diffuse radiation through the canopy are considered separately. The intensity of diffuse radiation is assumed to decline exponentially through the canopy, according to:

$$I_{\text{shade}}(L) = kI_d \exp(-kL), \quad (13)$$

where $I_{\text{shade}}(L)$ is the intensity of radiation incident on shaded foliage at canopy depth L , and I_d is the intensity of diffuse radiation incident at the top of the canopy. The intensity of direct-beam radiation does not decrease through the canopy, so the radiation incident on sunlit foliage at canopy depth L is given by:

$$I_{\text{sun}}(L) = k[I_b + I_d \exp(-kL)], \quad (14)$$

where I_b is the intensity of direct-beam radiation at the top of the canopy. The fraction of sunlit foliage at canopy depth L is given by $\exp(-kL)$, while the fraction of shaded foliage is $1 - \exp(-kL)$. Photosynthetic capacity is assumed to decline exponentially through the canopy according to:

$$A_{\max}(L) = A_{\max 0} \exp(-kL). \quad (15)$$

Integrating over the canopy, we obtain the following expression for canopy photosynthesis:

$$P_g = \frac{1 - \exp(-kL_c)}{k} \left(\frac{bA_{\max 0}^2 + A_{\max 0}d(A_{\max 0} + d)}{(A_{\max 0} + d)^2} \right) + \frac{1}{k} \frac{(bA_{\max 0})^2}{(A_{\max 0} + d)^3} \ln \left(\frac{(A_{\max 0} + d) \exp(-kL_c) + b}{A_{\max 0} + d + b} \right), \quad (16)$$

where L_c is the total canopy leaf area index, $b = \alpha I_b k$ and $d = \alpha I_d k$.

This expression is more complex than the big-leaf model (Equation 11 above) but is still relatively simple and mechanistic and does not require any additional information for parameters than the big-leaf model. Its advantage is that

by dividing the canopy into sun and shade classes it correctly weights the contributions of each to predicted canopy photosynthesis, giving better accuracy than any of the other models discussed above. The disadvantage is that it cannot be used with remotely-sensed radiation interception data. It also requires more information to parameterise and has greater computational overheads than the simpler maximum productivity and RUE models.

The analytic sun-shade expression for canopy photosynthesis (Equation 16) has been implemented in the G'DAY model (Medlyn *et al.* 2000), a model of carbon and nitrogen cycling in the plant-soil system. The G'DAY model has been applied to forest stands in Sweden and Australia, using parameter values obtained from photosynthesis measurements made on site. However, this model has not been validated, nor applied on larger scales. G'DAY is largely used to investigate long-term responses to global change. The sun-shade model was chosen for use with G'DAY largely because the effects of nitrogen and water availability and temperature could be readily incorporated into the model, directly using information obtained in leaf-scale experiments. Earlier versions of G'DAY used the RUE model, for which nitrogen, water and temperature effects were much more difficult to characterise (Kirschbaum *et al.* 1994).

An example of a model using the sun-shade approach to model NPP on large spatial scales is the CSIRO Biospheric Model (CBM) (Wang and Leuning 1998; Wang *et al.* 2001). The CBM is a model of canopy gas and energy exchange at half-hourly time intervals. Rather than the analytic sun-shade expression (Equation 16), this model uses a more detailed numerical approximation. The calculation of radiation absorption allows for different light extinction coefficients for direct and diffuse radiation, as well as scattered radiation. Canopy temperature and energy balance are calculated iteratively, and photosynthetic parameters are corrected for curvature of the leaf light-response curve. The CBM has been validated at stand scale against eddy flux measurements obtained for two wheat crops (Leuning *et al.* 1998) with photosynthetic parameters obtained from previous physiological studies (Leuning 1995). However, Wang *et al.* (2001) demonstrated that even with hourly measurements of energy, CO₂ and water fluxes over crop and pasture sites, there was only a limited constraint on model parameters in CBM. This result was due to correlation between data sets, leading to an under-determined optimisation problem and poor estimates of all model parameters. By holding some parameters constant, it was found that sufficient information resided in data to estimate three model parameters with confidence. In an attempt to incorporate additional information as constraints on parameters, Wang and Barrett (2002) used prior estimates of mean and standard error of NPP interpolated from ecological observations of litterfall and growth across Australia.

This approach allowed estimation of mean and standard error of $A_{\max 0}$ (Equation 15) and subsequently the prediction of the spatial distribution of monthly mean and standard error of NPP across the Australian continent.

Other models

One of the above four approaches to modelling the conversion of radiation into photosynthate is adopted in most, but not all models. Here we very briefly discuss some variations on the approaches described above, used in three well-known models of large-scale net primary productivity, and explain why these variations are used.

The Terrestrial Ecosystem Model (TEM) is a model of carbon and nitrogen pools and fluxes in terrestrial ecosystems and is designed to be applied at continental to global scales (Raich *et al.* 1991; Melillo *et al.* 1993). In this model, the vegetation is considered as a single pool. No information is available within the model about leaf biomass or leaf area, so it is not possible to apply any of the three models above that estimate radiation interception from leaf area. Rather than applying the fourth model, the maximum productivity model, which ignores the effects of incident radiation, however, the following simple formulation is adopted:

$$\text{GPP}_{\text{pot}} = P_{\text{max}} \text{PAR} / (k_i + \text{PAR}), \quad (17)$$

where GPP_{pot} is the potential gross primary production (modified by effects of water, nutrition, and temperature), P_{max} is the maximum rate of assimilation under optimum conditions, PAR is the incident photosynthetically-active radiation, and k_i is a constant parameter, set to $314 \text{ J cm}^{-2} \text{ d}^{-1}$ (Raich *et al.* 1991). The values of P_{max} for each biome are obtained by calibration against NPP data from calibration sites. This model has been very widely applied to estimate NPP at both regional and global scales (e.g. McGuire *et al.* 1995; Melillo *et al.* 1995; Pan *et al.* 1996; Xiao *et al.* 1997; McGuire *et al.* 2000).

The PnET model (Aber and Federer 1992; Aber *et al.* 1996) assumes an exponential distribution of radiation in the stand (Equation 8), but does not assume that photosynthetic capacity varies with depth, meaning that the simple integrations used in the big-leaf and sun-shade models are not applicable. Instead, radiation interception and resulting photosynthesis are calculated in 100 canopy layers and summed to give total canopy photosynthesis, either on a daily or monthly basis. The photosynthetic parameters required for this model are obtained from ecophysiological studies on representative forest types and include the foliar nitrogen content, the relationship of photosynthetic capacity with nitrogen, and a factor describing the light response of leaf photosynthesis. This model has often been applied at regional scale, particularly the north-eastern USA, where it was developed (Aber *et al.* 1995; Ollinger *et al.* 1998; Jenkins *et al.* 1999). In this region, the model performs well (Ollinger *et al.* 1998).

The IBIS model (Foley *et al.* 1996) also avoids the assumption that photosynthetic capacity varies with depth. However, since IBIS is a global-scale land surface model designed to operate at time scales of 10–60 minutes, a simple calculation scheme is required. The canopy is divided into just two sections, sunlit and shaded, and photosynthetic rates are assumed to be homogeneous within each section. Biome-specific parameter values are taken from leaf-level physiological studies in the literature. The ultimate aim of the model is to simulate vegetation dynamics on a global scale, and hence the model is tested by comparing the modelled near-equilibrium vegetation with maps of potential natural vegetation. The comparison showed on average a fair degree of agreement (Foley *et al.* 1996).

Comparison of alternative models

In this section, we examine the question of whether any of the methods of modelling canopy photosynthetic uptake discussed above are preferable to others, bearing in mind that speed, complexity and ease of parameterisation may be as important as accuracy when deciding which model is best for a given situation.

We have presented the four approaches in order of increasing complexity, which is also generally thought to be the order of increasing accuracy. However, it is difficult to directly test theoretical arguments about the relative accuracy of the different approaches. Typically, data sets available for testing models, such as data on NPP, test models in terms of their final outputs and do not provide tests of the accuracy with which component processes are modelled. Here, we have attempted to evaluate the different approaches against eddy covariance data, which provide estimates of whole-ecosystem gas exchange on a fine time scale, and hence are a better test of the radiation conversion components of models. We note that these data reflect changes in temperature and water availability, the effects of which are represented differently in each of the models, potentially influencing the comparison. We attempt to minimise this problem by using summertime (May–August) data from a Sitka spruce site in Scotland (Valentini *et al.* 2000) where water availability is not limiting, and temperatures are relatively constant. Griffin forest ($56^{\circ}36'N$, $3^{\circ}47'W$, 340 m above sea level) is an actively managed Sitka spruce forest, planted in 1981–1983. Stocking density is currently 2150 stems ha^{-1} and mean height in 2000 was 9 m. Average annual rainfall is 1200 mm. Eddy covariance data have been collected since mid-1996. To extract values of GPP from the eddy covariance data, it is necessary to subtract values of ecosystem respiration, which are estimated using a regression of night-time CO_2 exchange (representing respiration only) against temperature. Only data points where night-time wind speed was greater than 3 m s^{-1} were used, to avoid bias due to CO_2 storage. A good relationship was

found (Fig. 1), suggesting that respiration estimates are reasonable. It is wise to remember, though, when evaluating the results presented below, that the estimates of GPP from the flux data are also prone to error, not only from errors in estimating ecosystem respiration but also from errors of measurement (Moncrieff *et al.* 1996).

Estimates of daily, weekly and monthly incident radiation and GPP were obtained from four years of flux data. Data were gap-filled for monthly and weekly sums using average hourly values. Daily sums were only obtained for days where there were no gaps in the data. Each of the four approaches described above was then used to estimate GPP on each time scale. For the maximum productivity and RUE approaches, the parameters required were estimated from the data sets as a whole. For the big-leaf and sun-shade approaches, appropriate parameter values ($\alpha = 0.05 \text{ mol mol}^{-1}$ and $A_{\text{max}0} = 20 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) were derived from physiological studies on Sitka spruce (Meir *et al.* 2002). Convexity, θ , was taken to be 0. For all approaches estimating absorbed radiation, LAI was taken to be constant at $7 \text{ m}^2 \text{ m}^{-2}$ (Wingate 1998), the extinction coefficient k was assumed to be 0.5, and absorbed radiation was calculated from Beer's Law (Equation 8). For the big-leaf and sun-shade approaches, the models (Equations 11 and 16) were applied on the relevant time scale, with no attempt to correct for variation in incident radiation within the time-step.

The results of this model comparison are shown in Fig. 2 and Table 2. The most commonly used statistic to compare

model predictions to data are the correlation coefficient r^2 . However, the use of this statistic by itself can give a biased impression of model performance. Willmott (1981) suggests that a range of statistics, as given in Table 2, is necessary to fully evaluate goodness of fit. The index of agreement (d) presented by Willmott (1981) is particularly useful as it indicates the degree to which a model's predictions are error-free. This index is given by:

$$d = 1 - \frac{\sum (P_i - O_i)^2}{\sum (|P_i - \bar{O}| + |O_i - \bar{O}|)^2}, \quad (18)$$

where O_i are the observed and P_i the predicted values of GPP. The value of d increases from 0 to 1 as the degree of model-data agreement increases. Comparison of this statistic across models shows that in this exercise, the sun-shade model is the most accurate of the four models at all time scales, although the difference from the big-leaf model becomes marginal at shorter time scales. Interestingly, comparison of the RMSE statistic suggests that the RUE model is the worst performer at all time scales. Inspection of Fig. 2 shows that at the daily time-step, the RUE model fails to capture the non-linearity of the response of GPP to incident radiation. At the monthly time-step, in contrast, the relationship between GPP and radiation is linear, but the RUE model still performs badly because it assumes a proportional relationship, with no intercept. It should be noted, however, that the non-linearity in the relationship observed at the daily time scale at this site is unusual.

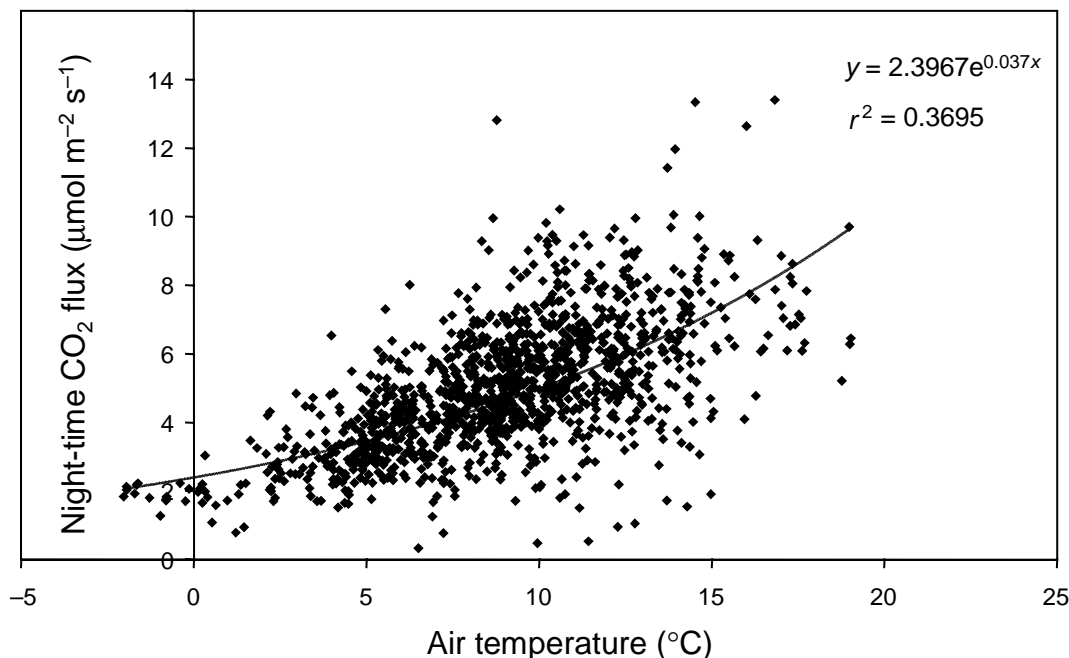


Fig. 1. Half-hourly night-time CO₂ flux data measured at Griffin forest, Scotland, plotted against air temperature. Summertime (May–August) values for periods when wind speed $>3 \text{ m s}^{-1}$. The regression line shown was used to estimate daytime whole-ecosystem respiration.

At other eddy flux sites, saturation of the photosynthetic response tends to occur at a higher level of incident radiation. The low saturation level at this site may be due to the high efficiency of use of incident radiation by Sitka spruce (Jarvis and Leverenz 1983). The RUE model would be expected to perform better for species with a higher light-saturation level.

This very simple comparison suggests that, at site scale, the sun-shade model is likely to be the most accurate model

of radiation conversion, even at monthly time scales. It is the most complex of the four models, but is still quite simple compared with multi-layer canopy models. It also has the advantage that parameters may be obtained from physiological studies. It is important to realise that, in the above comparison, parameters for the maximum productivity and RUE are derived directly from the data; normally parameters would have to be estimated, introducing an additional source of error.

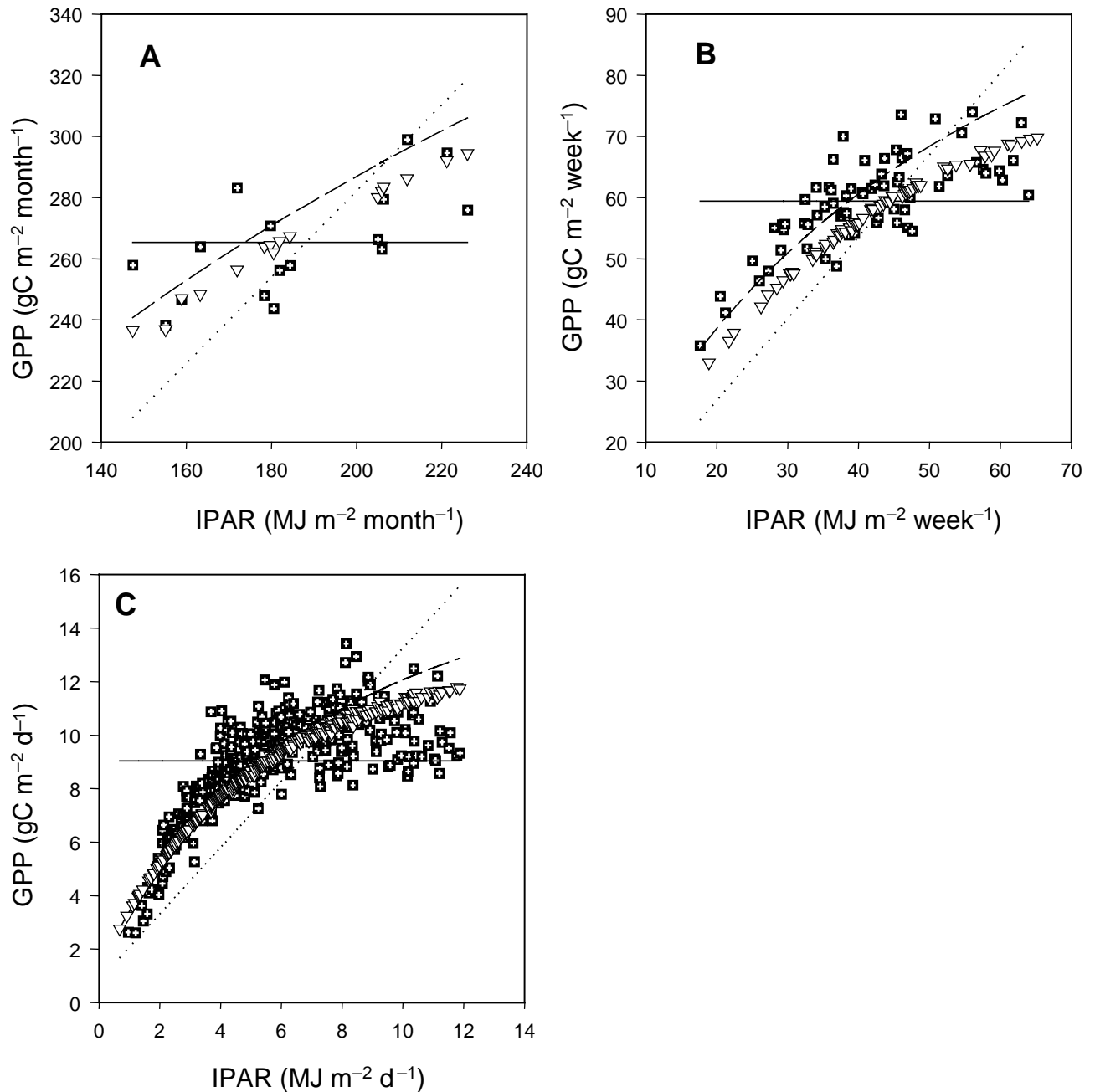


Fig. 2. Comparison of model estimates of GPP with estimates of GPP from eddy covariance data measured at Griffin forest, Scotland. Three different time scales are shown: (A) monthly (B) weekly (C) daily. EC = values measured by eddy covariance (■); Modelled values: MP = maximum productivity model (—); RUE = radiation use efficiency model (...); BL = big-leaf model (---); and SS = sun-shade model (-·-).

This comparison only concerns models applied to a single site, with constant LAI. It is possible that relative model performance may change when attempting to predict productivity across sites with different climates and vegetation. It seems likely, for example, that in such a simulation the RUE approach would outperform the maximum productivity approach. Thus far, however, there have been no definitive tests comparing the ability of these approaches to simulate productivity across sites. As noted above, it is difficult to test separate processes of a model individually; tests are generally made of complete models. Comparisons among models show that differences in model output are generally not attributable to differences in model structure. For example, the Potsdam NPP Model Intercomparison Project (Cramer *et al.* 1999) compared estimates of global NPP from models utilising a range of radiation conversion approaches, including RUE and big-leaf models. Differences between model estimates could not be attributed to any differences in modelling strategy, including the choice of radiation conversion model.

However, the Potsdam project also found that model estimates of radiation absorbed and RUE tended to compensate each other, such that each model arrived at a similar value of global NPP (Ruimy *et al.* 1999). The conclusion drawn tentatively in that study is that during model development, models were calibrated against similar NPP data sets, resulting in similar model outputs. Therefore, differences in model structure, such as choice of radiation conversion model, do not necessarily lead to differences in model estimates of productivity. A pessimistic response to this outcome might be to question how much confidence we can

have in model simulations, given that they have all been calibrated to give similar responses. An optimistic response, on the other hand, might be that all of the approaches currently in use to simulate radiation conversion are equally able to yield valid estimates of NPP on large spatial scales.

Scaling challenges: how well are we meeting them?

We outlined earlier three of the key challenges faced when up-scaling models, namely model identification, parameterisation, and validation, and have touched on how each of the different approaches to estimating regional scale canopy photosynthesis tackles these problems. In this section, we discuss each of these problems in more detail.

The first problem is that of model identification. In the case of photosynthetic uptake, we have confidence in the functional form of the leaf scale model because it has been extensively validated for a large range of vegetation types. Given this level of confidence we could, with perfect knowledge of the co-variances of forcing variables and parameters, use Equation 3 to accurately predict regional photosynthesis in an area of any size over any time interval. However, because of the impracticality of measuring co-variances of **M** and **P** over large regions, we must resort to approximations provided by simpler models when scaling the leaf scale model to regions.

The derivation of the four simplified models we have considered varies. The big-leaf and sun-shade models were derived from a detailed consideration of the fine-scale non-linearity and how it interacts with other environmental conditions, i.e. using a ‘bottom-up’ approach. The maximum productivity and RUE approaches were developed using a ‘top-down’ approach from empirical measurements at the scale of interest, and relationships to fine-scale processes were studied later.

Each of these functional forms is applicable at the stand scale, i.e. for areas of horizontally homogeneous vegetation. For non-homogenous vegetation, the functional forms applicable at the stand scale should possibly be modified (Raupach *et al.* 2002), but most modellers assume that the stand-level functional forms can be directly applied at the regional scale. The most typical approach is to divide the area under consideration into pixels, where each pixel is assumed to have homogeneous vegetation. The size of pixels used represents a trade-off; with more pixels, more detail of the underlying vegetation can be represented, but also more parameters and computing time are required. A number of studies have shown that estimates of regional NPP depend on the pixel size used, largely because as pixel size increases, less widely-distributed vegetation types become ignored (Turner *et al.* 1996; Kimball *et al.* 1999). Partly this is because in most models, the pixel is represented by the dominant vegetation type in that area, which may not be the same as the vegetation class contributing most to regional photosynthesis. For example, smaller wet areas of a

Table 2. Statistics of comparisons of modelled GPP vs GPP estimated from flux data measured at Griffin forest

GPP values are given in g C m^{-2} per time-step (month, week or day). The statistic d gives an estimate of model performance (Equation 18). The larger the value of d , the better the model fit. Further details are given in the text. n/a = not applicable

	Slope	Intercept	r^2	RMSE	d
Monthly ($n = 16$)					
Maximum productivity	0	265.3	n/a	17.16	0
RUE	1.28	-76.61	0.44	25.18	0.72
Big-leaf	0.74	78.54	0.43	17.97	0.75
Sun-shade	0.7	81.12	0.45	14.38	0.81
Weekly ($n = 68$)					
Maximum prod.	0	59.4	n/a	7.39	0
RUE	1.38	-26.72	0.53	10.8	0.74
Big-leaf	0.94	5.04	0.59	5.97	0.86
Sun-shade	0.85	8.33	0.62	5.11	0.88
Daily ($n = 345$)					
Maximum prod.	0	8.56	n/a	1.78	0
RUE	1.23	-2.99	0.49	2.5	0.73
Big-leaf	0.95	0.41	0.62	1.31	0.88
Sun-shade	0.88	0.77	0.67	1.14	0.9

landscape may contribute proportionally more to canopy photosynthesis than larger dry areas. An alternative approach, which may yield more accurate estimates of regional NPP, is to represent each pixel by a weighted mean of the different vegetation types present (Jenkins *et al.* 1999). Different soil types may pose the same problem, however, potentially making this type of scheme quite complex (Mummery and Battaglia 2002).

This question is intertwined with that of parameterisation. As noted above, for stand-scale simulations, parameters for the big-leaf and sun-shade models may be taken from leaf physiological measurements, while parameters for the maximum productivity and resource use efficiency models must be calculated from empirical measurements at the stand scale. For regional scale models, where pixels are assumed to be internally homogeneous, typical stand-scale parameter values for those vegetation types (species or functional groups) can be directly applied. There are two major problems with this approach. First, our knowledge of typical parameters for each vegetation type is imprecise, as the values may vary considerably for a given vegetation type (Gower *et al.* 1999), and secondly, vegetation is heterogeneous at all scales and will be present in all pixels no matter what their size. Since we are attempting to scale a non-linear process, linear averaging of parameter values will lead to bias in model outputs (Wang *et al.* 2001).

An alternative approach is to use 'effective' parameter values that accurately predict observations at the scale of interest (Raupach *et al.* 2002). However, parameters estimated in this way will differ from their mean values because this approach implicitly includes the 'bias terms' in Equation 3. Furthermore, as the scale changes, the magnitude of the bias terms will also change, so an effective parameter value is valid only at the scale for which it was estimated. Finally, direct empirical estimates of parameter values at pixel scale are generally impractical, so indirect methods must be used. One method is to use a hierarchy of models, dubbed the 'signal-transfer' approach by Luxmoore *et al.* (2000). In this approach, a detailed stand-scale model is run to develop parameter surfaces which can then be transferred into a large-scale model. This approach can account for much small-scale variation but does not solve the problem of inadequate data. An alternative method is to deconvolve integrated measurements, such as atmospheric gas concentrations, by estimating parameters to match measurements (Kercher and Chambers 2001; Wang and McGregor 2002). This approach also suffers from some important disadvantages: in particular, such signals generally carry relatively little information, permitting the estimation of a very limited number of parameters (Wang *et al.* 2001). In summary, there is no perfect way to estimate model parameter values; a combination of the methods proposed above is required to minimise model error due to

imperfect parameterisation (Wang and Barrett 2002; Wang and McGregor 2002).

Finally, we turn to the question of model validation. Comparing model outputs against stand-level measurements such as net primary productivity or standing biomass at a range of sites varying in climate and vegetation structure helps to increase confidence in the generality of the model, and a number of physically extensive databases of empirical measurements have been developed for exactly this purpose (Scurlock *et al.* 1999; Barrett 2001). However, although stand-scale validation can help to increase our confidence in model outputs, there is also a need to validate regional-scale models over the scales at which they are applied, which is not straightforward. Measurements at regional scale that have been used for model validation include atmospheric CO₂ concentrations, aircraft-based eddy flux measurements (e.g. Oechel *et al.* 2000) and remotely-sensed data (e.g. Coops *et al.* 2001a). Such measurements are of little use in validation if they have already been used to parameterise the model (Coops *et al.* 2001a). Another avenue for model testing at large scales is comparison between models, either between models operating at the same spatial scale (Cramer *et al.* 1999), or against models operating at finer scales (Reich *et al.* 1999), although questions of independence of models arise.

A further point regarding validation is that agreement between model and data does not necessarily confirm the correctness of the model, due to the problem of under-determination of models. With a large number of parameters, a model can almost always be made to fit a given data set by adjustment of the parameter values. Thus, a good fit between the two does not always imply that we can have confidence in the model structure (Hopkins and Leipold 1996). The Potsdam NPP Model Intercomparison Project clearly demonstrated this problem: while model outputs were similar, it was shown by Ruimy *et al.* (1999) that the model structures and parameters leading to these outputs were quite different.

Conclusion

We have presented and compared four alternative methods to model plant canopy photosynthetic uptake at regional scales. Each of the four methods has advantages, which can be enumerated as follows.

- (1) The sun-shade model is likely to be the most accurate of the four, particularly at diurnal and subdiurnal time scales, although the big-leaf model is also quite accurate at these time scales,
- (2) The sun-shade and big-leaf models can be parameterised directly from leaf-level measurements, which are easier to perform than stand-scale measurements required to parameterise the other models,

- (3) The big-leaf and RUE models have the advantage that they can be combined with estimates of radiation interception made using remotely-sensed data,
- (4) The RUE and maximum productivity models are simple to implement and swift to compute, and are particularly appropriate at monthly time-steps.

All four approaches have been shown to be capable of modelling canopy photosynthetic uptake. Validation tests of models incorporating the four different approaches have successfully simulated plant productivity at both stand and regional scales. We conclude that there is no overall 'best' model — just a 'best' model for any given modelling task.

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