Available online at www.sciencedirect.com
ScienceDirect
Agricultural and Forest Meteorology 145 (2007) 110–124
AGRICULTURAL AND FOREST METEOROLOGY
www.elsevier.com/locate/agrformet

Interpreting shallow, vertical nitrogen profiles in tree crowns: A three-dimensional, radiative-transfer simulation accounting for diffuse sunlight

Paul B. Alton *, Peter North

Geography Department, University of Swansea, UK

Received 17 January 2007; received in revised form 9 April 2007; accepted 13 April 2007

Abstract

The assumed concentration and distribution of active leaf nitrogen (N) within vegetation canopies has a major influence on the gross primary product (GPP) predicted by land-surface models. We couple a Monte Carlo, three-dimensional (3D), ray-tracing simulation to the land-surface model JULES in order to compare the vertical profiles of light and active leaf-N in three forest stands of diverse composition and structure. Our simulations, which are driven by real climate data, strengthen the view that tree canopies are only partially light-acclimated. Notably, our computation demonstrates the importance of both diffuse sunlight and the manner in which the light profile is quantified. For example, when our temperate, broadleaf stand is subjected to diffuse sunlight, the mean leaf irradiance declines steeply in the upper third of crown ($k_{ext} \gtrsim 1$, where k_{ext} is the exponential extinction coefficient) but is relatively shallow below that height ($k_{ext} \leq 0.75$). Under direct sunlight, the foliage divides into sunlit and shaded fractions and a more appropriate measure of the light environment is probably the mode irradiance rather than the mean irradiance. Under direct sunlight, the optimal vertical distribution of Rubisco (i.e. that which maximises GPP for a fixed amount of active leaf-N in the canopy) is calculated to be shallow in both the upper and lower portions of the canopy ($k_{rub} < 0.27$, where k_{rub}, is the exponential N-allocation parameter). Furthermore, an abrupt step, from high to low photosynthetic capacity, is predicted in the upper third of the crown. The theoretical gain in GPP for a stand that is fully light-acclimated compared to one that is only partially light-acclimated (i.e. with $k_{rub} = 0.15$, as measured in real tree canopies) is moderately important (8–13%). Our results are relatively insensitive to canopy architecture, i.e. crown structure, leaf-clumping and the leaf angle distribution.
Published by Elsevier B.V.

Keywords: Radiative-transfer; Diffuse sunlight; Light acclimation; Nitrogen cycle

1. Introduction

The acclimation hypothesis states that the vertical gradient of photosynthetic capacity is proportional to that of the average light profile through the canopy (Meir et al., 2002). The leaf photosynthetic capacity is equivalent to the photosynthetic rate at light saturation and is determined by the concentration of RUBP carboxylase-oxygenase (Rubisco) in the foliar photosynthetic apparatus. The acclimation hypothesis is implicit in the big leaf radiative-transfer (RT) scheme (Sellers et al., 1996) and is often assumed in other formulations of RT implemented in regional/global land-surface models (LSMs). Typically, these LSMs are coupled to a Global Circulation Model (GCM) and can, therefore, undergo quite computationally intensive simulations. The assumption of full acclimation facilitates the calculation of gross primary product (GPP) for the canopy considerably (e.g. Schulze et al., 1994). Furthermore, strong adaptation to the light

* Corresponding author.
E-mail address: p.alton@swansea.ac.uk (P.B. Alton).

0168-1923/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.agrformet.2007.04.006

environment might be expected for biomes of high Leaf Area Index (LAI) where GPP may be light-limited for prolonged periods of the day (Nemani et al., 2003). Although measurements of leaf-N and photosynthetic capacity can vary considerably at the same height within a tree (≃30%; Dang et al., 1998), a majority of empirical data in the literature suggest that light acclimation might be incomplete, at least within tree canopies (Carswell et al., 2000; Lewis et al., 2000; Meir et al., 2002; and references therein). The question of acclimation is important for several reasons: (i) the GPP predicted by LSMs varies strongly (20–35%) for typical uncertainties in both the photosynthetic capacity at the top of the crown and the vertical gradient of Rubisco (Alton et al., 2007a, 2007c); (ii) the distribution of active leaf-N is important for dynamic models of nutrient cycling; and (iii) the understanding of current constraints on plants and their ecosystems (light-, water- or N-limited) is a prerequisite to predicting the response of the terrestrial biosphere to future climate change (e.g. Nemani et al., 2003).

Various attempts have been made to explain the shallow Rubisco gradients measured in vegetation canopies (Chen et al., 1993; Kull and Kruijt, 1999; Friend, 2001). However, to cite Frak et al. (2002), '...there is presently no consensus about the factor(s) driving photosynthetic acclimation'. Furthermore, many previous studies are rather theoretical, containing ecological concepts which are difficult to test. In this paper, we adopt a different approach. We simulate light interception in tree canopies using a 3D, ray-tracing model which has recently been enhanced so that it discriminates between diffuse and direct sunlight (Alton et al., 2005). Our RT-scheme takes explicit account of leaf orientation and sunfieck penetration. This is an important consideration under sunny conditions when the dispersion in leaf irradiance, at any given height in the canopy, is observed to be large (Parker et al., 2002). Meir et al. (2002) attribute an important role to diffuse sunlight in influencing the Rubisco gradient within tree canopies. Until now, this idea remains untested as modellers have a tendency to concentrate on the impact of *direct* sunlight on the distribution of foliar N (e.g. Chen et al., 1993). The diffuse sky flux produced by clouds and aerosols is known to have a large impact on carbon assimilation, increasing light-use efficiency by up to a factor of two compared to direct sunlight (Hollinger et al., 1994; Gu et al., 2002; Niyogi et al., 2004; Alton et al., 2007b).

The current investigation differs from previous studies in several other important aspects: (i) our ray-tracing simulations are three-dimensional taking explicit account of crown shape and canopy heterogenity; (ii) we conduct simulations for three quite different tree stands with known biophysical parameters (a sparse, boreal needleleaf site; a dense, tropical, broadleaf stand; and a moderately dense, temperate, broadleaf location); and (iii) we use real climate data to infer the light environment in the canopy at each timestep, including the fraction of diffuse sunlight. Our RT-scheme is coupled to a LSM to ensure realistic simulation of other biophysical processes, such as stomatal conductance, as well as environmental variables such as canopy temperature and humidity.

Our main objective is to interpret the vertical profile of photosynthetic capacity (hence Rubisco) recorded in tree canopies. This is achieved in three steps: (i) by quantifying the light profile within the stand; (ii) by determining the exponential profile of Rubisco which maximises canopy GPP when the total amount of Rubisco within the stand is fixed (hereafter 'optimal' Rubisco distribution); and (iii) by using the theoretical results from (i) and (ii) to interpret the profiles of Rubisco and light measured in real tree canopies, particularly with respect to light acclimation.

2. Materials and methods

Our methodology requires the coupling of a 3D, ray-tracing simulation to a LSM. The latter is subsequently run for three separate sites using real climate data. The next two sections describe the ray-tracing simulation and the LSM. Section 3 describes simulations conducted to ascertain the average light profile and optimally distributed Rubisco distribution.

2.1. Radiative-transfer

The forest light (FLIGHT) simulation is a ray-tracing, numerical model employing Monte Carlo techniques to sample light propagation and leaf irradiance in both uniform, one-dimensional (1D) vegetation layers and heterogeneous, 3D canopies (North, 1996; Barton and North, 2001; Alton et al., 2005). Our current focus is on 3D canopies, although we also conduct 1D simulations in order to compare with previous modelling of light acclimation (Chen et al., 1993; Kull and Kruijt, 1999; Friend, 2001). For both 1D and 3D simulations, foliage is represented by volume-averaged parameters such as LAI and scattering phase function. Leaf inclinations are modelled explicitly within FLIGHT, rather than adopting a single (mean) leaf orientation which is standard practice in sunlit/shade RT models. Explicit leaf orientation accounts

much better for the range of leaf irradiance observed in real tree canopies at any given height above the ground (Parker et al., 2002). FLIGHT has recently been enhanced so that it estimates photosynthesis within 3D canopies under both direct and diffuse sunlight. Although simulations of anisotropic diffuse sky radiance are possible, in this study we assume diffuse sky radiance is uniform as this is found to be a good approximation under overcast conditions (Alton et al., 2005; Steven and Unsworth, 1980).

For the current study, we select three stands which vary greatly in architecture, LAI and latitude (Table 1). Although the Rubisco gradient is only measured at one of these sites (Manaus; Carswell et al., 2000), our chosen locations possess the considerable advantage of being amongst the better-studied FLUXNET sites with well-documented, biophysical parameters. Furthermore, flux (carbon, water and energy) measurements and a detailed micrometeorology (including diffuse sunlight for one site) is freely available for these locations for use in simulation studies. For our 3D simulations, crowns are represented by ellipses with a minor (horizontal) axis of 2, 5 and 5 m at Zotino, Harvard and Manaus, respectively. The major (vertical) radius is set to 5 m at all sites. The crown base is positioned randomly between a minimum and maximum height of 4 and 12 m at Zotino, 10 and 14 m at Harvard and 12.5 and 27.5 m at Manaus. The corresponding cover fraction for the crowns is 0.6, 0.95 and 1.0, respectively. These structural properties are approximately consistent with the properties measured at each site (see references in Table 1).

Canopy GPP is determined by sampling the irradiance for a random selection of leaves within the canopy and then multiplying the mean leaf photosynthetic rate by the canopy LAI. Leaf irradiance is ascertained by Monte Carlo sampling and reverse ray-tracing (Disney et al., 2000). The photosynthetic rate at the leaf is calculated using a colimitation submodel (Collatz et al., 1991), taking account of both leaf irradiance and the photosynthetic capacity due to foliar Rubisco concentration. The leaf-N-allocation parameter, k_{rub}, determines the exponential, vertical decline in Rubisco. Thus, the photosynthetic capacity is given by:

$$V_{\mathrm{cmax}}(z) = V^0_{\mathrm{cmax}} \exp(-k_{\mathrm{rub}} L) \tag{1}$$

where L is the cumulative LAI between the top leaf and a height z above the forest floor (Hirose and Werger, 1987). The photosynthetic capacity at the top leaf, V^0_{cmax}, is prescribed. In this study, V^0_{cmax} depends on k_{rub} and it is assigned a value which conserves the total amount of Rubisco in the canopy.

For uniform 1D canopies, this value can be derived analytically but, for 3D configurations, V^0_{cmax} follows from numerical integration, weighting for the fraction of foliage at each height in the crown. The leaf-N-allocation parameter k_{rub}, as expressed above, is analogous to the coefficient for light extinction k_{ext} (Sellers et al., 1996). Table 2 contains the vegetation and soil properties adopted in our RT simulations, including the default values of V^0_{cmax}, and k_{rub}. When the properties in Table 2 are adopted, observed GPP at our three sites is reproduced within 16% on average (Alton et al., 2007b; see also Fig. 1).

At each site, canopy GPP is calculated for permutations of the following biophysical properties: (1) downwelling shortwave (SW; $\lambda \simeq 0.3$–2.0) radiation (viz. surface intensity in the horizontal plane, the fraction of sky radiant flux density which is diffuse (fDIF) and the solar zenith angle (θ_s)); (2) canopy microclimate (viz. leaf temperature and the leaf internal concentration of CO_2); and (3) the allocation of leaf-N (k_{rub}). For each configuration of sky radiation, the

Table 1
Properties of three sites selected for ray-tracing with FLIGHT

Property	Zotino	Harvard	Manaus
Designation	Zo	Hv	Mn
Location	Siberia	N. America	Amazonia
Biome	Boreal needleleaf	Temperate broadleaf	Tropical broadleaf
Latitude (degree)	60.8N	42.5N	2.6S
Longitude (degree)	89.4E	72.2W	60.2W
Primary vegetation	Scots pine	Oak maple	Mixed species
LAI ($m^2\ m^{-2}$)	2.0	4.5	5.5
Green fraction	0.6	0.95	1.0

Sources for primary vegetation, projected one-sided leaf area index (LAI) and green fraction are as follows: Wirth et al. (1999) and Lloyd et al. (2002) for Zotino; Williams et al. (1996), Wofsy et al. (1993) and Goulden et al. (1996) for Harvard; Carswell et al. (2000) and Williams et al. (1998) for Manaus.

Table 2
Vegetation and soil parameters adopted in the FLIGHT simulations of canopy photosynthesis

Property	Zo	Hv	Mn	Description
V_{cmax} (μmol m^{-2} s^{-1})	60	90	60	Photosynthetic capacity at top of canopy
QE (mol/mol)	0.05	0.05	0.05	Quantum efficiency incident PAR
k_{rub}	0.15	0.15	0.15	N-allocation parameter
t_l (K)	271	277	285	Lower inhibition temperature for leaf photosynthesis
t_h (K)	301	307	315	Upper inhibition temperature for leaf photosynthesis
R_{PAR}	0.10	0.09	0.12	Leaf reflectance PAR
R_{NIR}	0.46	0.53	0.43	Leaf reflectance NIR
T_{PAR}	0.03	0.03	0.05	Leaf transmittance PAR
T_{NIR}	0.25	0.25	0.35	Leaf transmittance NIR
a_g	0.10	0.10	0.10	Ground albedo (PAR and NIR)

Reflectance and tranmittance for the leaves are given for photosynthetically active radiation (PAR; λ = 0.3–0.7 μm) and for near-infrared radiation (NIR; λ = 0.7–2.0 μm) and is taken from Williams (1991). We show the default values for k_{rub} and V_{cmax} which fix the total amount of Rubisco in the stand. The default value for k_{rub} (0.15) is consistent with recent empirical data for tree canopies (Carswell et al., 2000; Lewis et al., 2000; Meir et al., 2002). The inhibition temperatures t_l and t_h account for the lower kinetic enzyme activity observed at temperatures ≃15 K above and below the mean day-time air temperature during the growing season (Collatz et al., 1991; Cox, 2001; see also Baldocchi et al., 2001).

average, vertical profile of PAR is fitted with an exponential function of the form:

$$i(z) = \exp(-k_{ext}L) \tag{2}$$

where $i(z)$ is the irradiance relative to a position just above the canopy. For all θ_s, PAR is assumed to comprise 43% of sky radiance (Alton et al., 2007c).

The extinction coefficient k_{ext}, defining the light profile, is calculated in three different ways viz. (i) by using the mean irradiance in the horizontal plane (downwelling radiation only); (ii) by using the mode irradiance in the horizontal plane (downwelling radiation only); and (iii) by using the mean irradiance in the plane of the leaf (both upwelling and downwelling radiation). Sampling of irradiance, in our 3D simulations, is restricted to the crown interiors (thus gaps between crowns are not sampled). Our method (i) conforms to the traditional method of measuring light profiles in the field (e.g. Meir et al., 2002). We have introduced method (ii) in recognition of the large dispersion in leaf irradiance under direct sunlight (Parker et al., 2002). Under such circumstances, the mean value of irradiance does not necessarily provide a robust indicator of typical irradiance at any given height, owing to the division of the foliage into sunlit and shaded portions. The statistical mode (i.e. the value we measure most frequently; e.g. Boas, 1983) is ill-suited to a continuous variable and we adopt discrete bins in method (ii) in order to characterise the distribution of light interception adequately (bin-width of 2% maximum leaf irradiance). For completeness, it would have been desirable to ascertain the light profile using the mode irradiance in the plane of the leaf. However, the dispersion in leaf irradiance for sunlit foliage, especially for leaves of different inclination near the top of the canopy, is so great that the mode in this case is both difficult to determine and does not constitute a particularly useful indicator of typical leaf irradiance. For methods (i) to (iii), above, $i(z)$ is determined for 10 evenly spaced heights between the lowest and highest leaf within the canopy. For the mean and mode irradiance in the horizontal plane, k_{ext} is inferred by least-squares minimisation of the fitting function at all 10 heights. The same procedure is adopted for mean irradiance in the plane of the leaf, except average irradiance for the highest layer is excluded due to the rapidly changing light profile in this zone (see Section 4). Canopy GPP and the values of k_{ext}, inferred from (i) to (iii) above, are stored in a look-up table (LUT) for retrieval by the LSM.

2.2. Land-surface model

The Joint UK Land Environmental Simulator (JULES) is a LSM simulating flux exchange between the land-surface and the lower atmosphere. In its original form, JULES is a modularised version of the Met. Office Surface Exchange Scheme (MOSES; Cox et al., 1999; Harris et al., 2004). The latter is coupled to the Hadley Global Circulation Model (GCM) for use in simulations of climate change (Cox et al., 2000). JULES is driven by the following meteorological variables: downwelling shortwave radiation (λ = 0.3–2 μm), downwelling long-wave radiation (λ ∼ 10 μm), precipitation, surface pressure, top-of-canopy (TOC) air temperature, TOC specific air humidity and TOC wind speed. For the current study, hourly (Zotino and Harvard) or half-hourly (Manaus) climatic data are obtained from free-access distribution websites or by approaching the relevant

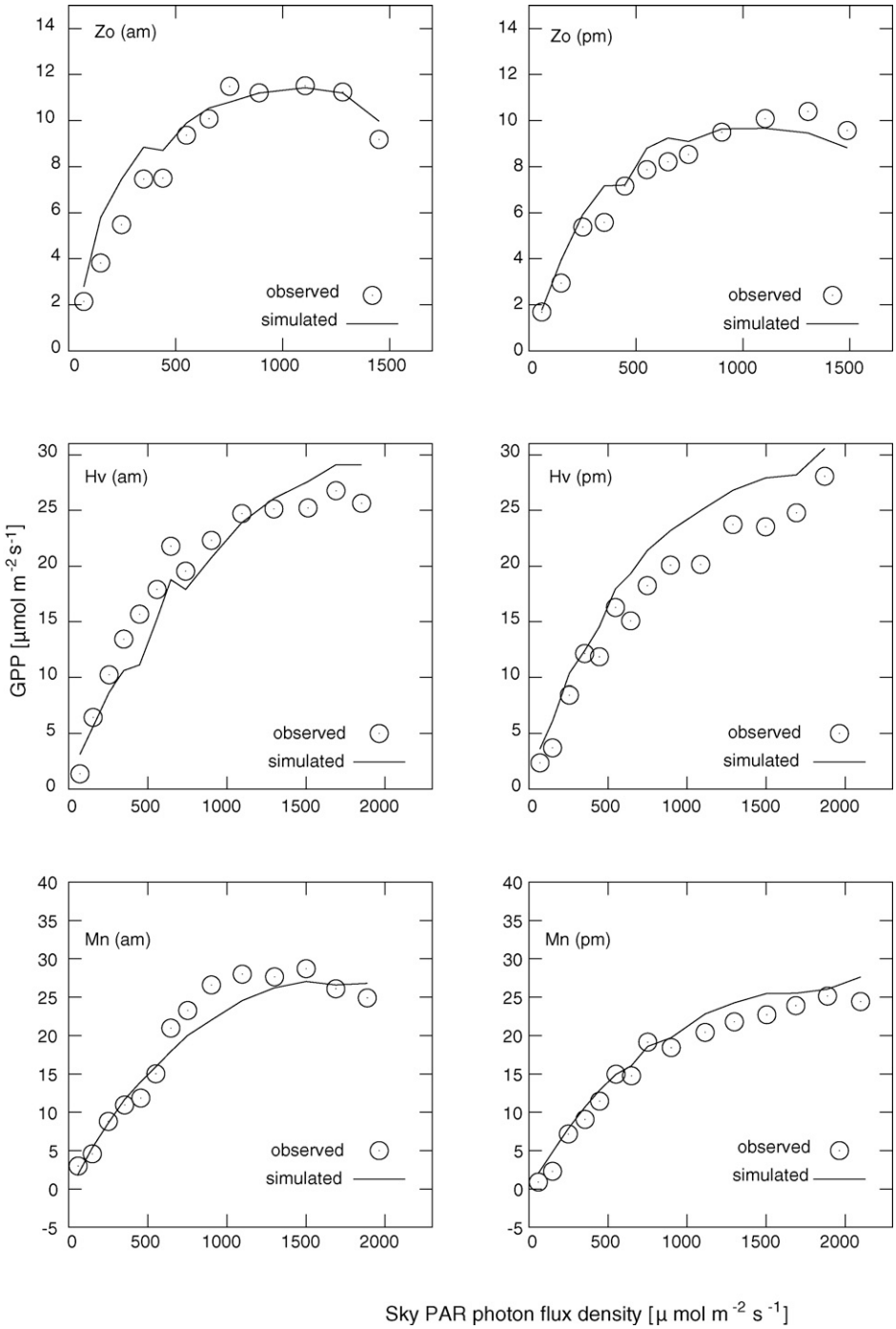

Fig. 1. Comparison of observed and simulated GPP at each of our study sites when using the canopy properties given in Table 2. Observed GPP is inferred in the standard way as GPP = $R_e - F - S$ (Lloyd et al., 2002). Quantity F is the carbon flow recorded 5–15 m above the canopy, S the storage of CO_2 recorded within the canopy airspace and R_e is the ecosystem respiration estimated from night-time respiration (Medlyn et al., 2003). The average canopy response to photosynthetically active radiation (PAR) is shown for morning (left) and afternoon (right) after binning measured and simulated values of GPP over the growing season (Julian Days 120–270) at Zotino (Zo) and Harvard (Hv) and part of the growing season (Julian Days 243–431) at Manaus (Mn). Uncertainties in observed GPP are twice the size of the markers.

FLUXNET Principle Investigators. The energy calculation central to the model is based on a Penman-Monteith approach (Monteith, 1965), ensuring that the downwelling shortwave and longwave fluxes are balanced by the outgoing fluxes of sensible heat, latent heat, conduction into the ground, reflected shortwave radiation and radiant thermal energy. Apart from meteorological driving data, input to the simulation occurs through a control file which prescribes certain time-invariant parameters for the canopy and the ground. For ground albedo, leaf reflectance and leaf transmittance these parameters are set to the values in Table 2 in order to ensure consistency with the RT simulation conducted with FLIGHT. By setting k_{rub}, in the control file, we also prescribe the subset of GPP values to be retrieved from the LUT created with FLIGHT.

At each timestep of the LSM simulation, canopy GPP is read from the LUT, according to the solar zenith angle (calculated internally from the latitude and time of day, etc.), downwelling sky radiant flux density (SW contained in the driving data), the fraction of sunlight energy which is diffuse (calculated internally) and canopy microclimate (leaf temperature and leaf internal CO_2 concentration, both prognostic variables). The fraction of diffuse sunlight, fDIF, is estimated at each timestep according to the ratio of SW and the top-of-atmosphere solar irradiance (Roderick et al., 2001). This method of estimating fDIF has an absolute error of ≤ 0.1 when compared against measurements conducted at the boreal site (Alton et al., 2005). Leaf temperature and leaf internal CO_2 concentration are estimated for the canopy as a whole. They follow from the Penman-Monteith surface energy balance and a simplified Leuning stomatal conductance model, respectively (Cox et al., 1998). Note that output from JULES encompasses numerous variables associated with flux exchange (e.g. evapotranspiration, run-off, soil and plant respiration) but this articles focuses on predictions of canopy GPP for various configurations of k_{rub}.

2.3. Simulations

The LSM is run for each of our three sites for a period of about 1 year. However, GPP is only extracted and integrated for the growing season or part thereof. For the boreal and temperate sites, this integration period is Julian Days 120–270 (i.e. June–August included). Meteorological driving data are taken from 1999 for Zotino and from 2002 for Harvard. For the tropical site, Manaus, climatic data are not available for a complete year. Data are taken from 1999 for the integration period of Julian Days 243–431 (begin September–begin March). Apart from September and October, this corresponds to the wet season at this location (Williams et al., 1998). To estimate productivity for the entire year at Manaus, GPP over the integration period is multiplied by a factor (431–243)/365, i.e. 1.9. In our default simulations, k_{rub}, is increased from 0.0 to 2.0 in steps of 0.5 for each site. An additional land-surface simulation is carried out with $k_{rub} = 0.15$ for comparison with Rubisco gradients measured in the field (see Section 4). Initially, fDIF is estimated at each timestep, according to downwelling shortwave radiation, as explained above. However, in order to ascertain the role of diffuse sunlight, all simulations are repeated separately either with pure direct sky radiation or pure diffuse sky radiation. Simulations are also run for a uniform vegetation layer by configuring FLIGHT in 1D mode (i.e. without crowns but otherwise adopting the same parameters given in Table 2). The 1D configurations permit a comparison with previous authors who use 1D models when examining light-acclimation. Comparison between our 1D and 3D simulations will reveal, to some extent, the sensitivity of our results to canopy structure. However, the clumping of leaves, and the gaps in the foliage thus created, are considered by certain authors to have a strong bearing on light propagation and canopy photosynthesis (e.g. Baldocchi and Harley, 1995). Therefore, for our temperate, broadleaf site, Harvard, a clumped 3D canopy is also configured within FLIGHT. For this clumped configuration, we adopt the same parameters as those in Table 2 but, on this occasion, we place foliage in spheres of radius 1.5 m.

Leaf inclination has a strong influence on how light is captured at different heights in the canopy and we test its role with respect to acclimation. Our default LAD is spherical and possesses a mean leaf angle (MLA) of 57° (average zenith angle of the leaf normal). This approaches the upper limit of MLA recorded in the field (27–64°; Campbell and Norman, 1998; Falster and Westoby, 2003). To gauge the impact of more horizontally orientated leaves, we repeat our simulations with a planophile LAD of MLA = 27°.

Friend (2001) and Chen et al. (1993), in their respective 1D simulations of acclimation in a temperate, broadleaf stand and a cotton canopy, use a leaf photosynthetic response which changes abruptly from a light-limited state to a N-limited state, i.e. colimitation (smoothing factors) are omitted from the leaf model. Furthermore, both these studies allow active N, associated with the light reaction (chlorophyll), to vary with height through the canopy. This is not possible in our default simulations due to the height-invariant parameterisation of quantum efficiency (Table 2).

Therefore, in a second batch of simulations, we implement the non-colimitation leaf model of Chen et al. in FLIGHT. The formulation of Chen et al. assumes a coupling between the leaf-N involved in electron transport (J_{max}) and that present in Rubisco (V_{cmax}). This coupling (Eqs. (6) and (7) in Chen et al.) approximates the relationship observed in real tree canopies (e.g. Fig. 2 in Meir et al., 2002) and accounts for the (partial) reallocation of active leaf-N from Rubisco to the light-harvesting apparatus that is typically observed in shade leaves (Warren and Adams, 2001; Eichelmann et al., 2005).

In summary, our experiments are organised as follows:

1. 1D and 3D simulations, all three sites, using the colimitation leaf model.
2. As (1) but replacing the spherical LAD with a planophile LAD.
3. A 3D simulation with clumped foliage for Harvard, using the colimitation leaf model.
4. As (1) using the non-colimitation leaf model of Chen et al.

3. Results

We present our results according to the sequence of experiments outlined above:

3.1. Experiment 1

Fig. 2 depicts GPP predicted by our primary simulations for different configurations of Rubisco (k_{rub}), canopy structure (1D/3D) and fraction of diffuse sky radiation (fDIF). In Table 3, the optimal value of k_{rub} is compared to values of k_{ext} inferred for light extinction. The optimal value of k_{rub} is determined from the turning point of a quadratic function fitted to the values of GPP displayed in Fig. 2. The quadratic function is fit using a least-squares minimisation over the k_{rub} range of 0.5–2.0 for Zotino and 0.15–1.5 for Harvard and Manaus. An example of this fitting procedure is illustrated in the bottom-middle panel of Fig. 2. From the figure and table we note the following:

1. For 1D canopy structure, the theoretically optimal value of k_{rub} ranges from 0.99 to 1.6 across the three test sites (column 2 of Table 3). For 3D canopy structure, the optimal Rubisco gradient is 0.78–1.4, i.e. slightly shallower (column 3).
2. The optimal value of k_{rub} is similar for pure diffuse and pure direct sunlight, although, for pure diffuse sky irradiance, a slightly steeper Rubisco distribution is favoured at the tropical and temperate sites (columns 4–7 of Table 3). For diffuse sky irradiance, we note an enhancement in canopy light-use efficiency of 20–40%, compared to pure direct sunlight (right and middle panels of Fig. 2). This is due to greater radiation-sharing under diffuse sunlight (Roderick et al., 2001; Farquhar and Roderick, 2003) and, for these particular sites, is discussed in detail elsewhere (Alton et al., 2007b).
3. The gain in GPP for an optimal distribution of Rubisco, compared to a uniform distribution ($k_{rub} = 0$), is 10–21% for a 3D canopy and 13–39% for a 1D structure.
4. Apart from the 1D representation of the boreal site, Zotino, the optimal value of k_{rub} (columns 2 and 3 of Table 3) is fairly close to the value of k_{ext} inferred

Table 3
Comparison of the optimal Rubisco distribution k_{rub} (columns 2–9) against the average light profile k_{ext} (columns 10–14)

Site (1)	k_{rub}								k_{ext}					
	fDIF (lD) (2)	fDIF (3D) (3)	Dir (lD) (4)	Dif (lD) (5)	Dir (3D) (6)	Dif (3D) (7)	Chen (lD) (8)	Chen (3D) (9)	Horiz (lD) (10)	Horiz (3D) (11)	Leaf (3D) (12)	Mode (3D) (13)	W-mode (3D) (14)	$\overline{f\mathrm{DIF}}$ (15)
Zo	1.60	1.37	1.75	1.50	1.50	1.25	1.64	1.31	1.13	1.20	8.0	1.50	1.38	0.7
Hv	1.06	0.92	1.05	1.15	0.91	1.00	1.06	0.73	0.99	1.01	5.7	1.35	1.24	0.7
Mn	0.99	0.78	0.95	1.08	0.73	0.88	1.08	0.85	0.98	1.10	4.9	1.47	1.65	0.8

Columns for k_{rub} refer to the following simulations: 1D and 3D canopy taking account of the fraction of diffuse sunlight fDIF (2 and 3); 1D canopy for pure and direct sunlight (4 and 5); 3D canopy for pure and direct sunlight (6 and 7); non-colimitation leaf photosynthesis of Chen et al. (1993) accounting for fDIF (8 and 9). Columns for k_{ext} take account for fDIF and quantify the extinction as follows: mean, downwelling irradiance in the horizontal plane for the 1D and 3D canopy (10 and 11); mean upwelling and downwelling irradiance in the leaf plane for 3D canopy (12); mode downwelling irradiance in the horizontal plane for 3D canopy (13); as column 13 but weighting GPP at each timestep using the default value of 0.15 for k_{rub} (14). The time-averaged value of fDIF is given in column (15). All time-averaged and GPP-weighted values refer to daylight hours of the integration period. Uncertainties in the extinction coefficients and the optimal values of k_{rub}, are 0.05 except column (12) where the uncertainty is 0.7.

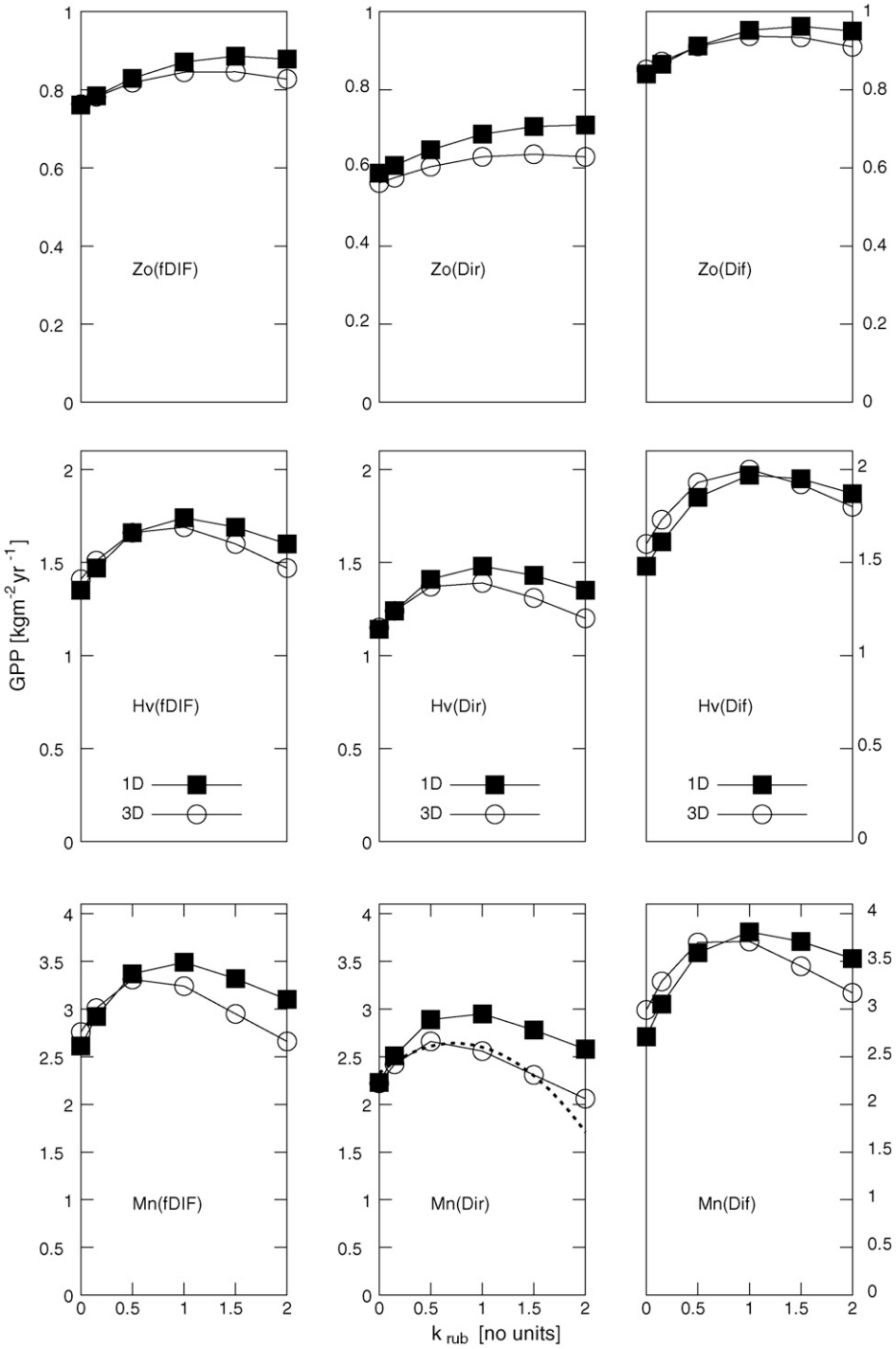

Fig. 2. GPP against the N-allocation parameter k_{rub} for all three sites: Zotino (top), Harvard (middle) and Manaus (bottom). These results correspond to our primary simulations (experiment 1 in the text). At each location, simulations are shown for a 1D and a 3D canopy (solid squares and open circles, respectively). Panels on the right correspond to pure diffuse sunlight. Those in the middle represent pure direct sunlight. For the left panels, the fraction of diffuse sunlight (fDIF) is estimated at each timestep of the simulation, as described in the text. In the bottom-middle panel, the dashed line demonstrates the quadratic fitting procedure used to locate the optimal value of k_{rub}.

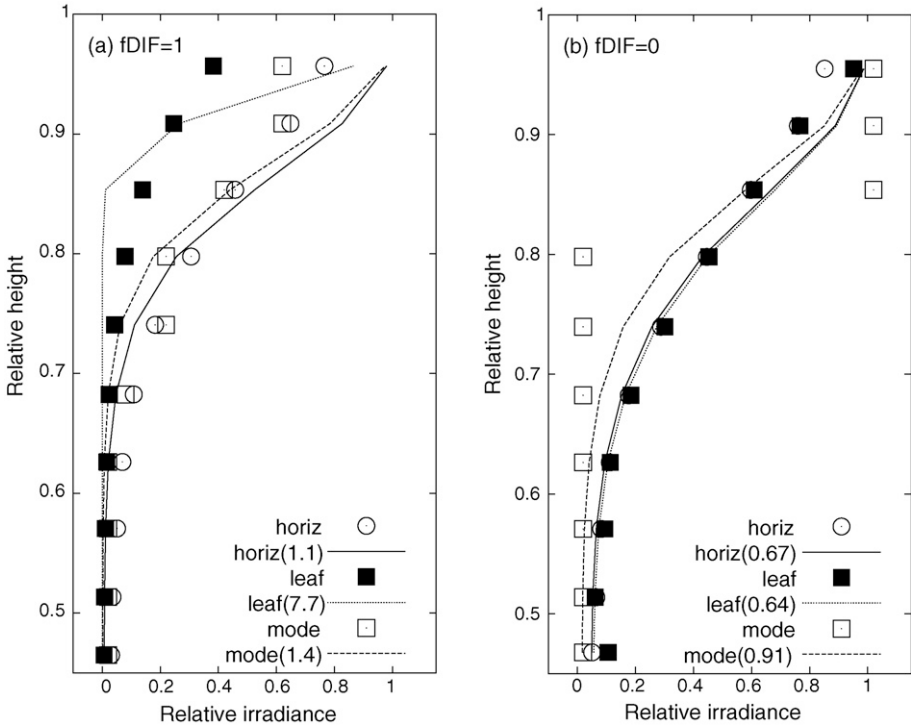

Fig. 3. Examples of the fitting procedure to determine k_{ext} under different conditions of sky radiation. For Harvard forest, we show irradiance relative to a position just above the canopy (Eq. (2)), obtained with 3D ray-tracing simulations. Panels depict light profiles for the following conditions: (a) pure diffuse sunlight; and (b) pure direct sunlight with $\theta_s = 46^\circ$ (mean, GPP-weighted solar zenith angle at this site for the growing season). Light profiles and the corresponding exponential fits are traced as follows: the mean, downwelling irradiance in the horizontal plane (open circles and solid line, respectively); the mean irradiance in the plane of the leaf (solid squares and dotted line); and the mode, downwelling irradiance in the horizontal plane (open squares and dashed line). Values of k_{ext} for the fits are given in parentheses in the legend. The fitted profiles appear non-exponential in this figure because irradiance is shown against relative height in the canopy, rather than against cumulative LAI.

from mean, downwelling irradiance in the horizontal plane (columns 11 and 12). Light extinction, as quantified by the mean irradiance in the plane of the leaf (column 13) or the mode irradiance in the horizontal plane (column 14), is steeper than the optimal Rubisco distribution. However, exponential profiles fit very poorly to both the mode irradiance, under direct sunlight, and the mean irradiance in the plane of the leaf under diffuse sunlight (Fig. 3).

5. Inferred extinction coefficients change little when weighting for GPP at each timestep. This is demonstrated in Table 3 for the mode irradiance (columns 14 and 15).
6. The mean value of fDIF is high at all sites for the integration period (≃0.7). The mean value of fDIF, weighted for GPP at each timestep, is only slightly lower (≃0.5).

3.2. Experiment 2

Results for the planophile LAD are broadly similar to those generated by our primary simulations using a spherical LAD (i.e. experiment 1). Table 4 summarises our results using a planophile LAD for the 3D canopy. Optimal k_{rub} ranges from 0.87 to 1.2 (cf. 0.78–1.4 using a spherical LAD). Light profiles appear to be very similar, although mean irradiance in the plane of the leaf declines less steeply with depth through the canopy using a planophile LAD.

3.3. Experiment 3

Clumping the foliage has little impact on the results from our 3D simulations of the temperate, broadleaf canopy, Harvard. The optimal value of k_{rub} is 0.86 (cf. 0.92 in experiment 1). The light profile is broadly similar to that produced using non-clumped foliage. Inferred values of k_{ext} are 1.1, 4.0, 1.9 and 1.7 using, respectively, the mean irradiance in the horizontal plane, the mean irradiance in the plane of the leaf, the mode irradiance and the GPP-weighted mode irradiance (cf. 1.0, 5.7, 1.4 and 1.2, respectively, given in Table 3 for experiment 1). For their respective optimal configurations of Rubisco, predicted GPP is 7% lower

Table 4
As Table 3 but adopting a planophile LAD

Site (1)	k_{rub} fDIF (3D) (3)	k_{ext}		
		Horiz (3D) (11)	Leaf (3D) (12)	Mode (3D) (13)
Zo	1.20	1.19	4.2	1.38
Hv	0.99	1.08	3.4	1.57
Mn	0.87	1.16	3.2	1.49

Columns are shown for the 3D simulation and are designated as in Table 3.

in the 3D simulation which clumps foliage compared to the non-clumped 3D simulation.

3.4. Experiment 4

The optimal value of k_{rub} does not appear to depend sensitively on the leaf model of photosynthesis. Results are shown in columns 8 and 9 of Table 3 using the non-colimitation leaf model of Chen et al. (1993).

4. Discussion

4.1. Theoretical light profiles

Even after accounting for clumping of the foliage within the crown, our light profiles do not appear to be very sensitive to canopy structure. In contrast, both diffuse sunlight and the manner in which we quantify the light profile bear strongly on the issue of acclimation. All our techniques for sampling irradiance indicate a steeper average light profile under diffuse sky radiation compared to direct sunlight. This is especially true when irradiance is measured in the plane of the leaf. Approximately half of the photons comprising diffuse sky radiation have zenith angles greater than 60°. These oblique photons are absorbed strongly in the upper 30% of the crown producing a steep light profile under diffuse sunlight (Fig. 3, panel a). Photons penetrating into the lower canopy have preferentially small zenith angles. Their incidence on foliage possessing a spherical LAD (MLA = 57°) is low, producing a gentler light profile in the lower portion of the canopy. The directionality of sky radiation under clouds and high aerosol loading is an aspect of acclimation and assimilation studies which has been considered very little in the past.

Under diffuse sunlight, the profile of mean irradiance in the plane of the leaf is poorly fit by an exponential function due to the strong absorption at the top of the crown, as mentioned above. Similarly, the mode irradiance in the horizontal plane is very difficult to fit using an exponential profile for conditions of direct sunlight (Fig. 3, panel b). For this latter case, the penetration of sunflecks produces a bi-modal distribution in light intensity more or less throughout the canopy. An abrupt change in the mode irradiance occurs in the upper third of the crown (Fig. 4).

Of the techniques we employ to quantify the light profile which measure of irradiance is relevant for studies of acclimation? Traditionally, k_{ext} is defined for mean, downwelling irradiance in the horizontal plane (Sellers et al., 1996). The horizontal light detectors utilised in field studies also capture irradiance in this way (e.g. Meir et al., 2002; Parker et al., 2002) although

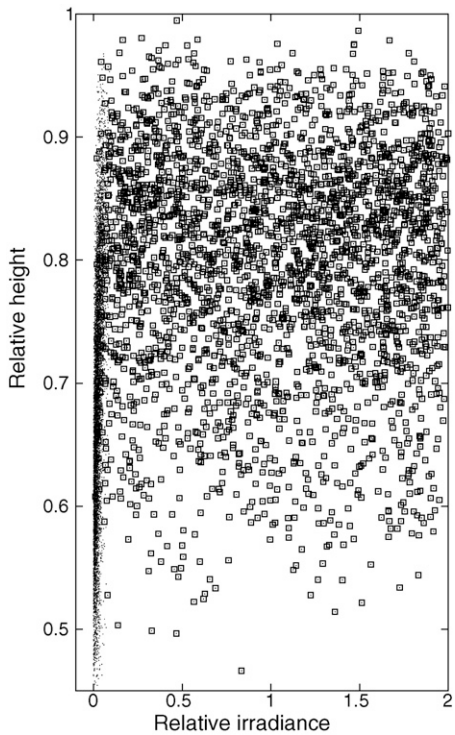

Fig. 4. Leaf irradiance corresponding to the simulation (b) in Fig. 3. Open rectangles and dots denote sunlit and shaded leaves, respectively. Note that the scale of the horizontal axis differs from that used in Fig. 3.

this may be motivated, in part, by the difficulty of orientating light detectors parallel to the leaf. Despite the traditional focus on downwelling irradiance in the horizontal plane, it is almost certainly the irradiance in the plane of the leaf which is relevant for leaf photosynthesis and, by corollary, important to studies of light-acclimation. Furthermore, the tendency of leaves to separate into two well defined groups when direct sunlight dominates, namely sunlit and shaded fractions, implies that the mean irradiance is not necessarily a reliable indicator of typical leaf irradiance. In this case, we might expect acclimation to occur with respect to the mode irradiance since this latter quantity typifies light intensity at any given height (Fig. 4).

4.2. Predicted optimal Rubisco distribution

The optimal Rubisco distribution for a 3D canopy is slightly shallower than that associated with a uniform vegetation layer. This is due to crown shape. For the 3D stand, the relative abundance of foliage in the mid-canopy, due to the circular or elliptical shape of the crowns, means that a shallower Rubisco gradient is favoured compared to a canopy where the same amount of foliage exists at each height (uniform 1D canopy). This aspect has been overlooked in the past since, typically, acclimation modellers configure 1D canopies (Chen et al., 1993; Kull and Kruijt, 1999; Friend, 2001). Given the steep profile for leaf irradiance under diffuse sunlight (Section 4.1), it is somewhat surprising that the optimal values of k_{rub} are so similar for pure diffuse and pure direct sky fluxes. It might be argued that crown shape plays a role here too, and that, despite the strong absorption of diffuse sunlight by the upper crown, it is the bulk of the leaves in the mid-canopy that influences the optimal Rubisco distribution. However, for our 1D simulations, where crown shape plays no role, the optimal values of k_{rub} are also broadly similar for diffuse and direct sunlight (Table 3). One possible explanation is an acclimation to the mode irradiance for which we derive fairly similar values of k_{ext} under direct and diffuse sunlight (Fig. 3).

4.3. Comparison of theory with measurement

It is already noted that the Rubisco gradient measured within real tree canopies is shallow compared to the corresponding light profile. Recent measurements by Carswell et al. (2000), Lewis et al. (2000) and Meir et al. (2002), which collectively encompass a diversity of broadleaf and needleleaf stands, indicate a range of 0.13–0.5 for k_{rub} with a median average close to 0.15. These values are two to three times smaller than the corresponding extinction coefficient measured in situ from the mean, downwelling irradiance in the horizontal plane (usually under direct sunlight). The extinction coefficients of our theoretical light profiles, based on mean irradiance in the horizontal plane, are close to unity and, therefore, consistent with the aforementioned field measurements of the light profile. For our tropical, broadleaf stand, Manaus, the light profile is measured by Carswell et al. (2000) using horizontally oriented detectors and by averaging over the daylight period in November. We infer $k_{ext} \simeq 0.6$ from their Fig. l, although their measurements are probably biassed towards small solar zenith angles when sky radiant flux density is greatest. The value of k_{ext} we derive from our 3D simulations of Manaus is 0.5 for pure direct sunlight and $k_{ext} = 0.9$ for pure diffuse sunlight.

The light profiles and optimal Rubisco distributions inferred from our simulations are all steeper than the observed range of k_{rub}. Our study corroborates, therefore, the claim that light acclimation is incomplete in tree canopies (Meir et al., 2002). We wish to explore reasons why the simulated optimal distribution of leaf-N differs so greatly from the distribution recorded in the field. Initially, we assume that light environment is the primary influence on the location of active leaf-N in the crown.

4.3.1. Parameterisation of the model

Our results might be sensitive to the exact configuration of our RT simulation, in particular to the adopted leaf optical properties or the total amount of leaf-N prescribed for the canopy (V^0_{cmax}). However, the parameters in Table 2 vary significantly across all three stands and probably encompass the real uncertainties in these parameters. Furthermore, our main conclusions are unaltered by implementation of a planophile LAD, despite leaf irradiance changing somewhat under diffuse sunlight. This insensitivity of the optimal k_{rub} to the LAD is probably explained by the manner in which we average over a wide range of solar zenith angles when considering acclimation.

4.3.2. Leaf photosynthetic model

Friend (2001) claims that only a heterogeneous leaf model (e.g. that of Kull and Kruijt, 1999) allows shallow N gradients to be reproduced in simulations of light-acclimation. This is due, purportedly, to the absence of colimitation (smoothing) factors, which allows the leaf response to saturate much more strongly

to incident light. We find, however, that our main conclusions are insensitive to the presence of colimitation factors in the leaf photosynthetic model. The formulation of Chen et al. (1993), which also allows for the coupling of leaf-N between Rubisco and chlorophyll, produces identical results within the errors. Furthermore, we note that, regardless of the leaf photosynthetic model employed in the simulation, the average photosynthetic response at any given height in the canopy is relatively smooth due to the range of leaf inclinations represented by the LAD.

4.3.3. Seasonal effects

Chen et al. (1993) carry out a 1D modelling study of acclimation in a cotton canopy. Compared to the present study, their optimised profile of leaf-N is much closer to the corresponding theoretical light profile (as quantified by the mean, downwelling irradiance in the horizontal plane). The differences between the current study and that of Chen et al. might be attributable to the climate data used to force the model. Chen et al. force their model re-iteratively with climate data from the same (sunny) day and allow the Rubisco, the total amount of which is fixed, to re-distribute itself in the canopy so as to maximise GPP. In the current study, simulations are conducted for a more protracted period (several months) and the optimal Rubisco distribution may change during this period. Restricting the acclimation period to either the month of June or the month of August does not, however, change our conclusions for the two sites where seasonal effects are most likely to be pronounced (the boreal and temperate stands). As before, we conclude that both the light profile and the corresponding optimal Rubisco profile possess a vertical, exponential fall-off which is close to or greater than unity, i.e. much steeper than the measured Rubisco profile.

4.3.4. Non-exponential Rubisco distribution

The optimal Rubisco profile may be poorly described by an exponential function. Indeed, our RT-simulations suggest that a hyperbolic or step function may be more appropriate for a light-acclimated canopy. For example, under diffuse sunlight, the irradiance in the plane of the leaf falls steeply in the upper 30% of the temperate, broadleaf canopy, but near the ground, the light profile is quite shallow (Fig. 3, panel a). Indeed, if we fit the light profile over the lower 70% of the temperate, broadleaf crown, using the mean irradiance in the plane of the leaf, we infer $k_{ext} = 0.75$, which is somewhat closer to the observed range of k_{rub}. Meir et al. (2002) conjecture that diffuse sunlight is important for acclimation. The mean value of fDIF at all our sites is high ($\simeq$0.7), even after weighting for GPP ($\simeq$0.5), and this underlines the importance of diffuse sunlight to canopy photosynthesis. Measured values of fDIF at our boreal site exhibit a bi-modal distribution, according to whether cloud cover is heavy or not (Alton et al., 2005). The mean value of fDIF, that we infer for our three selected stands, appears to typical of most 1 arc-degree landpoints (Alton et al., 2007a). For locations where direct sunlight dominates the growing season, we might expect a step function in the Rubisco distribution if leaf-N is influenced by the mode irradiance. For example, if we fit the light profile over the lower 70% of the temperate, broadleaf crown (Fig. 3, panel b), we obtain $k_{ext} = 0.0$. This uniform profile is produced by the dominance of shaded foliage (77% of leaves) in the lower 70% of the crown. If we include upwelling radiation in the mode irradiance, the corresponding value of k_{ext} is 0.27. These estimates of k_{ext}, for the lower two thirds of the crown, are close to the value of k_{rub} recorded in real tree canopies. Exclusion of the upper 30% of the crown, from the light profile, may seem somewhat arbitrary. However, the bulk of the foliage is located in the mid-canopy and it seems reasonable that the optimal distribution of Rubisco is heavily influenced by light interception in this part of the foliage. We note that the photosynthetic capacity measured by Carswell et al. (2000), for the tropical, broadleaf site Manaus, does not extend beyond 80% of the stand height (trunk + crown), presumably due to problems of access. The region where Rubisco may be quite steep, in the upper third of the crown, is therefore poorly sampled, if at all. The non-exponential form of light profiles is confirmed observationally by Parker et al. (2002). Within tall, coniferous stands of age 155–500 years, these authors identify three zones: a shaded region in the lower 20–40% of the stand; a sunlit region in the upper 10–30% of the stand; and a transitional region between the shaded and sunlit zones where mean irradiance, in the horizontal plane, changes rapidly with height and possesses a large horizontal variation. Outside the transitional zone, the light profile is rather shallow.

4.3.5. Considerations beyond light interception

Light is unlikely to the only influence on the distribution of leaf-N within the canopy. As pointed out by Meir et al. (2002), N is required for structural elements, both inside and outside the leaf, and, as a scarce resource, may be distributed throughout the plant so as to minimise herbivory. By comparing our model against measurements of photosynthetic capacity the

present investigation focuses on active leaf-N but we recognise that Rubisco may be used as a store of N by plants (Warren and Adams, 2001). Rubisco concentration also relates to the age and longevity of leaves in evergreen species (Kikuzawa, 2003; Niinemets et al., 2004; Miyazawa et al., 2004) and may change through the growing season (Warren and Adams, 2001). Drought is also likely to play a role in how active leaf-N is distributed since the top leaves of the canopy are more difficult to irrigate and stomatal pores may remain closed in this zone during large parts of the diurnal cycle (Williams et al., 1998). The current study concentrates on GPP. However, plant respiration may also be an important consideration for studies of acclimation. Optimising the Rubisco distribution with respect to net canopy assimilation (i.e. GPP $- R_l$, where R_l is the total leaf respiration) produces identical results, within the errors, for our simulations. We are reluctant to extend the modelling exercise to net primary product (NPP) since this involves many assumptions about how N is partitioned between above-ground biomass and the rootstock. Finally, our simulations indicate that the 'loss' in canopy productivity with Rubisco distributed as measured ($k_{rub} = 0.15$), rather than with a fully light-acclimated distribution, is not too great (8–13% across all three canopies). For the tropical and boreal sites, this constitutes only a third of the observed decrease in canopy photosynthesis that occurs during the early afternoon due to partial closure of the leaf stomata (Fig. 1). For canopies possessing a relatively low total N content, Leuning et al. (1991) predict a 10% reduction in carbon assimilation when Rubisco is distributed uniformly rather than optimally. This is at the lower end of the deficit predicted by our 3D simulations (10–21%).

5. Conclusions

We simulate light propagation and canopy photosynthesis in heterogeneous tree canopies by coupling a Monte Carlo, 3D, ray-tracing model to a state-of-the-art representation of the vegetated land-surface (JULES). We determine the vertical, exponential profile in Rubisco which maximises canopy GPP for a fixed total amount of leaf-N in the canopy (hence the optimal N-allocation parameter k_{rub}) and compare with the corresponding theoretical light profile. The simulations are conducted for three quite different tree stands where structural parameters and climate data are available (a sparse, boreal needleleaf; a dense, tropical broadleaf; and a moderately dense, temperate broadleaf). Our radiative-transfer takes account of diffuse sky radiation and its directionality.

The optimal values of k_{rub} are between 0.8 and 1.4. This is close to our estimates of the extinction coefficient as quantified by the mean, downwelling irradiance in the horizontal plane ($k_{ext} = 1.0–1.2$). Both our light profiles and our optimal profiles of Rubisco are much steeper than the profiles of k_{rub} inferred in a diverse range of real tree canopies (0.13–0.5; Carswell et al., 2000; Lewis et al., 2000; Meir et al., 2002). Our study, therefore, strengthens the view that light acclimation is incomplete in tree canopies. The interpretation of our results is not significantly influenced by canopy architecture (1D/3D structure, leaf-clumping and LAD). However, both diffuse sunlight and the manner in which we quantify the light profile are important considerations. For example, under diffuse sunlight, the mean irradiance in the plane of the leaf decreases both steeply and in a non-exponential manner in the upper third of the crown but is relatively shallow thereafter. Thus, for the temperate, broadleaf stand, we infer $k_{ext} = 0.75$ when just considering the lower 70% of the crown under diffuse sunlight.

Under direct sunlight, a more appropriate measure of light environment is probably the mode irradiance. When the foliage divides into sunlit and shaded fractions, the mean average constitutes a poor indicator of typical irradiance at any given height in the canopy. The mode irradiance in the horizontal plane possesses a step function under direct sunlight due to the dominance of sunlit foliage in the upper third of the crown and a preponderance of shade foliage below that height. Thus, if interception of *direct* sunlight is the primary criterion for the distribution of active leaf-N, we might expect to find shallow Rubisco gradients ($k_{rub} = 0–0.27$) in both the upper and lower portions of the canopy, with an abrupt step from high to low photosynthetic capacity in the upper third of the crown. Our simulations imply that better sampling of photosynthetic capacity in the upper third of the crown would be instructive. The theoretical gain in GPP for a stand that is fully light-acclimated compared to one that is only partially acclimated (i.e. with $k_{rub} = 0.15$, as measured in real tree canopies) is moderately important (8–13%).

Acknowledgements

We thank Steve Wofsy, Jon Lloyd and Phil Harris for making their FLUXNET datasets available to us. The investigators of the LBA project are acknowledged, in particular Drs. Nobre and Kabat. This study made use of

the FLUXNET sites at http://daac.ornl.gov/FLUXNET/fluxnet.html and ftp://ftp.as.harvard.edu/pub. This work was financed by the Natural Environment Research Council (NERC).

References

Alton, P., North, P., Kaduk, J., Los, S., 2005. Radiative transfer modelling of direct and diffuse sunlight in a Siberian pine forest. J. Geophys. Res. Atmos. 110, D23209.

Alton, P., Ellis, R., Los, S., North, P., 2007a. Improved global simulations of Gross Primary Product based on a separate and explicit treatment of diffuse and direct sunlight. J. Geophys. Res. 112, D07203.

Alton, P., North, P., Los, S., 2007a. The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes, Global Change Biol., accepted article online. doi:10.1111/j.1365-2486.2007.01316.x.

Alton, P., Mercado, L., North, P., 2007c. A sensitivity analysis of the land-surface scheme JULES conducted for three forest biomes: biophysical parameters, model processes and meteorological driving data. Global Biogeochem. Cycles 20 (1), GB1008.

Baldocchi, D., Harley, P., 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. II. Model testing and application. Plant Cell Environ. 18, 1157–1173.

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, Ch., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Xuhui, L., Yadvinder, M., Meyers, T., Munger, W., Oechel, W., Paw, K., Pilegaard, K., Schmid, H., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsey, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapour and energy flux densities. Bull. Am. Meteorol. Soc. 82, 2415–2434.

Barton, C., North, P., 2001. Remote sensing of canopy light-use efficiency using the photochemical reectance index. Model and sensitivity analysis. Remote Sens. Environ. 78, 264–273.

Boas, M., 1983. Mathematical Methods in the Physical Sciences. John Wiley & Sons, New York.

Campbell, B., Norman, J., 1998. Environmental Biophysics. Springer-Verlag, New York.

Carswell, F., Meir, P., Wandelli, E., Bonates, L., Kruijt, B., Barbosa, E., Nobre, A., Grace, J., Jarvis, P., 2000. Photosynthetic capacity in a central Amazonian rain forest. Tree Physiol. 20, 179–186.

Chen, J., Reynolds, J., Harley, P., Tenhunen, J., 1993. Coordination theory of leaf N distribution in a canopy. Oecologia 93, 63–69.

Collatz, C., Ball, J., Grivet, C., Berry, J., 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes laminar boundary layer. Agric. For. Meteorol. 54, 107–136.

Cox, P., Huntingford, C., Harding, R., 1998. A canopy conductance and photosynthesis model for use in a GCM land surface scheme. J. Hydrol. 212–213, 79–94.

Cox, P., Betts, R., Bunton, C., Essery, R., Rowntree, P., Smith, J., 1999. The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. J. Clim. Dyn. 15, 183–203.

Cox, P., Betts, R., Jones, C., Spall, S., Totterdell, I., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.

Cox, P., 2001. Description of the TRIFFID dynamic global vegetation model, Hadley Centre Technical Note 24. Ed. Met.Office, Bracknell, UK.

Dang, Q., Margolis, H., Collatz, G., 1998. Parameterization and testing of a coupled photosynthesis-stomatal conductance model for boreal trees. Tree Physiol. 18, 141–153.

Disney, M., Lewis, P., North, P., 2000. Monte Carlo methods in optical canopy reflectance modelling. Remote Sens. Rev. 18, 163–196.

Eichelmann, H., Oja, V., Rasulov, B., Padu, E., Bichele, I., Pettai, H., Maend, P., Kull, O., Laisk, A., 2005. Adjustment of leaf photosynthesis to shade in a natural canopy: reallocation of nitrogen. Plant Cell Environ. 28, 389–401.

Falster, D., Westoby, M., 2003. Leaf size and angle vary widely across species: what consequences for light interception? New Phytol. 158, 509–525.

Farquhar, G., Roderick, M., 2003. Pinatubo, diffuse light and the carbon cycle. Science 299, 1997–1998.

Frak, E., Le Roux, X., Millard, P., Adam, B., Dreyer, E., Escuit, C., Sinoquet, H., Vandame, M., Varlet-Grancher, C., 2002. Spatial distribution of leaf nitrogen and photosynthetic capacity within the foliage of individual trees: disentangling the effects of local light quality, leaf irradiance, and transpiration. J. Exp. Biol. 53, 2207–2216.

Friend, A., 2001. Modelling canopy CO_2 fluxes: are 'big-leaf' simplifications justified? Global Ecol. Biogeogr. 10, 603–619.

Goulden, M., Munger, J., Fan, S., Daube, B., Wofsy, S., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biol. 2, 169–182.

Gu, L., Baldocchi, D., Verma, S., Black, T., Vesala, T., Falge, E., Dowty, P., 2002. Advantages of diffuse radiation for terrestrial ecosystem productivity. J. Geophys. Res. 107, 10.1029.

Harris, P., Huntingford, C., Gash, J., Hodnett, M., Cox, P., Malhi, Y., Araujo, A., 2004. Calibration of a land-surface model using data from primary forest sites in Amazonian. Theor. Appl. Climatol. 78 (103), 27–45.

Hirose, T., Werger, M., 1987. Maximising daily canopy photosynthesis with respect to leaf N allocation pattern in the canopy. Oecologia 72, 520–526.

Hollinger, D., Kelliher, F., Byers, J., Hunt, J., McSeveny, T., Wier, P., 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. Ecology 75, 134–150.

Kikuzawa, K., 2003. Phenological and morphological adaptations to the light environment in two woody and two herbaceous plant species. Funct. Ecol. 17, 29–38.

Kull, O., Kruijt, B., 1999. Acclimation of photosynthesis to light: a mechanistic approach. Funct. Ecol. 13, 24–36.

Leuning, R., Wang, Y., Cromer, R., 1991. Model simulations of spatial distributions and daily totals of photosynthesis in *Eucalyptus grandis* canopies. Oecologia 88, 494–503.

Lewis, J., McKane, R., Tingey, D., Beedlow, P., 2000. Vertical gradients in photosynthetic light response within an old-growth douglas-fir and western hemlock canopy. Tree Physiol. 20, 447.

Lloyd, J., Shibistova, O., Zolotoukhine, D., Kolle, O., Arneth, A., Wirth, C., Styles, J., Tchebakova, N., Schulze, E., 2002. Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest. Tellus 54B, 590–610.

Medlyn, B., Barrett, D., Landsberg, J., Sands, P., Clement, R., 2003. Conversion of canopy-intercepted radiation to photosynthate: review of modelling approaches for regional scales. Funct. Plant Biol. 30, 153–169.

Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A., Jarvis, P., 2002. Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf N

concentration and leaf mass per unit area. Plant Cell Environ. 25, 343–357.

Miyazawa, S., Suzuki, A., Sone, K., Terashima, I., 2004. Relationships between light, leaf nitrogen and nitrogen mobilization in the crowns of mature evergreen *Quercus glauca* trees. Tree Physiol. 24, 1157.

Monteith, J.L., 1965. Evaporation and environment. Symp. Soc. Exp. Biol. 19, 205–234.

Nemani, R., Keeling, C., Hashimoto, H., Jolly, W., Piper, S., Tucker, C., Myneni, R., Running, S., 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300, 1560–1563.

Niinemets, Ü., Kull, O., Tenhunen, J., 2004. Within-canopy variation in the rate of development of photosynthetic capacity is proportional to integrated quantum flux density in temperate deciduous trees. Plant Cell Environ. 27, 293–313.

Niyogi, D., Chang, H., Saxena, V., Holt, T., Alapaty, K., Booker, F., Chen, F., Davis, K., Holben, B., Matsui, T., Meyers, T., Oechel, W., Pielke, R., Wells, R., Wilson, K., Xue, Y., 2004. Direct observations of the effects of aerosol loading on net ecosystem CO_2 exchanges over different landscapes. Geophys. Res. Lett. 31, 3120506.

North, P., 1996. Three-dimensional forest light interaction model using a Monte carlo method. IEEE Trans. Geosci. Remote Sens. 34, 946–956.

Parker, G., Davis, M., Chapotin, S., 2002. Canopy light transmittance in Douglas-fir-western hemlock stands. Tree Physiol. 22, 147–157.

Roderick, M., Farquhar, G., Berry, S., Noble, I., 2001. On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation. Oecologia 129, 21–30.

Schulze, E.-D., Kelliher, F., Korner, C., Lloyd, J., Leuning, R., 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate and plant N nutrition: a global ecology scaling exercise. Annu. Rev. Ecol. Syst. 25, 629–660.

Sellers, P., Randall, E., Collatz, G., Berry, J., Field, C., Dazlich, D., Zhang, C., Collelo, G., Bounoua, L., 1996. A revised land surface parameterization (SiB_2) for atmospheric GCMs. Part I. Model formulation. J. Clim. 9, 676–705.

Steven, Unsworth, 1980. The angular distribution and interception of diffuse solar radiation below overcast skies. Q. J. R. Met. Soc. 106, 57–61.

Warren, C., Adams, M., 2001. Distribution of nitrogen, Rubisco and photosynthesis in *Pinus pinaster* and acclimation to light. Plant Cell Environ. 27, 293.

Williams, D., 1991. A comparison of spectral reflectance properties at the needle, branch and canopy level for selected conifer species. Remote Sens. Environ. 35, 79–93.

Williams, M., Rastetter, E., Fernandes, D., Goulden, M., Wofsy, S., Shaver, G., Melillo, J., Munger, J., Fan, S., Nadelhoffer, K., 1996. Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest; the regulation of stomatal conductance by light, N and soil/plant hydraulic properties. Plant Cell Environ. 19, 911–927.

Williams, M., Malhi, Y., Nobre, A., Rastetter, E., Grace, J., Pereira, M., 1998. Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. Plant Cell Environ. 21, 953–968.

Wirth, C., Schulze, E., Schulze, W., von Stünzner-Karbel, D., Ziegler, W., Miljukova, I., Sogatchev, A., Varlagin, A., Panvyorov, M., Grigoriev, S., Kusnetzova, W., Siry, M., Hardes, G., Zimmermann, R., Vygodskaya, N., 1999. Above-ground biomass and structure of pristine Siberian Scots pine forest as controlled by competition and fire. Oecologia 121, 66–80.

Wofsy, S., Goulden, M., Munger, J., Fan, S., Bakwin, P., Daube, B., Bassow, S., Bazzaz, F., 1993. Net exchange of CO_2 in a mid-latitude forest. Science 260, 1314–1317.