An improved description of canopy light interception for use in a GCM land-surface scheme: calibration and testing against carbon fluxes at a coniferous forest

Venkata R Jogireddy, Peter M Cox, Chris Huntingford, Richard J Harding and Lina Mercado

22 March 2006

An improved description of canopy light interception for use in a GCM land-surface scheme: calibration and testing against carbon fluxes at a coniferous forest

Venkata R Jogireddy[a*], Peter M Cox[b], Chris Huntingford[c], Richard J Harding[c] and Lina Mercado[c]

[a]*Met Office Hadley Centre, 1 Fitzroy Road, Exeter, EX1 3PB, UK*

[b]*Centre for Ecology and Hydrology, Winfrith Technology Centre, Dorchester, DT2 8ZD,UK*

[c]*Joint Centre for Hydro-Meteorological Research, Centre for Ecology and Hydrology, Wallingford, OX10 8BB, UK*

Abstract

Recent comparisons of the Met Office Surface Exchange Scheme (MOSES) against land-atmosphere CO_2 flux measurements from eddy-covariance towers show a tendency for the model to underestimate the higher uptake rates in the middle of the day. Here we trace the reason for this bias to an underlying assumption that the plant canopy functions like a scaled big-leaf. An alternative treatment of canopy radiation interception is proposed based on an analytical two-stream model, and an explicit scaling-up from leaf-to-canopy. The new model (which will form part of the next generation Joint UK Land Environment Simulator, JULES) produces a better fit to the flux measurements from the pine tree site in Loobos, Netherlands, and also has the additional benefit of distinguishing between diffuse and direct radiation effects on photosynthesis. It is noted that changing the light interception component also influences best-fit parameters associated with other environmental factors.

1. Introduction

Significant progress has been made during the last twenty years in describing land-atmosphere fluxes of momentum, heat and vapour in climate and weather forecasting models. More recently, with interest in functioning of the global carbon cycle, such models have been enhanced to include CO_2 fluxes, and are utilised at spatial scales appropriate to coupling within Global Circulation Models (GCMs). Central to most land-surface schemes is application of the Penman-Monteith energy combination equation for single leaves (Monteith, 1981), a description of the dependence of stomatal opening on environmental conditions, and an integration algorithm for scaling from leaf to canopy level.

Despite their more recent and novel uses, a fundamental requirement for land-surface models is that they can replicate fluxes measured at single points. In most cases, this involves comparison against data from eddy-covariance towers, using simultaneous "weather" measurements to drive the surface model. Unfortunately, it is frequently found in such studies that predictions of Net Ecosystem Productivity (NEP) saturate too rapidly during the diurnal cycle, and there is a growing consensus that this might be in part due to leaf-to-canopy scalings that are too simplistic. To address this, new process descriptions are being developed to give land-surface models a more explicit canopy structure. Some "multi-source" models already exist (Shuttleworth and Wallace, 1985, Huntingford et al., 1995) but these have concentrated on internal canopy energy fluxes. Here we examine the impact of a more sophisticated treatment of canopy light-interception on the simulation of the diurnal cycle in NEP.

2. Data and Methods

2.1 Site description

The Loobos tower flux site is a long-term monitoring site of the CARBO-EUROPE and FLUXNET (Gu and Baldocchi, 2002) networks. The site is in the centre of the Netherlands (52° 10' 00" N, 05° 44' 38" E), with characteristics as given in Table 1. It consists of Scots Pine (*Pinus sylvestris*) with a canopy height of approximately 15m, a stem density of 434 trees per ha^{-1} and a LAI of between 1.7 and 2.2 (Dolman et al. 2002, /www.fluxnet.ornl.gov/fluxnet/). There is a grass under-storey (*Deschampsia flexuso*) on a sandy soil with a 10 cm organic surface layer (a value of 20 kg m^{-2} soil carbon is quoted by Sanderman et al., 2003). Eddy correlation measurements of vertical fluxes of CO_2 have been made at this site since 1996 and are continuing. For most of the tower flux sites the sum of the turbulent fluxes of energy (latent heat, LE, and sensible heat, H) are less than radiation input, when averaged over the year, indicating the familiar energy-closure problem. However, the measured energy balance ratio, (H+LE)/Rn, is 0.89 for the Loobos site for 1998, which is better than at most FLUXNET sites (Dolman et al., 2002, Wilson et al., 2002).

Table 1. The main characteristics of the Loobos site, data observed in 1998.

Site	Loobos
Location	52° 10' 00" N, 05° 44' 38" E
Canopy Height (m)	15.1
Density of trees (tree ha^{-1})	434
Diameter at breast height (DBH)	0.25
LAI(Maximum Leaf Area Index)	1.9
Rain (mm)	786
Measurement height for fluxes (m)	26

Estimates of the total uptake of carbon at this site range between 210 and 365 gC m^{-2} per year (depending on year and infill methodology), which is within the estimates from other temperate needleleaf forest sites (Falge et al., 2002, Valentini et al., 2000).

The driving data required is determined by the MOSES model, as described below in Section 2.2. Simultaneous measurements of downward shortwave radiation, $R_S\downarrow$ (Wm^{-2}) and downward net radiation, $R_{net}\downarrow$ (Wm^{-2}), CO_2 fluxes and meteorological conditions are available at the Loobos site. As MOSES is driven by radiative fluxes of downward shortwave radiation, and downward longwave radiation, $R_L\downarrow$ (Wm^{-2}), we calculate the latter as:

$$R_L\downarrow = R_{net}\downarrow - R_S\downarrow + R_L\uparrow + R_S\uparrow = R_{net}\downarrow - R_S\downarrow + \sigma T^4 + \alpha R_S\downarrow \quad (1)$$

where upward arrows mean upward energy fluxes, σ (W m^{-2}K^{-4}) is the Stefan Boltzmann constant and α (set as 0.1) is an estimate of the albedo. Surface climate is given by measurements of

temperature, T (K), vapour pressure deficit, D (kPa), air pressure, p (Pa), rainfall rate P (mm/day) and wind speed, U (m/s).

2.2 The MOSES land surface model

The MOSES land surface model (Cox et al., 1999) was designed for use within the Hadley Centre climate models, but it can also be operated independently of the GCM at a single point. For a prescribed climatology and vegetation Leaf Area Index (LAI), MOSES calculates canopy level Net Primary Productivity (NPP) and values of plant respiration for each of up to five vegetation classes (broadleaf tree, needleleaf tree, C3 grass, C4 grass, shrub) in each GCM gridbox (Essery et al., 2003). The NPP value is the difference between Gross Primary Productivity (GPP) and plant respiration (which includes both maintenance and growth respiration components). Heterotrophic soil respiration is calculated dependent on soil temperature and soil moisture (Cox, 2001), and is subtracted from the calculated NPP value to give the Net Ecosystem Productivity (NEP). It is this final quantity that we compare to the net CO_2 exchanges measured by eddy-covariance.

GPP is calculated within MOSES using a coupled leaf photosynthesis-stomatal conductance model (Cox et al., 1998). The C_3 and C_4 photosynthesis models within MOSES are based on the work of Collatz et al. (1991) and Collatz et al. (1992) as applied by Sellers et al. (1996). In both cases the rate of gross leaf photosynthesis, W (all fluxes of CO_2 here and below are in mol CO_2 m^{-2} s^{-1}), is calculated in terms of three potentially limiting factors:

$$W = min \{ W_c , W_l , W_e \} \tag{2}$$

where W_c is the carboxylation-limited rate of photosynthesis, W_l is the light-limited rate of photosynthesis, and W_e is the limitation associated with export of photosynthetic products for C_3 plants, or the PEP-Carboxylase limitation for C_4 plants (Collatz et al., 1992). The light-limited rate, W_l, is proportional to the Photosynthetically Active Radiation (PAR) absorbed by the leaf, while both W_c and W_l are proportional to the maximum-rate of carboxylation of Rubisco (V_{max}), which is itself assumed to be dependent on temperature (W_c) and leaf nitrogen content (W_l). The net leaf photosynthesis, A_L, is calculated as the difference between the gross photosynthesis and the dark respiration rate, R_D, modulated by soil water status:

$$A_L = \{W - R_D\} \beta. \tag{3}$$

Here β is a soil moisture factor which takes the maximum value of unity when photosynthesis is not moisture-limited. Full details of the MOSES stomatal conductance-photosynthesis model are given in appendix A of Cox (2001).

This paper is primarily concerned with a process-based scaling-up of the leaf level model to give larger-scale canopy fluxes which are more comparable to measurements from flux towers. The original MOSES model (Cox et al., 1999, Essery et al., 2001, Essery et al., 2003) uses the optimization-approach of Sellers et al. (1992), in which the primary determinants of photosynthesis (incident PAR, I_{PAR}, and the maximum-rate of carboxylation of rubisco, V_{max}) are assumed to vary proportionally down through the plant canopy. If the incident PAR follows a simple Beer's law dependence, this assumption also requires a similar decay of V_{max} with depth:

$$I_{PAR} = I_{PAR}(0) \exp \{-k L\} \tag{4}$$
$$V_{max} = V_{max}(0) \exp \{-k L\} \tag{5}$$

where k=0.5 is the PAR extinction coefficient used in MOSES, and L is the cumulative leaf area index of the canopy above the point in question. Hence the Sellers et al. (1992) optimization assumption ensures that W_c, W_l and W_e in Equation (2) all vary together down through the canopy, such that the canopy level net photosynthesis, A_C, is simply related to the net photosynthesis of leaves at the top of the canopy, $A_L(0)$:

$$A_C = A_L(0) \, F_{APAR} \, / \, k \qquad\qquad\qquad (6)$$

where $F_{APAR} = \{1 - \exp(-kL_T)\}$ is the "Fraction of Absorbed PAR" by a canopy with total leaf area index, L_T. Equation (6) provides a very simple scaling-up algorithm with a number of attractive features: (a) calculating canopy-level fluxes requires only the solution of the leaf-level model for a single leaf-layer, so this approach is computationally efficient, (b) the leaf-to-canopy scaling-up depends only on F_{APAR} which can be estimated from satellite data and (c) this scaling-up approach is broadly consistent with the idea that plants distribute their leaf-nitrogen to make optimal use of the incident PAR.

However, whilst Equation (6) has these advantages in aggregating from leaf to canopy, a further implicit assumption is that all environmental dependences of the canopy photosynthesis are identical throughout the canopy. Unfortunately, as demonstrated in Section 4 below, our tests of MOSES against the latest data from flux towers show that this "big-leaf" assumption leads to an underestimation of light-limitations on photosynthesis and therefore a poor simulation of the diurnal cycle in CO_2 uptake.

2.3 Improved Canopy Light-Interception

In order to examine the impact of the canopy light interception on the simulated diurnal cycle in CO_2 fluxes we utilize a two-stream canopy radiation model (Sellers, 1985). This approach is significantly more complex than Beer's Law, resolving upward and downward radiation streams as well as diffuse and direct radiation in various wavebands. Nevertheless, the two-stream model can be solved analytically to give the within-canopy profiles of (upward and downward) direct and diffuse radiation as a function of solar zenith angle, diffuse and direct radiation incident at the top of the canopy, and leaf radiative properties (reflection and scattering coefficients for each wavelength band).

The two-stream radiation canopy model is already available in MOSES to calculate surface spectral albedos (Essery et al. 2001), but here we also use it to infer PAR absorption in each of N equal leaf area increments down through the plant canopy - here we set N=10. These analytical forms can be differentiated with respect to cumulative leaf area index to produce expressions for the fraction of the incident direct and diffuse PAR absorbed per unit leaf area, for each level in the canopy. Figure 1 compares the profile of absorbed PAR calculated in this manner, with the profile assumed in the original MOSES (i.e. Beer's Law with k=0.5). The approaches agree well when the incident PAR is direct beam from a high sun angle, but otherwise differ markedly. In the two-stream model there is a strong zenith angle-dependence of the absorption profile, with PAR penetrating less deeply into the canopy as the sun moves towards the horizon (cosZ=0 where Z is sun angle). This also leads to the distinction between diffuse and direct radiation in the two-stream model, (with the diffuse radiation being absorbed as if it were direct beam radiation coming from a mean zenith angle of cos Z=0.5). These dependences of PAR absorption on the sun angle, and the diffuse-direct ratio are completely neglected in the original MOSES model.
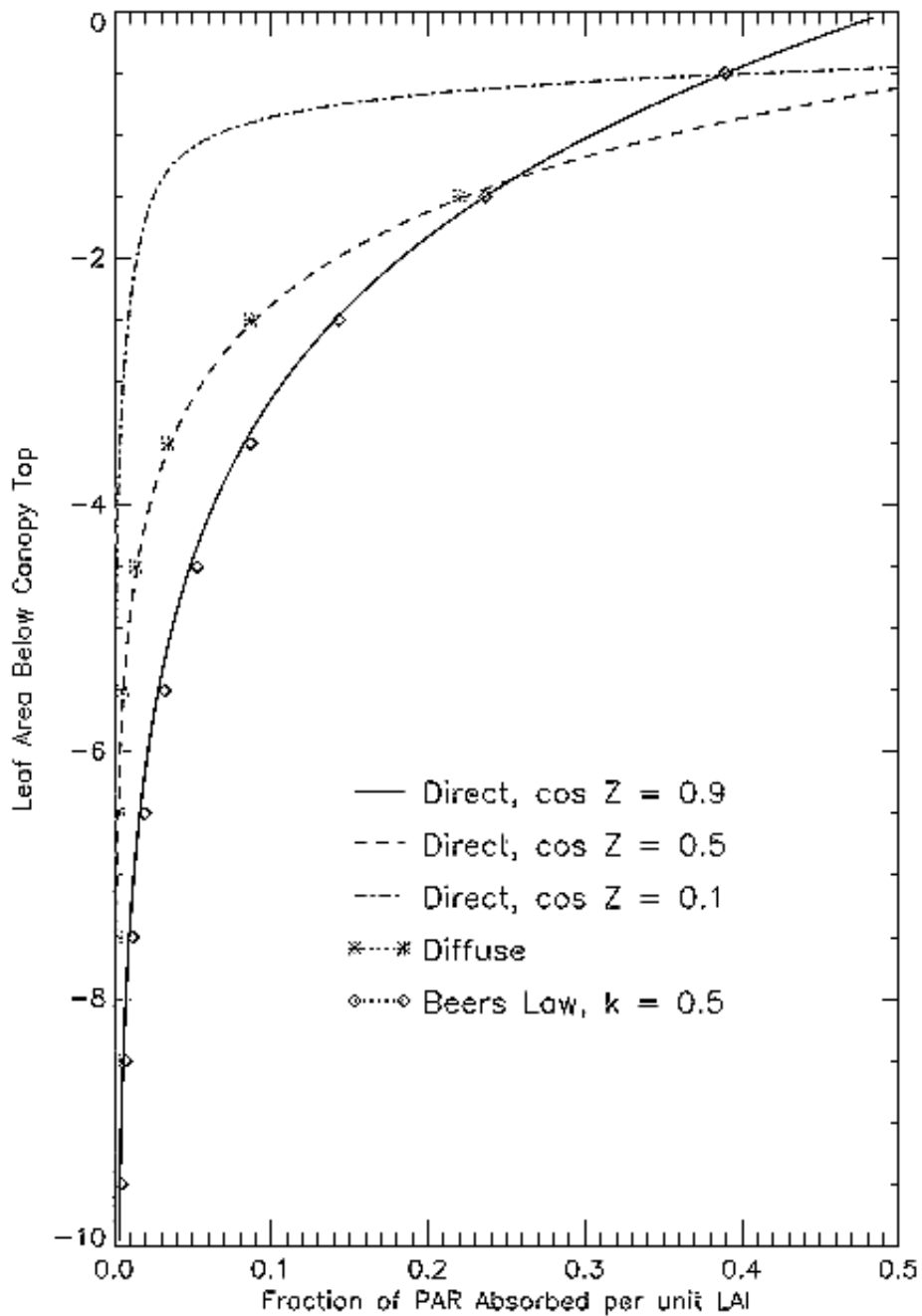
Figure 1: Comparison of PAR canopy interception profiles from the original big-leaf MOSES (diamonds), and the new JULES two-stream model. For the latter the absorption of direct PAR is shown for high sun (dot-dash line), low sun (continuous line), and an intermediate solar zenith angle (dashed line). The diffuse radiation absorption profile from the two-stream model is shown by the asterisks.

2.4 Revised Leaf-to-Canopy Scale-Up

The new canopy module makes use of the profiles of absorbed PAR calculated with the two-stream model to explicitly scale-up from leaf-to-canopy. In order to avoid spurious "big-leaf" behaviour the optimization of V_{max}, as defined by Equation (5) is also discarded. Instead we assume that leaf nitrogen concentration (and therefore V_{max}) is approximately constant with depth. Two versions of the model are considered for scaling from leaf to canopy. These are (i) the full 10-layer model, in

which the leaf stomatal conductance and photosynthesis model is called for each of the 10 leaf-layers resolved by the two-stream model. The canopy level fluxes and conductance are calculated as the weighted sum of the leaf-level values and (ii), a 2-layer model in which all leaves are classified as either light-limited or non-light limited, and the leaf-level model is called using mean conditions for each of these 2 classes. The level below which leaves are light-limited is defined by the point at which the absorbed PAR yields co-limitation: $W_l = min \{ W_c , W_e\}$ (i.e. a varying quantity dependent on meteorological driving conditions).

Figure 2 shows the dependences of Gross Primary Productivity (i.e. gross canopy photosynthesis) on incident PAR, leaf area index and solar zenith angle, for each of the leaf-to-canopy options for sscaling-up. Photosynthesis saturates rapidly with PAR in the original big-leaf MOSES (asterisks), but shows a much smoother response with the new options. The 2-leaf approximation is a good fit to the full 10-leaf model in all examples, suggesting that it is sufficient to use the more computationally-efficient 2-leaf version for large-scale applications.
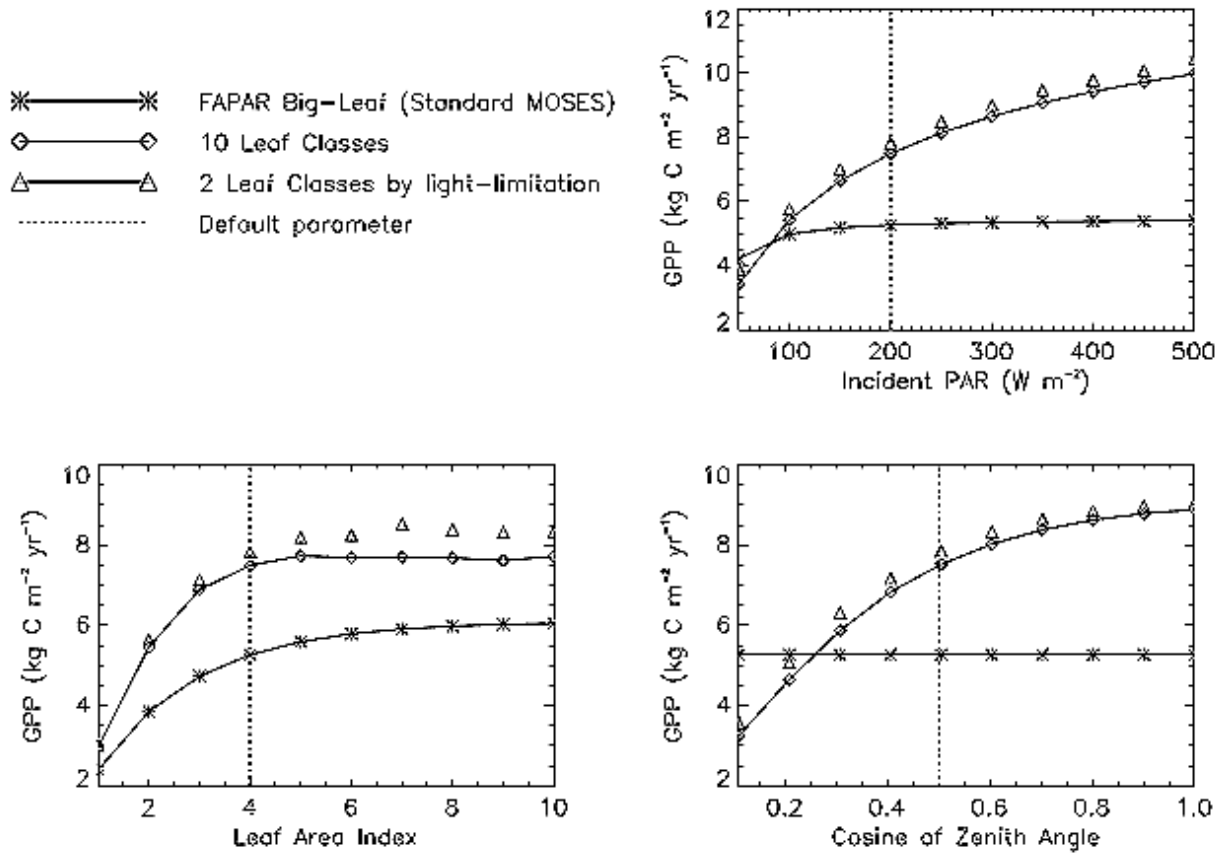

Figure 2: Comparison of Gross Primary Productivity (GPP) dependencies on incident PAR (top right), leaf area index (bottom left), and solar zenith angle (bottom right), for the original big-leaf MOSES model (asterisks) and the new JULES two-stream model. The line marked by diamonds is derived by explicit integration over ten-leaf layers, while the triangles show the two-leaf approximation. See text for details.

3.0 Modelling and Optimisation methods

The MOSES model contains a number of ecosystem parameters that may be calibrated. "Tuneable" parameters associated with photosynthetic uptake include f_0 (a calibration parameter associated with stomatal opening) and D^* (g kg^{-1}) (a leaf surface parameter that controls stomatal response to humidity deficit). Both of these parameters are used in the MOSES equation for the ratio of the leaf internal to external CO_2 concentration as a function of humidity deficit (kg kg^{-1}). (see Eqn. 30 of Cox et al., 1998). This relation is derived from a simplified version of the model for stomatal conductance proposed by Jacobs (1994) (and tested by many authors including Leuning, 1995) whereby stomatal conductance, g (mm s^{-1}) is linked directly to net photosynthetic activity.

Two other leaf parameters that which may require optimisation are leaf quantum efficiency, α, and leaf nitrogen content, N_{lo} (kg N (kg C)$^{-1}$). The first variable controls vegetation response to Photosynthetically Active Radiation (PAR), whilst the latter is linked to substrate saturated rubisco capacity and in turn temperature response. In addition, we calibrate the critical soil moisture content level below which stomata start to close in response to water stress (V_{crit} (kg H_2O (kg soil)$^{-1}$)).

These five parameters were optimized using a simple least squares method, minimising the differences (S^2) between modelled and measured values of NEP. An initial attempt to use standard optimisation software failed resulting in "false minima" (i.e. the global best fit was not obtained). Instead, for different parameters (all varied simultaneously) and taking advantage of spare computing capacity, MOSES simulations were repeatedly made to calculate a set of S^2 values, the average of sum of squares for between half-hourly model and data values of NEP, for each simulation. For this exercise we utilised the 1998 Loobos data and limited the model-data comparison to daytime fluxes (10am to 4pm) in order to avoid uncertainties in the measured night-time fluxes.

The five parameters f_0, D^* α, N_{lo} and V_{crit} were varied across a range guided by values obtained from the plant physiological literature. Each parameter was perturbed ten times resulting in an ensemble of 10^5 simulations. In each instance the big-leaf and two-layer models were run (closeness between the two and ten-layer models as presented in Figure 2 implies little advantage in high vertical complexity).

4. Modelling Results

Figure 3 is a scatter plot of the measured and modelled NEP against the incident shortwave radiation for the individual 30 minute periods. The data shows, as expected, that higher CO_2 flux measurements generally coincide with high incident SW values (or equivalently, high incident PAR). However, the original uncalibrated MOSES model fails to capture the higher NEP values, instead demonstrating a tendency for CO_2 uptake to saturate when the incident shortwave values exceeds about 100 Wm^{-2}. With the new two-leaf version of MOSES (lower panel of Figure 3) light-saturation occurs more at higher values, which is more consistent with the measurements (upper panel of Figure 3).

The best fits for the big-leaf and two-leaf configurations are determined by selecting the highest Percentage of Variance Explained (PVE) (a function of S^2) from amongst the multiple simulations

with each model. The original MOSES parameters and optimized parameters corresponding to the best overall fits are presented in Table 2.

MODEL	Fit (PVE)	N_{lo} (kgN/kgC)	f_0	D^* (kg/kg)	V_{crit} (kg H_2O /kg soil)	α
MOSES - original	-25.9%	0.03	0.875	0.06	0.03	0.08
MOSES - best fit	57.4%	0.1033	0.70	0.0822	0.05	0.04
JULES 2 leaf – best fit	60.1%	0.0411	0.86611	0.04667	0.11667	0.06
Observed Range		0.008-0.034	0.61-0.84	0.006-0.015	0.05-0.25	0.02-0.10

Table 2: Fit of models to the Loobos CO_2 flux measurements in terms of the "Percentage of Variance Explained (PVE)". Listed are the leaf model parameters used to obtain this fit. Also listed are literature ranges of parameters (Cox et al., 2003).

The original (untuned) MOSES big-leaf model has a negative percentage of variance explained suggesting a very poor fit to the data. The fit is significantly improved by tuning even in the big-leaf model, reaching a PVE of 57.4%. However, this fit is achieved by moving the leaf nitrogen concentration (N_{lo}) to a value which is far outside the range which is measured for needleleaf plants (Schulze et al. 1994). By contrast the new JULES canopy model, achieves an improved fit (increasing to PVE = 60.1%), and importantly with more realistic parameter values. The most notable result is that the change from big-leaf to two-leaf model has a major influence on the best fit values for N_{lo}.

In Figure 4, mean NEP values for each daytime half-hourly interval are plotted to assess the simulation of the diurnal cycle. The calibrated big-leaf and two-leaf models perform reasonably well. By contrast the original uncalibrated big-leaf MOSES produces a very flat NEP diurnal cycle with maximum uptake rates about half that observed. The uncalibrated two-leaf version produces a more realistic daily maximum.

Figure 5 shows the effect of parameter variation on model fit (both big-leaf and two-leaf). The most notable result is that the change from big leaf to two-leaf model, whilst based predominantly on response to PAR, has a major influence on the best fit values of other parameters, such as N_{lo}.
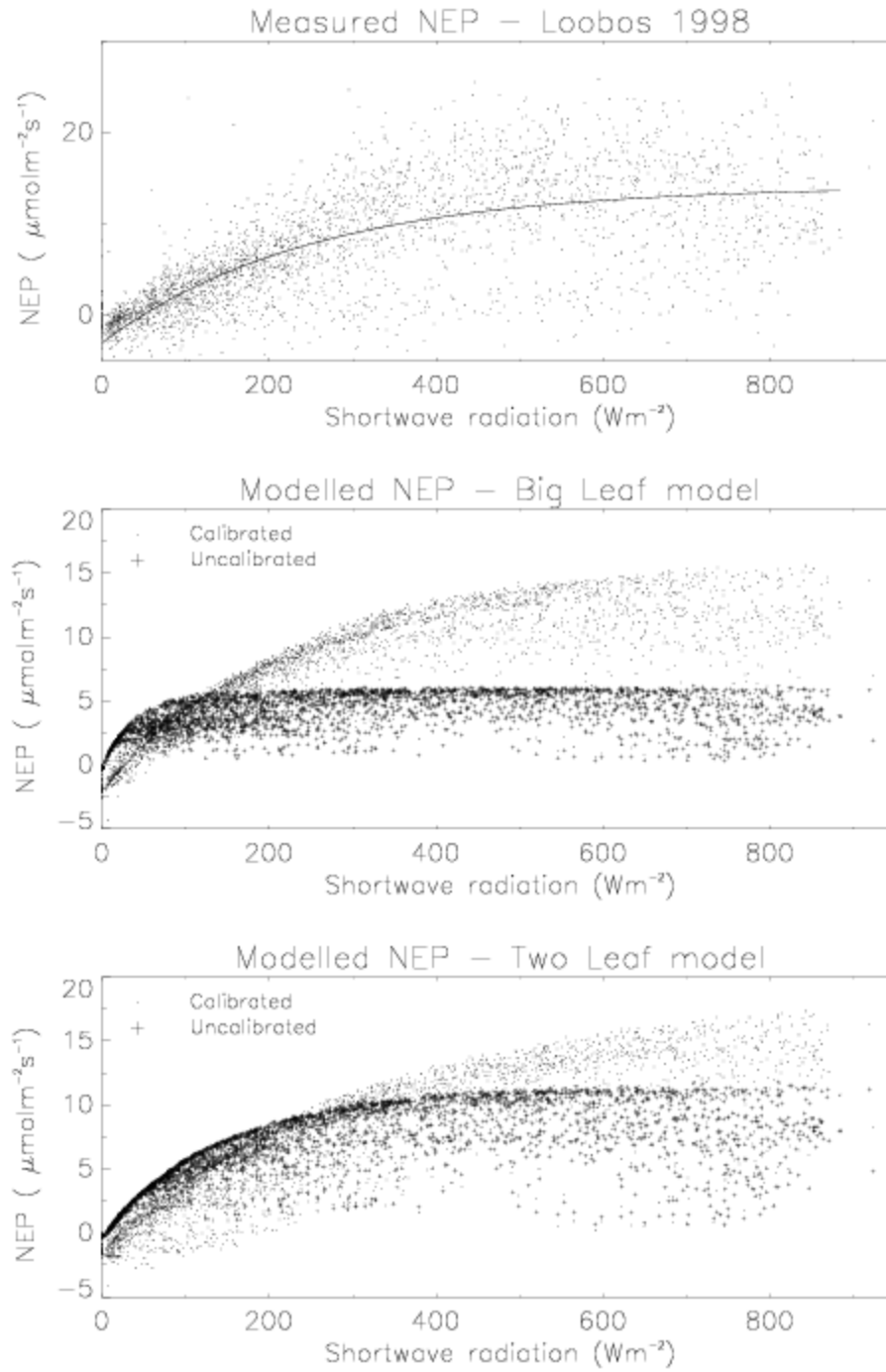
Figure 3: Measured and modelled NEP values for the Loobos needleleaf tree site, plotted against incident shortwave radiation. The top panel is of NEP measurements, whilst the middle and bottom panels are for the "Big Leaf" and "Two-Leaf" versions respectively.
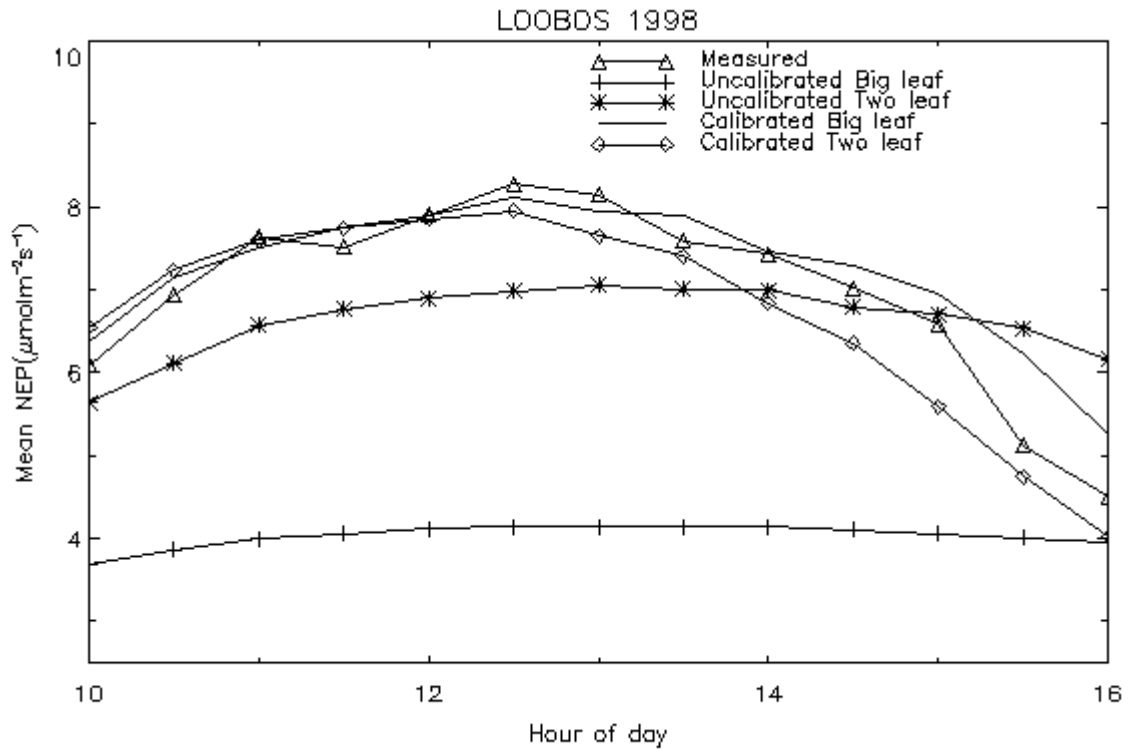
Figure 4: Diurnal cycle in net CO_2 exchange; Loobos measurements and simaultions with various configurations of MOSES.

5. Conclusions

Tests of MOSES against the latest CO_2 flux measurements from eddy covariance towers show a tendency for the model to underestimate net CO_2 fluxes in the middle of the day when the incident solar radiation is large. This bias can be traced to an underlying assumption concerning the distribution of nitrogen down through the plant canopy, which leads to the canopy responding to photosynthetically active radiation (PAR) like a "big-leaf".

A revised canopy PAR-interception model has been devised based on an analytical two-stream model for within-canopy radiation transfer. Absorbed PAR is calculated for each of 10-layers through the canopy. There are two new options for scaling-up from leaf-to-canopy, which produce very similar results; an explicit summing of the leaf level fluxes (and conductance) for each of the 10 PAR absorption levels; or a 2-leaf approximation in which only light-limited and non-light-limited classes are resolved.

The new model produces a better fit to the CO_2 flux data from the pine forest site at Loobos in the Netherlands, without the need to tune leaf-level photosynthesis parameters far outside of their measured ranges. This improved canopy light-interception model will from an integral of the next generation UK community land-surface scheme, "JULES".
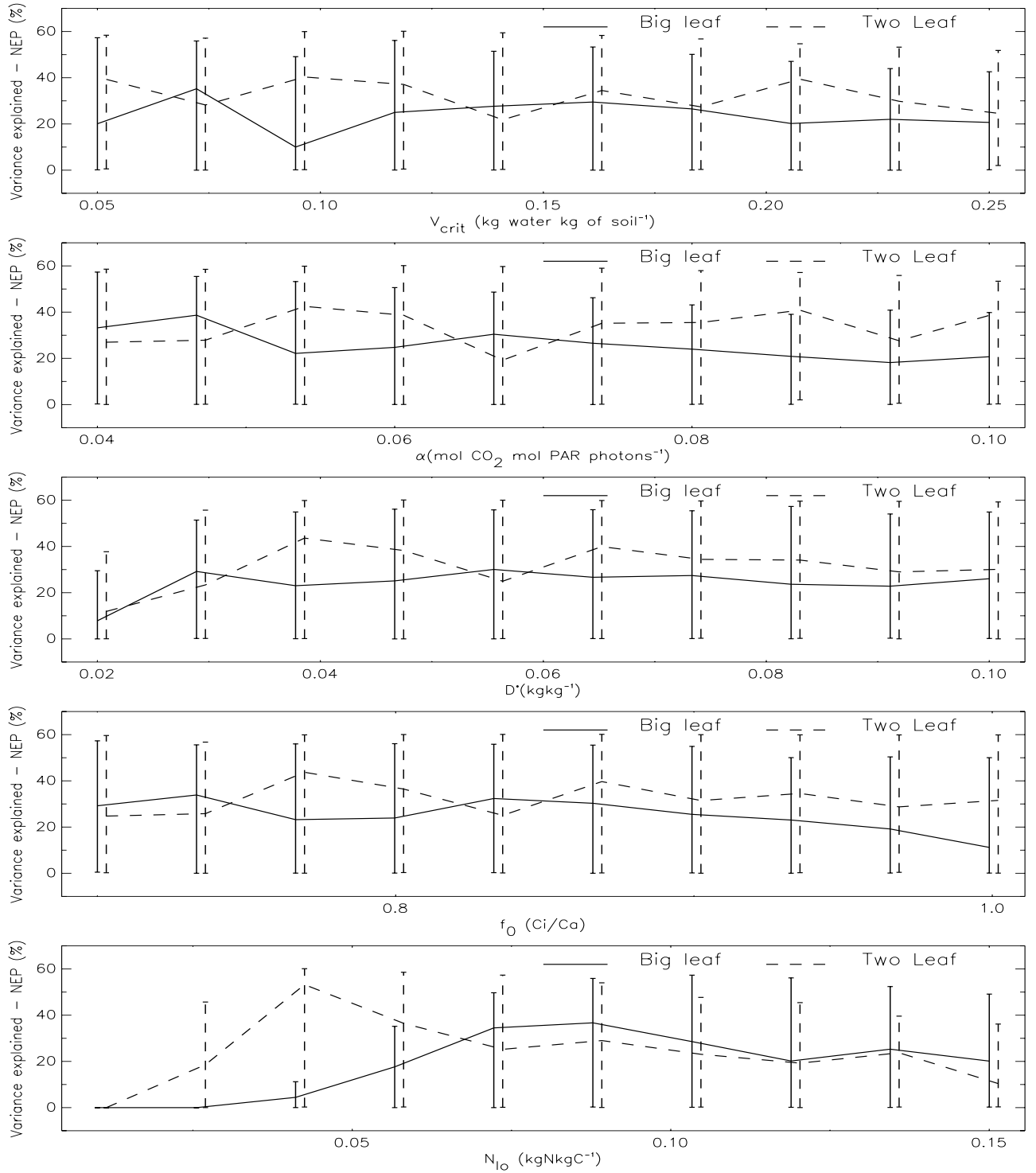
Figure 5: Percentage of Variance Explained (PVE) by the big-leaf and two-leaf variants of MOSES as a function of the value of each calibration parameter. The vertical bars represent the maximum and minimum PVE value obtained from the set of ensemble members with the same specified parameter.

References

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

Collatz, G.J., Ribas-Carbo, M., Berry, J.A., 1992. A coupled photosynthesis-stomatal conductance model for leaves of C4 plants. Aus. J. Plant Physiol. 19, 519-538.

Cox, P.M., 2001. Description of the TRIFFID dynamic global vegetation model. Technical Note 24, Hadley Centre, Met Office, Bracknell, RG12 2SY.

Cox, P.M., Betts, R.A., Bunton, C.B., Essery, R.L.H., Rowntree, P.R. Smith, J., 1999. The impact of new land surface physics on the GCM sensitivity of climate and climate sensitivity. Clim Dyn. 15, 183-203.

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

Cox, P.M., Jogireddy, V.R., Huntingford, C., 2003. Central estimates and plausible ranges for TRIFFID parameters using EuroFlux data. DEFRA CPP deliverable, 080403.

Dolman, A.J., Moors, E.J., Elbers, J.A., 2002. The carbon uptake of a mid latitude pine forest growing on sandy soil. Agric. For. Meteorol. 111,157-170.
Essery, R.L.H., Best, M.J., Betts, R.A., Cox, P.M., Taylor, C.M., 2003. Explicit representation of sub-grid heterogeneity in a GCM land-surface scheme. J. Hydrometeorol. 4 , 530-543.

Essery, R.L.H., Best, M.J., Cox, P.M., 2001. MOSES 2.2 Technical Documentation. Hadley Centre Technical Note, 30.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Guomundsson, J., Hollinger, D., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monsonn, T.K., Munger, J.W., Oechel, W., Paw, K.T., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Valentini, R., Wilson,K., Wofsy, S., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. Agric. Forest Meteorol. 113(1-4), 53-74.

Gu, L.H., Baldocchi, D., 2002. Fluxnet 2000 synthesis – Foreword, Agric. Forest Meteorol. 113 (1-4): 1-2 DEC 2 2002.

Huntingford, C., Allen, S.J., Harding, R.J., 1995. An intercomparison of single and dual-source vegetation-atmosphere transfer models applied to transpiration from Sahelian savannah. Boundary-Layer Meteorol. 74, 397-418.

Jacobs, C., 1994. Direct impact of atmospheric CO2 enrichment on regional transpiration. PhD thesis, Wageningen Agricultural University.

Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C3 plants. Plant, Cell and Environ. 18, 357-364.

Monteith, J.L., 1981. Evaporation and surface temperature. Quart. J. Roy. Meteorol. Soc. 107, 1-27.

Sanderman, J., Amundson, R.G., Baldocchi, D.D., 2003. Application of eddy covariance measurements to the temperature dependence of soil organic matter mean residence time. Global Biogeochem. Cycles 17(2), 1061.

Schultze E.D., Kelliher F.M., Korner C., Lloyd C., Leuning R. 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition : a global ecology scaling exercise. Annual Review of Ecological Systems 25, 629-660.

Sellers P.J., 1985. Canopy reflectance, photosynthesis and transpiration. Int. J. Remote Sens. 6, 1335-1372.

Sellers P., Berry J., Collatz G., Field C., Hall F., 1992. Canopy reflectance, photosynthesis and transpiration. III a reanalysis using enzyme kinetics – electron transport models of leaf physiology. Remote Sens. Environ. 42, 187-216.

Sellers P., Randall D., Berry J., Collatz G., Field C., Dazlich D., Zhang C., and Collelo G., 1996. A revised land surface parameterisation (SiB2) for atmospheric GCMs. Part I: Model formulation. J. Climate 9, 676-705.

Shuttleworth, W.J., Wallace, J.S., 1985. Evaporation from sparse crops - an energy combination theory. Quarter. J. Roy. Meteorol. Soc. 111, 839-855.

Valentini, R., Matteucci, G., Dilman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Grainier, A., Gross, P., Jensen, N.O., Pllegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Bubinet, M.C.R., Kowalski, A.S., Vesala, T., Rannlk, U., Berbgier, P., Loustau,D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861-865.

Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Berhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B.E., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., Verma, S., 2002. Energy balance closure at FLUXNET sites. Agric. Forest Meteorol. 113(1-4), 223-243.