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Reduced carbon sequestration in terrestrial ecosystems under overcast skies compared to clear skies

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ABSTRACT

There is still no consensus on the impact of cloud on terrestrial carbon sequestration. Nevertheless, the fraction of sky irradiance which is diffuse (fDIF) is close to half as a global annual average, owing mainly to the presence of clouds. Furthermore, as a consequence of human-induced perturbations, the occurrence and opacity of cloud is changing both regionally (due to deforestation and drainage) and globally (shortwave "solar" dimming). In this study, we quantify the impact of cloud on carbon assimilation at an unprecedented number of FLUXNET sites (38) and for six plant functional types (PFTs). We compare results from previously established empirical and statistical methods with novel land-surface and three-dimensional (3D) radiative-transfer (RT) simulations that take explicit account of diffuse sunlight. We record a much lower enhancement in canopy light-use efficiency (LUE) under diffuse sunlight relative to direct sunlight (factor 1.12–1.80) compared to previous authors (factors 2–3). Increased radiation-sharing, due to varied leaf orientation within the canopy, is the primary cause of LUE-enhancement rather than beam penetration within an open crown structure. Under cloud, we consistently record a decrease in primary productivity (≥10–40%) and an unequivocal decline in daily carbon sequestration (60–80%), owing to the dramatic reduction in total (direct plus diffuse) irradiance that occurs when clouds obscure the solar disk (≥60% attenuation). A cooling-induced reduction in ecosystem respiration offsets the decline in primary productivity by about one third.

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1. Introduction

Theoretically, the diffuse sunlight produced by clouds and aerosols enhances canopy light-use efficiency (LUE) compared to direct solar radiation (Roderick et al., 2001). Photons arriving from different angles of the sky share the radiation load more evenly across the canopy and this reduces the fraction of foliage which is light-saturated. Thus, Gu et al. (2003) claim a 20% increase in forest photosynthesis in the wake of the 1991 Pinatubo eruption owing to the presence of volcanic aerosols. The impact of cloud is arguably more complicated than aerosols since water vapour droplets are relatively efficient in back-scattering incoming solar radiation (Farquhar and Roderick, 2003). Consequently, clouds are less conservative with respect to total (diffuse plus direct) downwelling short-wave radiation. The resulting attenuation under cloud may offset the LUE-enhancement attributable to diffuse sunlight although, as stated recently (Farquhar and Roderick, 2003; Niyogi et al., 2004), the underlying mechanisms of LUE-enhancement and the overall impact of cloud on carbon sequestration remain to be established.

Under diffuse sky radiance, canopy LUE has been shown to increase by 110% for crops (Choudhury, 2001) and 110–180% for temperate forest (Gu et al., 2002). With such high levels of enhancement, an increase in gross primary productivity (GPP) and ecosystem carbon sequestration are conceivable under

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cloud despite the concomitant reduction in insolation. In contrast, for three forest sites (two broadleaf and one needleleaf), Alton et al. (2007a) estimate an LUE-enhancement under diffuse sunlight of only 6–33%, i.e. much lower than previously considered and conceivably insufficient to increase productivity and carbon sequestration under cloud. The most direct measurement recorded at carbon-monitoring (FLUXNET) sites is net ecosystem exchange (NEE) but conclusions drawn from net exchange also provide an inconsistent, or at least highly contrasting, picture. Hollinger et al. (1994) claim a 50% increase in carbon sequestration within a New Zealand beech forest under cloud compared to seasonally equivalent cloudless days. In contrast, carbon sequestration within a tundra shrubland of low leaf area index (LAI) appears to be neutral with respect to cloud (Letts et al., 2005).

In summary, important differences remain to be resolved for the inferred level of LUE and the observed change in NEE both within and between PFTs. The lack of consensus on the impact of diffuse sunlight can be attributed to at least five factors: (i) both empirical (Gu et al., 2002) and process-based (Alton et al., 2007a) models are applied to the problem, making results potentially model-dependent; (ii) carbon exchange under diffuse and direct sunlight is not always compared at the same sky irradiance (e.g. Choudhury, 2001); (iii) although authors are generally careful to distinguish between the effects of aerosols as opposed to clouds, the two scattering media are often treated together despite the latter being much less conservative with respect to total downwelling shortwave radiation (e.g. Niyogi et al., 2004); (iv) different studies treat carbon fluxes from different carbon-monitoring sites; (v) different PFTs may exhibit highly contrasting behaviour under cloud.

In addition to the above problems, clarity is still required on the underlying mechanisms. For example, is enhanced canopy LUE attributable to varied leaf orientation (Alton et al., 2005) or increased light penetration within an open crown structure (Baldocchi and Harley, 1995; Farquhar and Roderick, 2003)? Under cloud, what role is played by concomitant changes in micro-meteorological variables such as air temperature and vapour pressure deficit (VPD) with respect to leaf photosynthesis and ecosystem respiration (Lloyd et al., 2002)?

The explicit treatment of diffuse sunlight in global land-surface models (LSMs) offers a novel approach in determining the impact of cloud. Until now, the problem is addressed for only a few sites using either an empirical LUE-model (Gu et al., 2002, 2003) or a statistical approach (Hollinger et al., 1994). The advantage of a process-based LSM is that any change in carbon sequestration can be attributed as well as quantified. Furthermore, once coupled to a global circulation model, an LSM has the potential to generate feedbacks, such as increased cloud-formation owing to enhanced transpiration. Until now, global LSMs used in climate predictions (e.g. Cox et al., 2000) adopt average light profiles when calculating canopy photosynthesis. These average light profiles cannot reproduce LUE-enhancement under diffuse sunlight (Alton et al., 2007b). The need to calibrate global LSMs with FLUXNET measurements has been emphasized by several authors (e.g. Falge et al., 2002).

In the current investigation we quantify and attribute the impact of cloud on carbon sequestration at an unprecedented number of sites (38 compared to a previous maximum of 6). The sites cover six plant functional types (PFTs), namely broadleaf forest (BL), needleleaf forest (NL), mixed woodland (MX), C_3 grassland (C_3), C_4 grassland (C_4) and shrub (SH). The total number of site-years (1 year at any given site is referred to as a site-year hereafter) is 98. Both to compare with previous authors and to derive new insights we combine a number of established empirical and statistical methods with novel, process-based land-surface and RT simulations. Our aim is to answer four major scientific questions, namely:

1. What is the observed level of LUE-enhancement under diffuse sunlight for different PFTs?
2. How can the observed levels of enhancement be explained in terms of (i) biophysical properties such as LAI, leaf orientation and crown shape; and (ii) micro-meteorological variables such as VPD and air temperature?
3. Given that total downwelling shortwave radiation generally declines under thickening cloud cover, are the observed levels of LUE-enhancement sufficient to increase GPP under cloud, compared to seasonally equivalent cloudless skies?
4. Taking account of changes in GPP and ecosystem respiration, does the vegetated land-surface sequester more carbon on cloudy days compared to seasonally equivalent cloudless days?

In the following sections, we describe and present results from five different methods. The discussion follows the four scientific questions given above.

2. Materials and methods

2.1. Data

All our methods use gap-filled half-hourly measurements of carbon exchange and micrometeorology, available in the Marconi FLUXNET archive (Falge et al., 2002). Although the database is strongly biased towards forests of N. America and Europe (Baldocchi et al., 2001), measurements are available for 37 sites and usually 2–3 years per site. Law et al. (2002) provide a complete listing of the Marconi sites with references for the original publication of data at each site. A summary of location and vegetational composition is given in Table 1. For control purposes we add measurements for three forest sites where some of the current methods have been applied (Alton et al., 2007a). The total number of sites is 38 and the total number of site-years is 98. For each site-year, GPP is inferred in the standard way as $R_e - \Delta C - F$, where F is carbon flow above the canopy (upward flow is negative), ΔC is the change in CO_2 stored in the canopy airspace and R_e is the ecosystem respiration (Lloyd et al., 2002). R_e is estimated from nighttime carbon flow (GPP = 0) under moderate wind-speed (Medlyn et al., 2003) using, initially, a linear function of soil temperature. Only fluxes from the growing season, generally Julian Day 135–255, are considered since we are testing the hypothesis that increased GPP increases ecosystem carbon sequestration. Furthermore, meteorological variables in the Marconi database are often incomplete outside this period.

Table 1 – Summary of site locations used in the current investigation

Site	Latitude (°N)	Longitude (°E)	PFT
Manaus, Brazil	−1.4	−59.8	BL
Gunnarsholt, Iceland	63.8	−20.2	BL
Hesse, France	48.7	7.1	BL
Harvard, USA	42.0	−72.2	BL
Soroe, Denmark	55.4	11.7	BL
Vielsalm, Belgium	50.3	6.0	BL
Walker Branch, USA	35.9	−84.3	BL
Willow Creek, USA	45.8	−90.1	BL
Castelporziano, Italy	41.8	12.4	BL
Sky Oaks (old), USA	33.4	−116.6	BL
Sky Oaks (young), USA	33.4	−116.6	BL
Aberfeldy, Scotland	56.6	−3.8	NL
Blodgett Forest, USA	38.9	−120.6	NL
Bordeaux, France	44.1	0.1	NL
Duke, USA	36.0	−79.1	NL
Flakaliden, Sweden	64.1	19.5	NL
Howland, USA	45.2	−68.7	NL
Hyytiala, Finland	61.9	24.3	NL
Saskatchewan, Canada	53.9	−104.7	NL
Loobos, Netherlands	52.2	5.8	NL
Metolius, USA	44.5	−121.6	NL
Manitoba, Canada	55.9	−98.5	NL
Norunda, Sweden	60.1	17.5	NL
Niwot Ridge, USA	40.0	−105.6	NL
Tharandt, Germany	51.0	13.6	NL
Weidenbrunnen, Germany	50.2	11.8	NL
Wind River, USA	45.8	−121.9	NL
Zotino, Siberia	60.8	89.4	NL
Braschaat, Belgium	51.3	4.5	MX
Park Falls, USA	45.9	−90.2	MX
Ponca City, USA	36.8	−97.0	C_3
Bondville, USA	40.0	−88.3	C_3/C_4
Little Washita, USA	35.0	−97.9	C_4
Shidler, USA	36.9	−96.6	C_4
Atqasuk, USA	70.5	−157.4	SH
Barrow, USA	70.3	−156.6	SH
Happy Valley, USA	69.1	−148.8	SH
Upad, USA	70.3	−148.8	SH

Plant functional types (PFTs) are designated as follows: broadleaf (BL), needleleaf (NL), mixed broadleaf/needleleaf (MX), C_3 grassland (C_3), C_4 grassland (C_4) and tundra shrubland (SH).

2.2. *Analysis techniques*

The gap-filled carbon fluxes are analysed in the following five ways:

1. Method 1 extends the statistical approach of Hollinger et al. (1994). We determine NEE on both cloudy and non-cloudy days by assigning a cloud factor to each half-hourly measurement and deriving the average cloud factor for the entire day. The cloud factor at each half-hourly timestep is $1 - (SW/SW_{cl})$ where SW is irradiance measured at the top of the canopy and SW_{cl} is the surface irradiance under clear-sky opacity (Campbell and Norman, 1998, p. 172). Days with an average cloud factor > 0.4 are considered cloudy, consistent with the observation that average attenuation is 60% when broken cumulus clouds obscure the solar disk (Gu et al., 2001). In our discussion we consider alternative definitions of cloudiness such as an overcast sky. By defining composites, we only compare daily NEE from cloudy and non-cloudy days within the same 14-day period. This minimises the influence of soil moisture and physiological change on our results.
2. In Method 2, we fit inferred GPP with a generalised rectangular hyperbola (Gu et al., 2002). The LUE parameters, initial quantum efficiency (QE) and closeness to linear response (CLR), are inferred for both diffuse and direct irradiance from a least-squares minimisation after rejection of 2σ outliers. The advantage of this fitting procedure is that, subsequently, GPP can be predicted for given values of SW and fDIF. Since sky irradiance is rarely purely diffuse or purely direct, we determine canopy LUE at a reference (average daytime) shortwave irradiance for predominantly diffuse (fDIF = 0.75) and predominantly direct (fDIF = 0.25) sunlight. A similar separation into diffuse and direct regimes is adopted by previous authors (e.g. Niyogi et al., 2004). Furthermore, this technique allows comparison with a previous study of the control sites where GPP is compared for fDIF < 0.5 and fDIF ≥ 0.5 (Alton et al., 2007a). Using the hyperbola fit we also predict the change in GPP for values across the full range in fDIF.
3. Method 3 extends the non-linear regression adopted by Hollinger et al. (1994). GPP is fitted stepwise against environmental variables. First, GPP is regressed to SW, then the resultant residuals in GPP are regressed to air temperature and then the final residuals in GPP regressed to fDIF. This is carried out for morning and afternoon fluxes separately since plant stomata are often observed to close down around midday. We also fit air temperature against SW. The residuals in R_e resulting from the linear model in soil temperature are regressed to air temperature to take account of changes in autotrophic respiration. For fitting, we use a Taylor polynomial expansion containing five terms, i.e. a quartic. Compared to functions fitted by previous authors (e.g. Hollinger et al., 1994), this technique confers a greater amount of flexibility. The advantage of this method is that we take account of concurrent changes in air temperature and fDIF when examining the response of GPP and NEE to perturbations in SW.
4. Method 4 simulates GPP using a LSM. This is only possible where a complete meteorology is available in the Marconi database to force the model (71 out of 98 site-years). The LUE-enhancement predicted by the model is compared against: (i) observed LUE-enhancement derived in Method 2; (ii) above-canopy micro-meteorological variables such as VPD and air temperature.
5. Method 5 simulates GPP with a Monte Carlo ray-tracing model called FLIGHT (North, 1996). The radiative-transfer (RT) simulation calculates leaf photosynthesis in the same way as the LSM from Method 4. In addition, however, three-dimensional (3D) crown structure is represented with ellipsoids (Alton et al., 2005). The complexity of the model precludes simulations for all Marconi sites. Therefore, GPP is predicted for ecosystems possessing a range of architectural parameters (e.g. crown height, vegetation fraction, LAI and leaf angle) assuming different conditions of sky radiance.

Our five methods provide complementary insights into potential changes in carbon sequestration. Method 1

indicates, in the most direct manner, whether carbon sequestration is greater or smaller under clouds compared to seasonally equivalent non-cloudy skies. NEE follows directly from the sum of carbon flow at the canopy top (F) and the change in canopy storage (ΔC). Thus, this technique is more or less independent of inferred or modelled variables. By comparing NEE over both the daytime and a 24-h period, Method 1 reveals whether R_e or GPP is driving the change in carbon sequestration. Methods 2 and 3 permit a comparison with empirical procedures adopted by previous authors (Choudhury, 2001; Gu et al., 2002). All but one of the eight FLUXNET sites studied collectively by Niyogi et al. (2004), Gu et al. (2002) and Baldocchi and Harley (1995) are included in the current study. Assuming GPP is responsible for any change in carbon sequestration, Methods 4 and 5 allow interpretation of our results by comparing LUE-enhancement against influential biophysical parameters and micro-meteorological variables. Specifically, Method 5 reveals the respective roles of canopy architecture (Baldocchi and Harley, 1995; Farquhar and Roderick, 2003) and leaf orientation (Alton et al., 2005).

2.3. *Inferring fDIF*

Since diffuse sunlight is rarely measured at FLUXNET sites, we follow previous authors (e.g. Gu et al., 2002) in inferring the fraction of diffuse sunlight from the ratio of total downwelling radiation at the top of the canopy and above the atmosphere (x). As x decreases, fDIF is observed to increase as follows:

$$\mathrm{fDIF} = 1.45 - 1.81x \quad (1)$$

For $x < 0.28$ and $x > 0.75$, fDIF is set to 0.95 and 0.1, respectively (Roderick et al., 2001). Although the exact form of Eq. (1) depends somewhat on the duration of the measurement period (hourly or daily), comparison for one of our control sites, where fDIF is measured directly, indicates an acceptable level of error ($\pm$0.1; Alton et al., 2005). Adopting an equivalent relation given by Spitters et al. (1986) does not change significantly the results of our analysis. We also use Eq. (1) to infer the change in fDIF for a systematic perturbation to SW and *vice versa* (Methods 3 and 4). Although aerosols are present under our clear-sky measurements, we expect cloud to dominate the observed diffuse SW irradiance when comparing measurements across the growing season.

2.4. *Land-surface modelling*

The LSM adopted in Method 4 is the Joint UK Land Environmental Simulator (JULES), which is an enhanced version of the Met.Office Land-Surface Scheme (MOSES; Cox et al., 1999). Meteorological forcing data are obtained from the Marconi database, except longwave radiation which we estimate from air temperature (Campbell and Norman, 1998, p. 164). 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, reflected shortwave radiation, radiant thermal energy and conduction into the ground. Surface albedo and the penetration of light into the canopy are estimated according to the two-stream formulation (Sellers et al., 1996). The latter is enhanced to take account of sunfleck penetration, explicit leaf orientation and the fraction of sunlight that is diffuse (Alton et al., 2007a). Stomatal conductance, transpiration and photosynthesis are calculated in each canopy layer, before summing to produce total values for the canopy (Mercado et al., 2007). Five layers provide sufficient numerical accuracy. To expedite the calculation of momentum and energy transfer in global simulations the leaf temperature derived in the Penman–Monteith calculation is assumed to be uniform across the canopy. Leaf C_3 and C_4 photosynthesis are derived using the co-limitation model of Collatz et al. (1991) which is conceptually similar to the biochemical model of Farquhar et al. (1980). Apart from meteorological driving data, input to the simulation occurs through a control file prescribing general and PFT-specific biophysical parameters. Phenology is supplied by satellite-derived LAI of 10-day and 0.25° (≈28 km) resolution (Los et al., 2000). The LAI timeseries is normalised to the maximum LAI recorded *in situ* (Law et al., 2002) in order to account for sub-gridscale heterogeneity. The Ball–Berry algorithm is adopted for stomatal conductance and an exponential dependence on soil-moisture content is assumed for canopy photosynthesis (Sellers et al., 1996).

For each site-year in the Marconi database, the JULES simulation is calibrated by adjusting the photosynthetic capacity at the top of the canopy (V_{cmax}) to produce a least-squares minimisation between measured and simulated hourly GPP across the growing season. V_{cmax} is one of the most influential biophysical parameters entering the model (Wang et al., 2001) and this calibration procedure produces realistic values of photosynthetic capacity and leaf nitrogen (Alton et al., 2008) when compared to collated field measurements (Schulze et al., 1994). Other biophysical parameters are taken from field measurements available in the literature (Alton et al., 2008).

3. Results

Our results are generally aggregated by PFT. Site-years for crops are allocated either to C_3 or C_4 grasses, according to what is being cultivated. Tundra is categorised as shrub.

Our results are organised according to our five methods:

1. For all PFTs, we record a significant reduction in ecosystem carbon uptake (i.e. NEE more positive) on cloudy days compared to seasonally equivalent non-cloudy days. The possible exception is shrubland where carbon exchange is close to 0 across the 24-h cycle (Table 2). The difference in exchange between cloudy and non-cloudy days is typically 0.12–0.22 mol/(m^2 day) when integrating over 24 h. This is equivalent to a 61% reduction in sequestration when averaging across all PFTs. The difference in NEE between cloudy and non-cloudy skies is larger when integrating over just daylight hours. This indicates a cooling-induced reduction in respiration during the night following a cloudy day. The offset in nighttime respired CO_2 is equivalent to one third of the daytime reduction.
2. We observe a significant enhancement in LUE when sky irradiance is dominated by diffuse rather than direct

Table 2 – Net ecosystem exchange compared for cloudy and non-cloudy days

PFT	Daylight				24 h			
	ΔNEE (μmol/(m^2 s))	NEE (μmol/(m^2 s))	$\frac{\Delta NEE}{NEE}$	n	ΔNEE (μmol/(m^2 s))	NEE (μmol/(m^2 s))	$\frac{\Delta NEE}{NEE}$	n
BL	2.05 (0.22)	−8.17 (0.57)	−0.25	34	1.54 (0.16)	−3.54 (0.28)	−0.44	36
NL	2.05 (0.18)	−6.07 (0.38)	−0.34	36	1.45 (0.12)	−2.43 (0.20)	−0.60	36
MX	1.94 (0.15)	−4.86 (0.29)	−0.40	6	1.40 (0.11)	−1.49 (0.18)	−0.94	6
C_3	2.61 (1.38)	−6.10 (1.33)	−0.43	2	1.53 (0.68)	−2.14 (0.64)	−0.72	2
C_4	4.10 (0.82)	−9.93 (2.40)	−0.41	5	2.56 (0.50)	−3.82 (1.40)	−0.67	5
SH	1.94 (0.15)	−0.74 (0.15)	−2.62	5	0.15 (0.12)	−0.46 (0.09)	−0.32	5

NEE refers to non-cloudy days. ΔNEE denotes NEE under cloud minus NEE for non-cloudy days. Positive increments correspond to reduced sequestration. Averaging is carried out over both daylight hours and a 24-h period. In each case, we show the average value per PFT, after rejection of 2σ outliers, and the standard error in the mean (S.E.) in parentheses (S.D./$\sqrt{n}$). The number of site-years per PFT is given by n.

sunlight (1.12–1.80; Table 3). For the four site-years available for comparison (Walker Branch, Hyytiala, Shidler and Ponca City), our results are consistent with Gu et al. (2002). We infer an average LUE-enhancement of 1.32 whilst the LUE-parameters of Gu et al., yield a corresponding value of 1.36 when comparing fDIF = 0.75 with fDIF = 0.25. Method 2 is also consistent with Alton et al. (2007a) where GPP is compared for fDIF < 0.5 and fDIF ≥ 0.5 for the three control forest sites (average enhancement 1.22 against 1.27 recorded here). There is no significant difference between LUE-enhancement for measurements taken before and after solar noon. Furthermore, averaged across all site-years, the canopy response is only 5% lower during the afternoon compared to the morning when comparing at the average daylight irradiance. When fDIF is prescribed at each timestep, and SW adjusted according to Eq. (1), GPP is maximum for fDIF = 0.4–0.7 for trees and shrubs and 0.2–0.3 for grasses (Fig. 1). Note that without any adjustment to fDIF, the mean diffuse fraction for each PFT is 0.62 (BL), 0.65 (NL), 0.52 (C_3), 0.51 (C_4), 0.69 (SH) and 0.67 (MX). Except for shrubs, there is an unequivocal decrease in GPP when irradiance is completely diffuse compared to the mean diffuse irradiance of each PFT (22–42% reduction). The total irradiance also exhibits a considerable fall over this range in fDIF (Fig. 1, panel f). The rectangular hyperbolae employed in Method 2 reproduce inferred GPP with a high degree of fidelity (typically, $r = 0.92$, $n = 3000$).

Table 3 – Observed and simulated enhancement in light-use efficiency (LUE) under diffuse sunlight

PFT	Observed		Simulated	
	LUE-enhancement	n	LUE-enhancement	n
BL	1.30 (0.05)	35	1.39 (0.08)	21
NL	1.34 (0.04)	38	1.42 (0.06)	32
MX	1.29 (0.04)	6	1.58 (0.03)	5
C_3	1.12 (0.01)	2	1.42 (0.16)	2
C_4	1.19 (0.05)	5	1.15 (0.05)	5
SH	1.80 (0.30)	5	2.06 (0.49)	3

We define the LUE-enhancement as the ratio of GPP at fDIF = 0.75 to GPP at fDIF = 0.25 for the average daylight irradiance within each site-year. GPP(fDIF) follows from the rectangular hyperbola fitted with Method 2. The average LUE-enhancement is shown (after 2σ outlier rejection) for n site-years per PFT. The standard error is given in parentheses. The simulated LUE-enhancement is based on the GPP simulated by the land-surface model in Method 4. Note that simulations are not possible for all site-years since a full set of meteorological variables is required to force the model.

3. We record a significant reduction in mean GPP when SW is decreased systematically at each timestep. The increment in GPP, at each timestep, is inferred from the statistical relations established between GPP and the micro-meteorological variables SW, air temperature and fDIF. As SW changes, Eq. (1), in conjunction with the statistical relation established between air temperature and SW, indicate how concurrent changes in air temperature and fDIF affect GPP. Thus, we predict a decrease of 11–46% in average GPP for a 50% reduction in mean SW, the greatest decline being for grasses (Fig. 2). The results from Method 2 for prescribed fDIF show a similar behaviour when superimposed. GPP is reduced by 15–43% for a 35–47% deficit in SW. However, in this case, predicted values of mean GPP are higher as the same value of fDIF is assumed for all timesteps, including those of high irradiance. The predicted change in NEE *vis-a-vis* a systematic perturbation in SW uses the differential of R_e with respect to air temperature in addition to the statistical relations already established for GPP (Fig. 3). Aggregating across all PFTs, we predict an 80% reduction in ecosystem carbon sequestration (i.e. NEE more positive) when SW falls to 50% of its average value. The ecosystem switches from a carbon sink to a carbon source for attenuations greater than this. The regressional relationships established with Method 3 reproduce observed NEE with a high degree of fidelity (typically, $r = 0.95$, $n = 2500$).
4. Our JULES land-surface simulation reproduces fairly well the magnitude of the observed LUE-enhancement (Table 3). Indeed, except for mixed forest and C_3 grassland observed LUE-enhancement is reproduced within the errors. However, reproduction for individual site-years is only fair ($r = 0.55$, $n = 71$) as the carbon fluxes are quite noisy compared to the magnitude of the LUE-enhancement (Fig. 4). On average, the model underestimates GPP under direct sky irradiance by 9%. The LSM is believed to be somewhat oversensitive to above-canopy VPD and, consequently, underestimates stomatal conductance under direct sunlight. It is difficult to relate LUE-enhancement for each site-year to micro-meteorological variables other than shortwave irradiance. Observed LUE-enhancement correlates weakly with the difference in air temperature

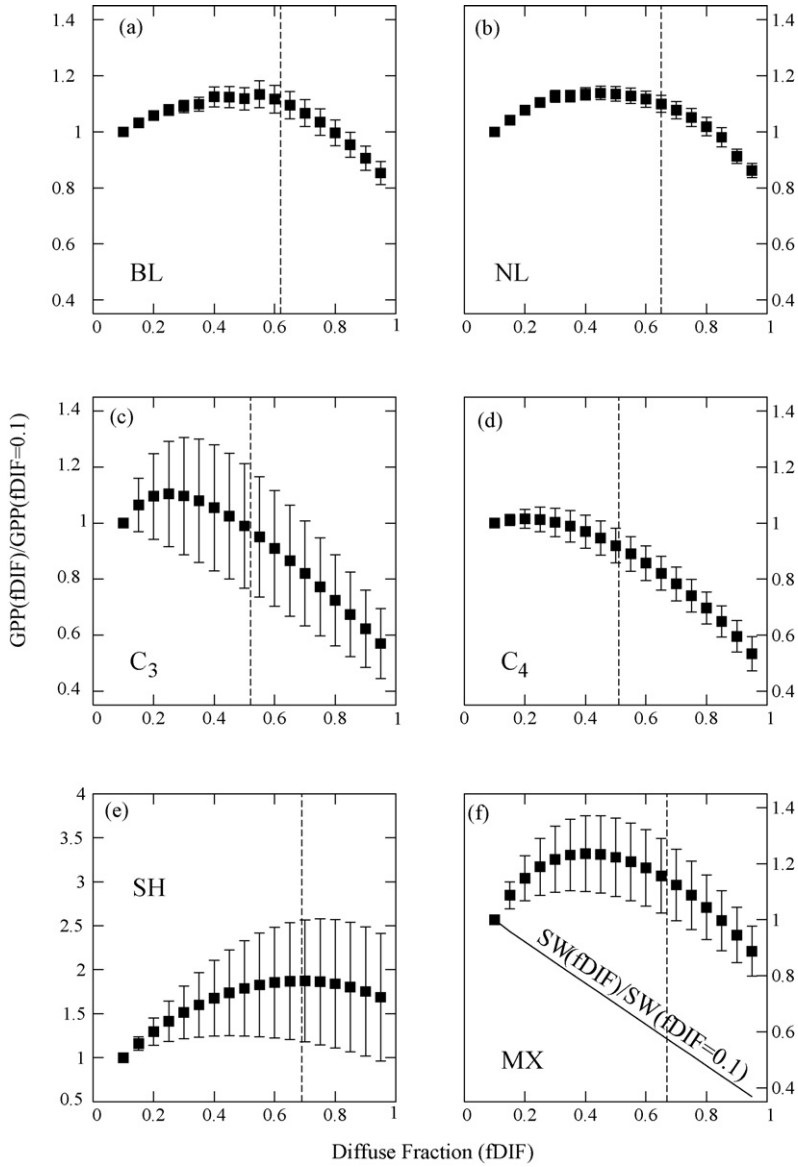

Fig. 1 – (a–f) Gross primary productivity (GPP) for prescribed values in the fraction of diffuse irradiance (fDIF). Values are normalised with respect to fDIF = 0.1 (the lowest diffuse fraction generally measured in the field). Markers and error bars denote the average and standard error, respectively, for each plant functional type (PFT). A dashed, vertical line indicates the average fDIF within the PFT. In panel (f) we show the decrease in total irradiance as fDIF increases assuming the relation given in Eq. (1). Note that there is a change in vertical scale for shrubs in panel (e).

between direct and diffuse conditions ($r = 0.14$, $n = 93$). The ratio of above-canopy VPD for direct and diffuse sunlight also correlates poorly with LUE-enhancement ($r = -0.16$, $n = 72$). We emphasize that simple RT schemes based on Beer's Law, as adopted in many global and regional LSMs, fail entirely to reproduce the LUE-enhancement under diffuse sunlight (Fig. 5).

5. The Monte Carlo RT model accounting for 3D crown architecture, FLIGHT, indicates that V_{cmax} has one of the greatest influences over canopy LUE. However, the simulation has difficulty in accounting for LUE-enhancements in excess of 1.2 even when taking account of the probable range in biophysical parameters describing canopy architecture (Fig. 6).

4. Discussion

We address the four scientific questions raised in Section 1.

4.1. *What is the observed level of LUE-enhancement?*

We infer an increase of 1.12–1.80 in LUE when sky irradiance is dominated by diffuse (fDIF = 0.75) rather than direct (fDIF = 0.25) sunlight. The average for all site-years is 1.32 ± 0.02 (S.E.). The LUE-enhancement is lower in grasses, compared to trees and shrubs, although more site-years are required to confirm this difference.

Method 2 elucidates the seeming inconsistency between the "low" enhancement of 1.12–1.32 given by Alton et al.

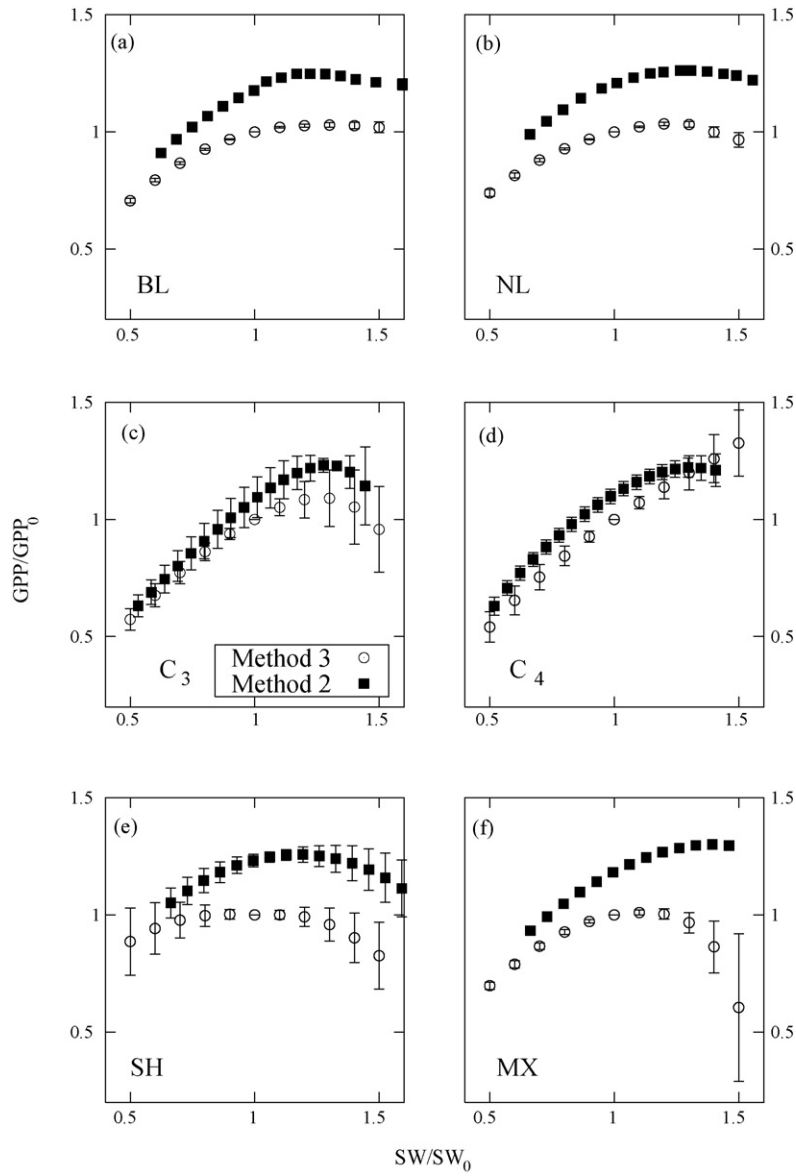

Fig. 2 – (a–f) Fractional change in gross primary productivity (GPP) for a systematic increase or decrease in SW. SW_0 and GPP_0 denote the unperturbed state. Predictions are derived using Methods 2 and 3. For the former, we use Eq. (1) to relate changes in fDIF to changes in SW, as well as the GPP response to fDIF that is depicted in Fig. 1. Error bars represent the standard error in the mean.

(2007a) for the three control sites (all forest) and the "high" ratio of initial QE (2.3) derived by Gu et al. (2002) for pure diffuse and pure direct sunlight in three forest and two grassland sites. The difference arises partly from the choice of fDIF = 0.25 and 0.75, in the current study, to characterise direct and diffuse sky conditions (rather than 0 and 1, respectively). However, the rectangular hyperbola used to describe GPP in Method 2 depends strongly, at moderate irradiances at least, on the values fitted for both initial QE and CLR. This means that the ratio of initial QE (and the CLR ratio for that matter) provides a rather poor measure of LUE-enhancement. We feel that using the average irradiance for a site in order to compare GPP is a more useful indicator. Our results are consistent with Urban et al. (2007) who record a LUE-enhancement of $\leq$1.5 for a young needleleaf forest.

For crops, Choudhury (2001) reports a LUE-enhancement 110% under cloud. However, the LUE (or yield) is measured at a significantly lower total irradiance under diffuse (cloudy) conditions compared to direct sunshine. The hyperbolic response to SW, that typifies vegetation canopies, ensures that LUE increases for lower light levels, i.e. d(GPP)/d(SW) increases as SW $\rightarrow$ 0 (e.g. Fig. 5).

4.2. *How can the LUE-enhancement be explained in terms of biophysical parameters and micro-meteorological variables?*

Land-surface simulations with JULES capture fairly well the *magnitude* of the LUE-enhancement under diffuse sunlight ($\approx$30%; Fig. 4) when compared against the 100–200% enhancement claimed by some previous authors (Choudhury, 2001; Gu

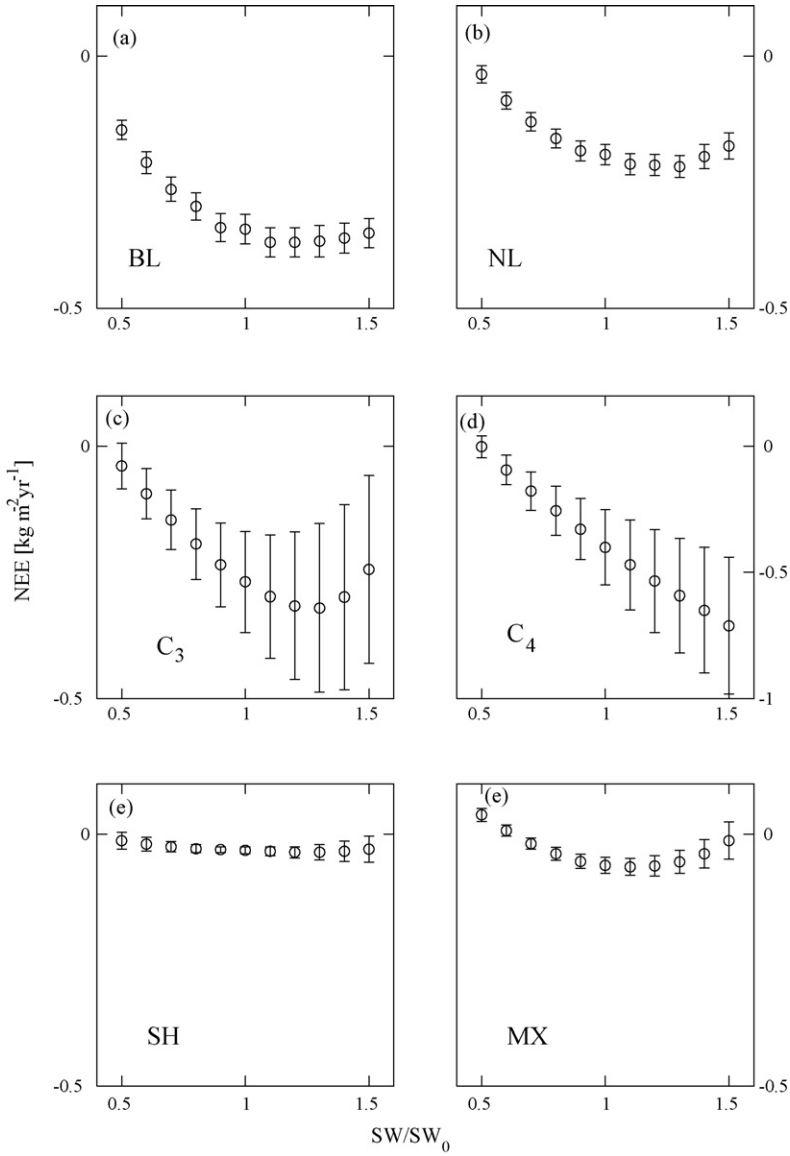

Fig. 3 – (a–f) Absolute change in annual net ecosystem exchange (NEE) with respect to the unperturbed state for a systematic increase or decrease in SW. SW_0 denotes the unperturbed state. Error bars depict the standard error in the mean. Negative values denote carbon uptake by the land-surface. Note that there is a change in vertical scale for C_4 grasses in panel (d).

et al., 2002). However, only about a third of the variance is explained by the model ($p < 0.0005$, $n = 71$), suggesting that further progress is still required before LSMs fully account for canopy behaviour under different conditions of sky radiance. We emphasize that most global LSMs adopt average vertical light profiles for leaf irradiance (Alton et al., 2007b). Thus, they fail completely to reproduce the LUE-enhancement and predict the same GPP regardless of the nature of sky radiance (diffuse or direct; see Fig. 5). The current LSM takes explicit account of leaf orientation and simulates the penetration of sunflecks into the canopy from direct sunlight. Previous authors (Baldocchi and Harley, 1995; Chen, 1996) emphasize the importance of crown shape within vegetation to allow effective beam penetration. However, for the continuous canopies that typically comprise FLUXNET, we conclude from our 3D RT modelling that canopy architecture plays only a minor role in the enhancement of LUE under cloud. For all but the most open canopies, the oblique photons constituting diffuse sunlight (average zenith angle 60°) are absorbed at the top of the canopy where photosynthetic capacity is greatest. A range of leaf angles permits the crown to intercept diffuse photons with a high degree of efficiency. Under direct sunlight a greater fraction of irradiance is generally absorbed by foliage in the lower part of the canopy where Rubisco-limited photosynthetic rates are least (Carswell et al., 2000; Lewis et al., 2000; Meir et al., 2002). Our simulations indicate that increased radiation-sharing under diffuse sunlight, particularly amongst foliage at the top of the canopy, leads to the enhancement in LUE under cloud.

The 3D RT simulation has difficulty accounting for LUE-enhancements greater than 1.2 in closed canopies, i.e. where vegetation cover fraction ≥ 0.7. However, the average

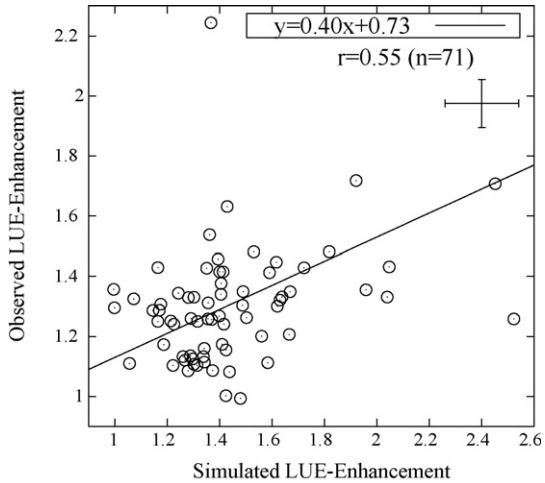

Fig. 4 – A comparison of simulated and observed enhancement in light-use efficiency (LUE) for all site-years where a complete meteorology is available to force the land-surface model. At the top-left we indicate the least-squares linear fit and the typical uncertainty in deriving LUE.

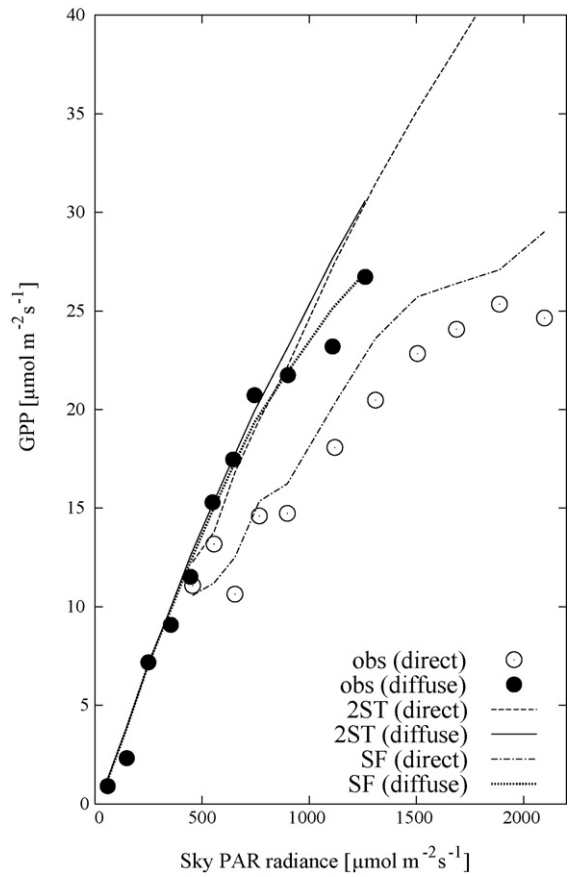

Fig. 5 – Gross primary productivity (GPP) inferred for an Amazonian broadleaf canopy near Manaus from measured carbon fluxes (open and closed symbols). Measurements and simulated values are shown separately for predominantly diffuse (fDIF > 0.5) and predominantly direct (fDIF ≤ 0.5) sunlight. In contrast to the standard representation of light interception adopted in climate predictions (2ST), the LSM adopted in this study (SF) accounts correctly for the dispersion in leaf irradiance at any given height within the canopy arising from varied leaf orientation and sunfleck penetration. Under diffuse sunlight, this dispersion is relatively small reducing the fraction of foliage which is light-saturated.

enhancement that we observe is 1.32 ± 0.02. We surmise that a second environmental variable, other than light, contributes to the LUE-enhancement. Previous authors invoke concomitant reductions in temperature and VPD as factors increasing LUE under cloud (Gu et al., 2002; Lloyd et al., 2002). Indeed, VPD and air temperature are both significantly higher when direct rather than diffuse sunlight predominates at the Marconi sites. Under such conditions, plants may reduce stomatal conductance in order to conserve water, reducing leaf assimilation rates and thus reinforce the LUE-enhancement. Our results, however, suggest that VPD and air temperature play only a secondary role. In Method 4, we record a poor correlation between above-canopy VPD and observed LUE-enhancement ($r = -0.16$). In Method 2, GPP is only 5% lower in the afternoon compared to the morning, although the highest above-canopy VPD occurs during mid-afternoon. Finally, air temperature emerges as a second-order variable in Methods 3 and 4 when predicting GPP and accounting for the observed LUE-enhancement. The absence of a strong correlation may be due to canopy microclimate which often behaves in a quasi-independent manner of above-canopy conditions if the vegetation is dense and the transpiration rates are high (e.g. Dolman et al., 1991). Moreover, leaf temperature may differ greatly from above-canopy air temperature, particularly when the radiation load is high but transpiration is low (Linacre, 1972; Campbell and Norman, 1998, p. 227). Future investigations of LUE-enhancement should focus on the temperature and humidity recorded within the canopy airspace once such measurements become widely available.

4.3. *Are the observed levels of LUE-enhancement sufficient to increase GPP under cloud?*

The LUE-enhancement is not sufficient to offset the dramatic fall in light levels that occurs when clouds obscure the solar disk. For an assumed 60% reduction in average SW under broken cloud (Gu et al., 2001), Methods 2 and 3 indicate a decrease of 20–60% in productivity. The reduction is greatest for grasses and smallest for trees and shrubs. This prediction is based on a decrease in mean SW and corresponds, therefore, to the steepest part of the curve in Fig. 2. Assuming the initial state is a cloudless sky, a 60% reduction in SW incurs only a 10–40% drop in GPP for trees and grasses and a possible increase in GPP for shrubs (fDIF = 0.1 → 0.9 in Fig. 1). However, our assumption of 60% attenuation under cloud is conservative (e.g. Campbell and Norman, 1998, p. 172). For overcast days, defined as ≥7 Oktas, i.e. cloud covering ≥88% of the sky, the attenuation recorded with respect to clear sky is ≥80% (Lam and Li, 1996).

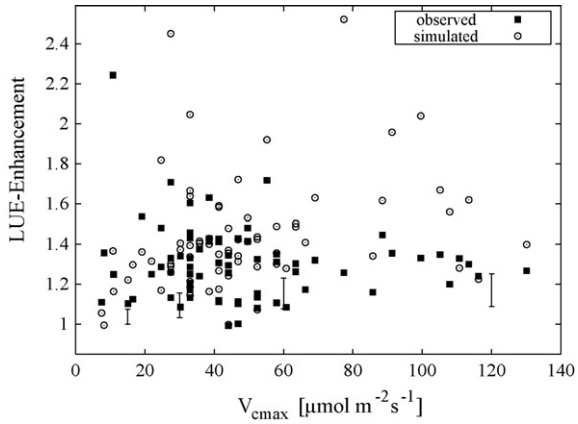

Fig. 6 – The observed and simulated enhancement in light-use efficiency (LUE) plotted against the top-of-canopy photosynthetic capacity (V_{cmax}), the latter inferred from the JULES calibration for each site-year. Vertical error bars denote the range of LUE-enhancement produced in an ensemble of 3D ray-tracing simulations spanning the likely range in biophysical parameters for the Marconi sites, namely: crown height from 1 to 25 m, LAI from 1 to 8 m^2/m^2, solar zenith angle from 0° to 60°, leaf angle distribution from erectophile to planophile and vegetation cover fraction from 0.4 to 1.0. These simulations are conducted at the average daylight irradiance for all site-years during the growing season (375 W/m^2).

Our findings contrast with the enhancement in GPP recorded under aerosols (Gu et al., 2003). Aerosols are much more conservative with respect to total downwelling radiation although under thick haze we may expect GPP to fall rather than rise. LUE-enhancement produces a quasi-stability in productivity since small perturbations in insolation are offset by changes in both fDIF and, to a lesser extent, temperature-dependent respiration. Thus, for trees and shrubs, the change in mean GPP for a 10% increase/decrease in average insolation is rather modest (3%), suggesting that primary production is fairly well adapted to light environment for these PFTs (Fig. 2). We note that the global trend in insolation, over the latter half of last century, is a decline of 5–10% (Stanhill and Cohen, 2001; Liepert, 2002). Interannual variability in insolation is ≤8% on spatial scales of ≈100 km resolution (Alton et al., 2007b).

An LUE-enhancement in excess of 2 is required for GPP to increase under broken cloud. Simulations with the 3D RT model indicate that only a LUE-enhancement as high as 1.6 is possible through considerations of sky radiance, leaf orientation and canopy architecture alone. This is predicted to occur when $V_{cmax} \geq 120$ μmol/(m^2 s), for a vegetation cover fraction of 0.1 (e.g. individual trees separated by twice the crown width) and an overhead sun. Such conditions are unusual since V_{cmax} is approximately 40–60 μmol/(m^2 s) for trees/shrubs and about half that value in grassland (Schulze et al., 1994). Furthermore, undisturbed canopies are generally closed except at temperature-limited (e.g. boreal) and moisture-limited (e.g. Sahelian *acacia*) tree lines. For closed tropical canopies, we speculate that diffuse sunlight may be of particular importance for emergent crowns.

4.4. *Does the vegetated land-surface sequester more carbon on cloudy days?*

Methods 1 and 3 demonstrate unequivocally and consistently that carbon sequestration is reduced under cloud due to the dramatic drop in primary productivity. This is despite accounting, by means of Method 1, for a cooling-induced reduction in respiration under cloud (estimated offset one third). Thus, for our conservative assumption of 60% SW-attenuation under cloud, we estimate a 60–80% decrease in carbon sequestration. The fractional change in ecosystem carbon sequestration is larger than that for primary productivity, despite the significant, counteracting role of temperature for the former. This is because net exchange is much closer to 0 compared to primary productivity. Within global trends of insolation associated with increased cloud optical depth (10% reduction in mean SW from 1960 to 1990 and a reversal thereafter; Wild et al., 2005), our predicted change in net primary productivity (NPP), assuming NPP ≈ 0.5GPP (DeLucia et al., 2007), is 3–5%, i.e. somewhat smaller than the impact of human-released fossil fuel on the carbon cycle (≈10% NPP; e.g. Schlesinger, 1997). Our methods, however, assume that SW changes by the same fraction at all timesteps and, as such, they neglect any temporal re-distribution in irradiance.

Previous studies of diffuse sunlight give rise to disparate conclusions on the impact of cloud on carbon sequestration. Hollinger et al. (1994) claim an increase rather than a decrease in ecosystem carbon sequestration for a New Zealand beech forest under cloud. However, the purported increase varies dramatically (0.01–0.316 mol/(m^2 day)) across the few adjacent days that are monitored. Within low-LAI peatland shrubs, Letts et al. (2005) find that NEE is neutral against clearness index > 0.35 (equivalent to $SW/SW_0 \geq 0.86$ in Fig. 3, panel e). Within the errors, this is consistent with the current study. Niyogi et al. (2004) infer a LUE-enhancement of 30–50% after analysing the carbon flow at six FLUXNET sites (forest, crops and grassland) and this accords with the current investigation. However, these authors leave open the question of whether ecosystem carbon sequestration decreases on cloudy days owing to reduced shortwave radiation. In artificial shading experiments, crop yields are undiminished for 20% reductions in insolation (Evans, 1993). However, we find that, of all the PFTs, grassland and crops appear to be the most sensitive to changes in surface irradiance (Fig. 3, panels c and d).

4.5. *Caveats and limitation of the study*

1. Our estimates of fDIF pertain to half-hour intervals but the distribution of SW and fDIF within this time interval may vary strongly depending on the type of cloud present. Under broken cloud, for example, fDIF may switch rapidly from high to low values. Although stomatal response (typically 10–20 min; Woods and Turner, 1971) will slur such effects, it would be instructive to monitor leaf photosynthesis under varying conditions of cloud. We emphasize that the cloud factor derived in Method 1 correlates strongly with the cloud optical depth that we infer from satellite imagery (Fig. 7).
2. Although we claim an unequivocal decrease in both productivity and ecosystem sequestration when the sky

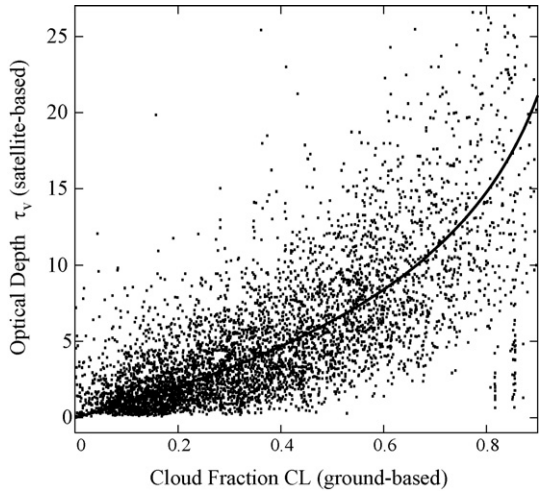

Fig. 7 – Visual (λ = 0.6 μm) optical depth (τ_v), retrieved from the International Satellite Cloud Climatology Project (ISCCP; Rossow and Schiffer, 1999), compared against the cloud factor (CL) inferred in Method 1. The comparison is made for the growing periods of 1997 and 1998 at the Marconi sites (48 site-years). The best-fit, denoted by the solid line, has the form CL = $1 - \exp(-Q\tau_v/\langle\cos\theta_s\rangle)$ where Q = 0.06 (cosine mean solar zenith angle $\langle\cos\theta_s\rangle$ = 0.55). Despite significant differences in spatial resolution (≈10 and 280 km for the Marconi and ISCCP data, respectively) and temporal resolution (0.5 and 3 h, respectively), the best-fit accounts for 72% of the variance (n = 5300).

is overcast (SW-attenuation ≥ 80%) compared to clear skies, the canopy response to cloud is non-linear. Indeed, productivity for trees appears to increase slightly (≈10%) when some cloud is present such that fDIF and SW-attenuation are, respectively, 0.55 and 30% (Figs. 1 and 2). An analysis of NEE for more than two categories of the cloud factor (Method 1) does not yield statistically significant results due to the small number of site-years for some PFTs and the small change in NEE for trees over a broad range of SW (Fig. 3).

3. Our canopy response under high fDIF is biased to large solar zenith angles (i.e. sun near the horizon) compared to direct sunlight. Since the canopy response in the early morning may be enhanced by CO_2 respired during the night, we may overestimate the LUE-enhancement in closed, dense canopies.
4. Apart from in Method 1, we average fluxes over the whole growing season. However, the canopy light-response may vary somewhat over this period owing to physiological change (Lloyd et al., 2002) or drought-stress (Reichstein et al., 2003). For sites-years where the fluxes are less noisy, we find that comparing canopy response over a limited part of the growing season does not change our conclusions. We emphasize that our methods account for the change in LAI throughout the growing season.
5. The data currently available for grasses and shrubs are not very representative for those PFTs. Thus, our results for shrubs apply to tundra environments and may not be relevant to shrubs situated at lower latitudes.

5. Conclusions

We determine the impact of cloud cover on light-use efficiency, primary productivity and ecosystem carbon sequestration for six vegetational types and at an unprecedented number (38) of carbon monitoring (FLUXNET) sites. Established statistical and empirical methods are combined with novel techniques based on a land-surface model and a three-dimensional radiative-transfer simulation. Our primary objectives are to reconcile the contrasting results from previous studies and to identify the biophysical mechanisms whereby carbon exchange may vary. The main findings are as follows:

(i) Relative to previous authors (Choudhury, 2001; Gu et al., 2002), all our methods indicate a much lower enhancement in canopy light-use efficiency under diffuse sunlight produced by clouds compared to direct sunlight. For forest (broadleaf, needleleaf and mixed) and grassland (C_3 and C_4) we record LUE-enhancements of only 1.30 ± 0.05 (79 site-years) and 1.15 ± 0.05 (7 site-years), respectively, when sky radiance is dominated by diffuse (fDIF = 0.75) rather than direct sunlight (fDIF = 0.25). For tundra shrubs the corresponding value is 1.80 ± 0.30 (5 site-years). Some, but not all, of the difference with previous authors (LUE-enhancement 2–3) arises from the values of fDIF and irradiance adopted when determining LUE.

(ii) The LUE-enhancement we record is of insufficient magnitude to increase primary productivity under cloud compared to cloudless skies. Owing to the dramatic fall in total downwelling shortwave radiation when clouds obscure the solar disk, we predict a fall in GPP of at least 10–40% under cloud. The greatest decline is for grassland.

(iii) Our 3D radiative-transfer simulations indicate that a LUE-enhancement ≥ 2 is required in order for primary productivity to increase under cloud. The appropriate solar-crown geometry (isolated crowns and overhead sun) is unlikely to occur for the closed canopies comprising our sample. In the current investigation LUE-enhancement can be attributed to (i) varied leaf orientation rather than crown shape and (ii) an unidentified factor not relating to architecture nor above-canopy meteorological conditions (i.e. shortwave radiation, VPD and air temperature).

(iv) Despite a significant cooling-induced reduction in respiration under cloud (offset ≈ 1/3), the vegetated land-surface sequesters 60–80% less carbon on cloudy days compared to seasonally equivalent non-cloudy days. This result contrasts with previous authors who, for individual sites, find either no change in NEE (Letts et al., 2005) or even a 50% increase in carbon sequestration (Hollinger et al., 1994).

(v) For reductions in mean insolation comparable to those associated with global "solar" dimming (≈10%), we predict changes in NPP (3–5%) somewhat less than the equivalent impact of human-released CO_2 on the global carbon budget (≈10% NPP; e.g. Schlesinger, 1997).

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