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The impact of diffuse sunlight on canopy light-use efficiency, gross photosynthetic product and net ecosystem exchange in three forest biomes

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Abstract

For three forest canopies (a sparse, boreal needleleaf; a temperate broadleaf; and a dense, tropical, broadleaf stand) light-use efficiency (LUE) is found to be 6–33% higher when sky radiance is dominated by diffuse rather than direct sunlight. This enhancement is much less than that reported previously for both crops (110%; Choudbury, 2001) and moderately dense temperate woodland (50–180%). We use the land-surface scheme JULES to interpret the observed canopy response. Once sunflecks and leaf orientation are incorporated explicitly into the scheme, our simulations reproduce convincingly the overall level of canopy gross photosynthetic product (GPP), its enhancement with respect to diffuse sunlight and the mean 15% reduction in productivity observed during the afternoon due to stomatal closure. The LUE enhancement under diffuse sunlight can be explained by sharing of the canopy radiation-load, which is reduced under direct sky radiance. Once sunflecks are accounted for the advantage of implementing more sophisticated calculations of stomatal conductance (e.g. Ball–Berry and SPA submodels) is less obvious even for afternoon assimilation. Empirical relations are developed between observed carbon flux and the environmental variables total downwelling shortwave radiation (SW), canopy temperature (*T*) and the fraction of diffuse sky radiance (fDIF). These relations allow us to gauge the impact of increased/reduced insolation on GPP and net ecosystem exchange (NEE). Overall the three stands appear to be fairly stable within global trends and typical interannual variability (SW changing by $<$15%). Greatest sensitivity is exhibited by the boreal site, Zotino, where NEE falls by 9 ± 4% for a 15% reduction in SW.

Keywords: carbon cycle, diffuse sunlight, radiation

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Introduction

Terrestrial vegetation has a major impact on climate partially balancing anthropogenic sources of atmospheric CO_2 (Cox *et al*., 2000; Knorr & Heimann, 2001; Adams & Piovesan, 2002), determining surface temperature (Sellers *et al*., 1997) and returning a sizeable fraction of rainwater to the lower troposphere through transpiration (Salati *et al*., 1979; Gat & Matsui, 1991; Williams *et al*., 2004). A key issue to be resolved, however, is how climate change will affect the ability of plants to photosynthesize and how this in turn will amplify or suppress those climatic trends.

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A systematic reduction of 5–10% in global insolation is estimated for global insolation in the latter half of last century with drops of 15–30% for certain areas of the Northern Hemisphere (Stanhill & Cohen, 2001). An increase in the optical depth of clouds due to anthropogenic tropospheric aerosols is cited as the probable cause of this decline (Liepert, 2002). Increased cloud reduces insolation but increases the fraction of shortwave radiation that is diffuse, that is to say not emanating directly from the solar disc (e.g. Roderick *et al*., 2001). Under diffuse sky radiance, canopy light-use efficiency (LUE) is believed to increase by $>$50% for both crops (Choudbury, 2001) and temperate woodland (Hollinger *et al*., 1994; Gu *et al*., 2002) compared with the equivalent quantity of direct sunlight. For systems of

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Table 1 Main geographical and structural features of the canopies featuring in this study

		Site		
Property	Units	Zotino	Harvard	Manaus
Designation		Zo	Hv	Mn
Location		Siberia	North America	Amazonia
Biome		Boreal needleleaf	Temperate broadleaf	Tropical broadleaf
Latitude	Deg.	60.8N	42.5N	2.6N
Longitude	Deg.	89.4E	72.2W	60.2W
Primary vegetation		Scots Pine (*Pinus sylvestris*)	Oak, Maple (*Quercus rubra, Acer rubrum*)	Mixed species (*Floresta ombrophila densa*)
LAI	$m^2 m^{-2}$	2	4.5	5.5
Stand density	Trees ha^{-1}	470	?	635

LAI and stand density are adapted from values collated in Alton *et al*. (2007b).
LAI, leaf area index.

low leaf area index (LAI; e.g. grassland and shrubs), the corresponding enhancement is probably close to zero (Niyogi *et al*., 2004; Letts *et al*., 2005). Given that the leaf photosynthetic response saturates to high light levels, canopy LUE is expected to be higher under diffuse sky radiance, compared with direct sunlight, due to a more even radiation loading across the foliage (Farquhar & Roderick, 2003). What is less clear is whether the increase in LUE is sufficient to compensate for the loss in total SW (i.e. direct + diffuse) and, therefore, whether the gross photosynthetic product (GPP) of the entire canopy is higher or lower under cloudy skies.

In this paper, we test the hypothesis that the enhancement in LUE under cloudy skies is sufficient to increase both canopy GPP and ecosystem net ecosystem exchange (NEE) compared with seasonally equivalent clear skies. We do this by referring to carbon flow measured at three forest stands each of which represents a different forest biome (sparse boreal needleleaf, dense tropical broadleaf and moderately dense temperate broadleaf). In order to be able to attribute any LUE enhancement unequivocally to diffuse light (and not to any concurrent changes in temperature or vapour pressure deficit VPD) we simulate and interpret the observations using a land-surface model specifically modified to take account of the directionality of sky radiance and explicit leaf orientation. This is deemed important given that the directionality of incoming sky radiation is poorly represented in current land-surface schemes (Farquhar & Roderick, 2003; Sitch *et al*., 2003). Since stomatal closure is observed to suppress canopy photosynthesis usually around mid-day (e.g. Jones, 1992) we introduce, separately, two computationally expensive stomatal submodels into the land-surface scheme in order to compare with the comparatively simple calculation of stomatal conductance in the default configuration.

This study is structured as follows: in the following section, we show how canopy GPP and LUE is inferred for conditions of diffuse and direct sunlight. We then present our land surface scheme and the modifications necessary to the land-surface scheme necessary to simulate and thus interpret the observations and in the subsequent section, empirical relations are developed for GPP, allowing us to estimate the impact on canopy production and NEE for given changes in downwelling shortwave radiation. In the penultimate section, our results are discussed in the context of the findings of previous authors.

Materials and methods

GPP and LE from observations

We select three forest sites from different latitudes which span a wide range in LAI and stand density: Zotino in Siberia, Manaus in Amazonia and Harvard Forest in New England (Table 1). These locations form part of FLUXNET where carbon and energy fluxes have been monitored using eddy covariance techniques. The flux towers also record micrometeorology and *in situ* physiological measurements (e.g. leaf nitrogen and LAI) are easily available in the literature. For each of our forest stands, flux and meteorological data are obtained for periods when carbon storage is measured (Valentini *et al*., 2000). This is done by either accessing public web sites or by contacting the relevant Principal Investigators directly.

GPP is inferred in the standard way from ecosystem respiration (R_e), carbon flow 5–15 m above the canopy

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Table 2 Regression coefficients for empirical relations based on least-squares optimization

Relation	Site	Type	a	b	c	r^2
GPP vs. SW (am)	Zotino	3	12.1	189	12	0.65
GPP vs. SW (pm)	Zotino	3	10.1	175	10	0.57
GPP vs. T (am)	Zotino	1	0.01	−2.90	0.0	0.02
GPP vs. T (pm)	Zotino	1	−0.11	32.4	0.0	0.28
GPP vs. fDIF (am)	Zotino	2	4.9	−3.7	−1.3	0.09
GPP vs. fDIF (pm)	Zotino	2	6.3	−6.1	−1.0	0.04
T vs. SW (am)	Zotino	4	0.44	280	0.56	0.61
T vs. SW (pm)	Zotino	4	0.44	283	0.55	0.56
R_e vs. T (am and pm)	Zotino	5	0.30	0.07	260	0.81
GPP vs. SW (am)	Harvard	3	28.9	236	27	0.81
GPP vs. SW (pm)	Harvard	3	27.1	339	26.9	0.78
GPP vs. T (am)	Harvard	1	0.10	−29.4	0.0	0.14
GPP vs. T (pm)	Harvard	1	0.06	−17.7	0.0	0.06
GPP vs. fDIF (am)	Harvard	2	15.9	−11.0	−4.2	0.29
GPP vs. fDIF (pm)	Harvard	2	19.1	−14	−4.9	0.24
T vs. SW (am)	Harvard	4	0.44	282	0.54	0.60
T vs. SW (pm)	Harvard	4	8.27	269	0.20	0.65
R_e vs. T (am and pm)	Harvard	1	0.076	−18.6	0.0	0.84
GPP vs. SW (am)	Manaus	2	8.18e–2	−6.10e–5	1.60	0.65
GPP vs. SW (pm)	Manaus	2	5.06e–2	−2.85e–5	1.60	0.72
GPP vs. T (am)	Manaus	1	−0.14	42.3	0.0	0.06
GPP vs. T (pm)	Manaus	1	−0.19	57.7	0.0	0.19
GPP vs. fDIF (am)	Manaus	2	2.7	−0.70	−1.20	0.08
GPP vs. fDIF (pm)	Manaus	2	12.9	−9.6	−3.20	0.16
T vs. SW (am)	Manaus	3	16.7	799	311.7	0.92
T vs. SW (pm)	Manaus	3	11.5	498	308.7	0.82
R_e vs. T (am and pm)	Manaus	1	−0.115	40.2	0.0	0.05

'Type' refers to the type of the equation fitted: 1 = linear [$ax + b$]; 2 = quadratic [$ax + bx^2 + c$]; 3 = exponential [$c - a \times \exp(-x/b)$]; 4 = hyperbola [$ax^c + b$]; and 5 = exponential [$a\exp(b \times (x-c))$]. All relations, except ecosystem respiration (R_e), are fitted separately for morning and afternoon (col.1). Units for GPP, SW, T and R_e are $\mu mol\,m^{-2}\,s^{-1}$, $W\,m^{-2}$, K and $\mu mol\,m^{-2}\,s^{-1}$, respectively.
GPP, gross photosynthetic product.

(F) and storage of CO_2 within the canopy airspace (S). Thus:

$$GPP = R_{e^-}(F + S), \quad (1)$$

with upward flow denoted as positive (e.g. Lloyd *et al.*, 2002). For Manaus and Harvard, ecosystem respiration is derived from night-time fluxes recorded under moderate airflow (Medlyn *et al.*, 2003) assuming a linear temperature dependency (Table 2). Estimates for the mean daytime R_e during the growing season at Harvard and Manaus are 3.6 ± 0.1 and $5.7 \pm 0.2\,\mu mol\,m^{-2}\,s^{-1}$, respectively. At Zotino, a second eddy covariance device, located near the forest floor, allows the direct subtraction of respiration associated with both the soil and herb layer. Autotropic respiration is estimated at 1.3 and $1.7\,\mu mol\,m^{-2}\,s^{-1}$ for 1999 and 2000, respectively (Shibistova *et al.*, 2002). This appears to dominate mean daytime R_e ($1.9 \pm 0.2\,\mu mol\,m^{-2}\,s^{-1}$) at the boreal site. For all sites latent heat (LE) is derived from the upward flow of water vapour measured above the canopy.

We extract fluxes for a limited part of the growing season when physiological and phenological changes can be largely neglected. For Zotino, this study period was Julian day from 152 to 243 (June–August incl.) from 1999 and 2000. For Harvard the relevant period was Julian day 150 to 260 (June–mid-August) from 2002 and 2003. For Manaus the study period was Julian day 243 to 431 (beginning of September until the beginning of March), corresponding, apart from September and October, to the wet season at this site (Williams *et al.*, 1998). Observations were selected randomly over the aforementioned study periods and separated into categories of predominately diffuse (fDIF ≥ 0.5; hereafter simply 'diffuse') and predominantly direct (fDIF < 0.5; hereafter simply 'direct') sunlight. We only consider measurements where solar elevation is $>17°$. In general, fDIF is not measured directly at our sites. Thus, we follow previous authors (e.g. Gu *et al.*, 2002) in inferring the diffuse fraction from the ratio of SW at the top of the canopy with its top-of-atmosphere value (x). As

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x decreases fDIF has been observed to increase as follows:

$$\mathrm{fDIF} = 1.45 - 1.81x. \quad (2)$$

For $x < 0.28$ and > 0.77, fDIF is set to 0.95 and 0.05, respectively (Roderick *et al.*, 2001). Although the exact form of Eqn (1) depends somewhat on the duration of the measurement period (hourly or daily), comparison for one of our sites, where fDIF is measured directly for some of the study period (Zotino), indicates an error of <0.1 in our estimate of fDIF for solar elevation angles $>17^\circ$ (Alton *et al.*, 2005). Adopting an equivalent relation given by Spitters *et al.* (1986) does not change the results of our analysis.

To preclude any bias in physiology or soil-moisture stress, we ensure that each direct/diffuse category samples smoothly and evenly through the study period. Given that stomata are seen to close down in real canopies near mid-day, we treat prezenith (morning) and postzenith (afternoon) measurements separately. Figure 1 depicts measured GPP against diffuse and direct sky radiance for all three canopies.

Simulation of GPP and LE

We use the land-surface scheme JULES to simulate and interpret the observations. JULES is modular version of the Met. Office Land-Surface Scheme (MOSES). The latter is coupled to the Hadley Centre Global Circulation Model (GCM) and has been employed *inter alia* in simulations of climate change under increased atmospheric loading of CO_2 (Cox *et al.*, 2000). JULES is driven by meteorological data observed typically at hourly or half-hourly intervals. At each (half-) hourly timestep, the downwelling fluxes of shortwave radiation ($\lambda = 0.3$–$2\,\mu$m; SW) and longwave radiation ($\lambda \sim 10\,\mu$m: LW) are balanced by the outgoing fluxes of H, LE, ground flux (G), reflected SW and thermal energy released radiatively (all in $\mathrm{W\,m^{-2}}$). Thus

$$\mathrm{SW}(1 - a_t) + \mathrm{LW} = \sigma T_s^4 + \mathrm{LE} + H + G, \quad (3)$$

where σ is the Stefan–Boltzmann constant and T_s is the surface temperature (Cox *et al.*, 1999). A SW-albedo a_t is derived for each of nine tiles (five plant functional types and four nonvegetated types) and the energy balance of Eqn (1) performed independently within each tile using a Penman–Monteith approach (Monteith, 1965; Cox *et al.*, 1999). Model output encompasses a range of variables associated with the carbon, energy and water cycles but, for the present study, we extract only GPP and LE.

We effect two major changes to the land-surface calculation. As is typical of most land-surface schemes, JULES assumes a vertical light profile within the canopy that is smooth under both direct and diffuse sky radiance. A single (mean) leaf orientation is also adopted. In the unmodified scheme the two-stream approximation yields the light transfer within 10 horizontally uniform layers and, under direct sunlight, the light profile declines approximately exponentially according to Beer's law. The combination of a smooth light profile and a single (mean) leaf orientation produces a single leaf irradiance at each depth within the canopy. However, real canopies display a large range of leaf irradiance (Parker *et al.*, 2002) and we emulate this dispersion by introducing into JULES a probability function for sunfleck penetration and an explicit range of leaf orientations. Note that the mean light profile and average leaf angle are unchanged by these enhancements.

To emulate more realistically the water-use efficiency exhibited by trees we also implement two stomatal submodels, which are both more sophisticated and computationally expensive than the default calculation. The first of the introduced algorithms is the Ball–Berry formulation with best-fit C3 parameters of $m = 9$ and $b = 0.01\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ (Collatz *et al.*, 1991). The second is the SPA representation of Williams *et al.* (1996). In the unmodified scheme, stomata are closed under increasing VPD according to a prescribed reference value (Cox *et al.*, 1998). Both the Ball–Berry and SPA submodels are sensitive to VPD but stomatal conductance, in both these cases, is modified according to the photosynthetic rate of the leaf. Thus, if light levels are too low for efficient photosynthesis the stomata are unlikely to be fully open even if humidity conditions are favourable (i.e. at low VPD). The SPA formulation is a process-based submodel which can be expected to emulate realistically the water-use efficiency displayed by real plant canopies (Jones, 1992). It also contains a greater number of parameters than either the Ball–Berry or default submodel. The cost function embodied within SPA allows for the benefit to leaf photosynthesis in opening stomata when leaf water is available. A capacitance term allows for storage of water within the crown and belowground resistance determines the availability of soil water. For all canopies we use a soil-to-leaf resistance of $2000\,\mathrm{s\,m^{-2}\,MPa\,mol^{-1}}$ and a capacitance of $2.3\,\mathrm{mol\,m^{-2}\,MPa^{-1}}$ when implementing SPA in our simulations (Williams *et al.*, 1996; Fisher *et al.*, 2005). As a minimum increment in the cost function we adopt 0.07% (Williams *et al.*, 1996).

For all stomatal submodels conductance is solved iteratively at each of the 10 layers within the canopy. Note that, whether sunflecks are being simulated or not, leaf photosynthetic rate is always calculated using the colimitation model of Collatz *et al.* (1991). Thus, we adopt a quantum efficiency $\alpha = 0.05\,\mu\mathrm{mol\,\mu mol^{-1}}$ for all

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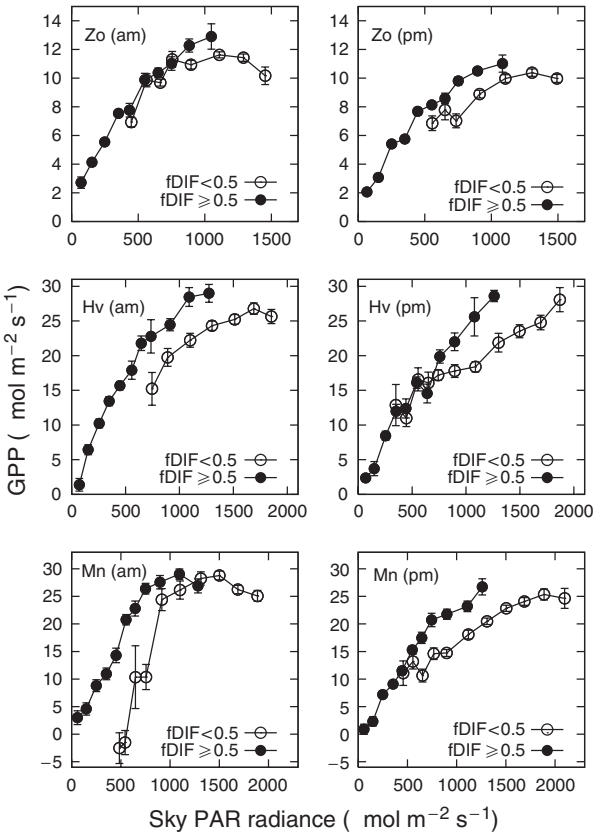

Fig. 1 Gross photosynthetic product (GPP) inferred from observed carbon fluxes at three forest stands: Zotino at the top (Zo), Harvard (Hv) in the middle and Manaus (Mn) at the bottom. In all cases GPP is plotted against top-of-canopy radiance with • denoting conditions of diffuse light (fDIF ≥ 0.5) and open markers representing photosynthesis under direct sunlight (fDIF <0.5). Measurements recorded before (after) noon are contained in the left (right) panel. Note that the scales vary according to each site.

three sites. The Rubisco-limited photosynthetic rate at the top of the canopy (V_{cmax}) is set to 45 μmol m^{-2} s^{-1} at Harvard (Wullschleger, 1993) and to 60 μmol m^{-2} s^{-1} at both Zotino (Alton *et al*., 2005) and Manaus (Williams *et al*., 1998; Carswell *et al*., 2000; Domingues *et al*., 2005). For all simulations, we also make the following assumptions: (1) the Rubisco-limited rate declines with depth through the canopy as exp (−0.15LAI) (Lewis *et al*., 2000; Meir *et al*., 2002); (2) the fraction of bare ground is zero; (3) the leaf angle distribution is spherical (Campbell & Norman, 1998; Falster & Westoby, 2003). Coefficients for leaf reflectance, leaf transmission and ground albedo correspond to the values collated in Alton *et al*. (2007b).

Although simulations were generally run for a more extended period, predicted fluxes were only extracted for the time intervals of the measurements selected above for Fig. 1. Figure 2 shows predicted GPP with various combinations of the stomatal and sunfleck/nonsunfleck submodels.

Inference of GPP and NEE under changing SW

For morning and afternoon periods at each site empirical relations are developed between GPP and the environmental variables SW, *T* and fDIF. We follow Hollinger *et al*. (1994) in fitting the dominant variable, SW, against GPP and fitting the residuals in GPP against temperature. Finally, the residuals from the GPP vs. *T* relation are fitted against fDIF. Linear, quadratic, exponential or hyperbolic equations are used in the least-squares regression in that order of preference (Table 2 and Figs 3 and 4). A relation is also developed between *T* and SW (Table 2). The above relations, in conjunction with that relating SW to fDIF [Eqn (2)], allow us to predict the change in GPP for a systematic increase/decrease in SW. Furthermore, empirical relations already established in the subtraction of ecosystem respiration (and developed additionally for Zotino) allow us to extend our predictions to NEE. We use the differential of these relations, d(GPP)/d(SW), to establish the mean perturbation to GPP (all measurements integrated over the study period) assuming a systematic increase/decrease in SW (Fig. 5).

Results

Figures 1 and 2 illustrate inferred and predicted GPP, respectively, for each of our three sites under diffuse and direct sky radiance. The following features are noted:

1. An enhancement in canopy LUE is inferred for all sites under diffuse sunlight. The increase spans 6–33% (Table 3).
2. Averaging across all three locations, observed GPP is 15% higher in the morning compared with the afternoon. However, while productivity falls quite noticeably at the boreal and tropical sites during the afternoon (24–30%), canopy photosynthesis actually increases slightly at the temperate site after solar mid-day (Table 3).
3. The inclusion of sunflecks reproduces the saturation observed at high sky radiance and manifests an enhancement in LUE under diffuse light comparable with that found observationally. The standard simulation, using a smooth light profile and a single (mean) LAD, produces a too linear response and does not reproduce the observed enhancement (e.g. Fig. 2 bottom panel).
4. Once sunflecks are included, the simulation produces broadly similar results regardless of the sto-

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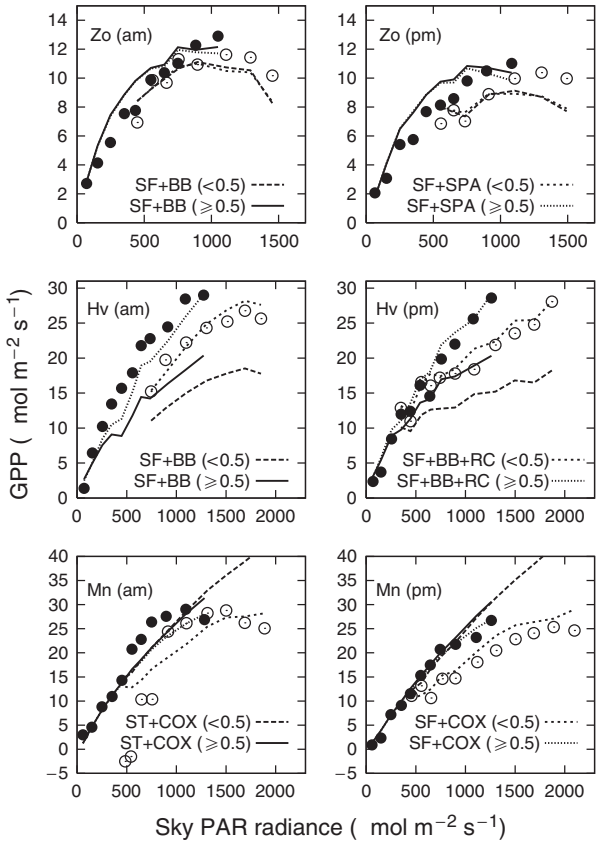

Fig. 2 As Fig. 1 but overlaying various simulations of gross photosynthetic product (GPP) from the JULES land-surface scheme. For clarity the error bars have been removed from the measurements. Note that the key for each site is split across left and right panels. The following designations have been used: SF for sunfleck canopy-photosynthesis; ST for standard/default (two-stream) canopy-photosynthesis; BB for the Ball–Berry stomatal submodel; SPA for the Soil–Plant–Atmosphere stomatal submodel and COX for the standard/default stomatal submodel. Thus 'SF + BB' denotes predicted GPP using sunfleck canopy-photosynthesis in conjunction with the Ball–Berry submodel. 'RC' denotes recalibration of the Rubisco-controlled leaf parameter V_{cmax} (see text for details). The fraction of diffuse sunlight is indicated in parentheses.

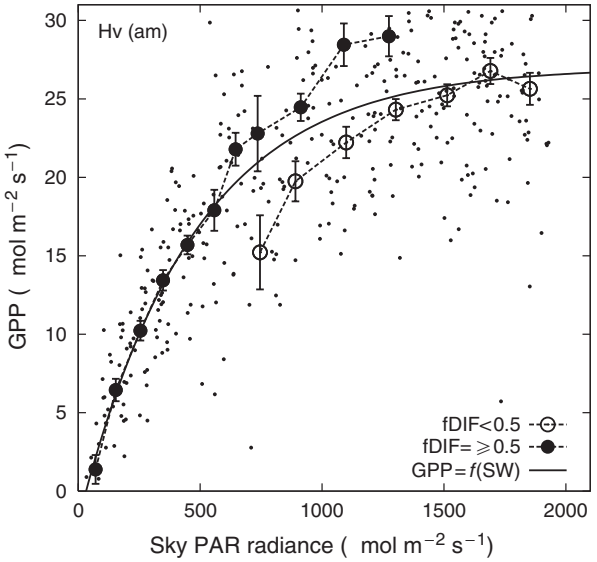

Fig. 3 An empirical fit between gross photosynthetic product (GPP) (morning measurements) and SW (solid line) for the temperate broadleaf site, Harvard. The function has the form GPP = 27–29 × exp(SW/−236). Measurements are denoted by dots. We overlay the markers from Fig. 1 (middle panel, left) where data are binned for conditions of diffuse and direct sunlight. Note that we use IPAR(μmol m^{-2} s^{-1}) = 2 × SW(W m^{-2}), consistent with independent measurements of photosynthetically active radiation and SW available in the micrometeorological data for Zotino and Harvard.

matal submodel employed (e.g. Fig. 2 top panel). In particular, with sunflecks, all simulations manifest a drop in photosynthesis due to stomatal closure in the afternoon. A slightly better performance is noted for the Ball–Berry model with GPP being predicted within 14% (r.m.s.) for the boreal and tropical sites (Table 4). Simulations of the Harvard site using the Ball–Berry algorithm require a 100% increase in the Rubisco-limited rate, V_{cmax}, (from 45 to 90 μmol m^{-2} s^{-1}) in order to produce a consistency within 10% (r.m.s.) between observed and predicted GPP (Fig. 2 middle panel). On average, LE is only predicted to within 31% of its measured value for the combined sunfleck/Ball–Berry model. However, evaporation from the soil is expected to contribute significantly to LE, at least for the tropical and temperate sites, and it is difficult to judge unequivocally the performance of the stomatal-photosynthesis submodels with respect to evapotranspiration.

As expected, Table 2 reveals SW as the dominant environmental variable determining GPP (mean r^2 is 0.70). GPP saturates with respect to SW at Zotino and Harvard (exponential relations fitted) but for the tropical site, Manaus, there is actually a slight fall in GPP when sky radiance exceeds approximately 1500 μmol m^{-2} s^{-1} (quadratic fitted). This slight decrease, discerned in Fig. 1 for the morning period, may be due to increased dark respiration or reduced stomatal conductance under high light incidence. Both dark respiration and stomatal conductance are either directly or indirectly temperature-dependent (the latter through VPD). However, as there is a strong correlation between T and SW (mean r^2 is 0.69), it is conceivable that dark respiration and stomatal conductance influence the fit between SW and GPP. We also note that, after accounting for SW and T, the dependence of GPP

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on fDIF is weak, as evidenced in Table 2 (mean r^2 is 0.15) and Fig. 4.

Figure 5 reveals only small changes in canopy GPP (<5%) for modest changes (<10%) in the mean value of SW at each of our sites. We attribute this quasi-stability to the saturating response of GPP to SW, coupled with a weak dependence of GPP on fDIF (as alluded to above). Thus, in general, the small reduction in GPP due to falling light levels is largely compensated by the modest increase in GPP due to increasing fDIF. In contrast, the impact of a perturbed SW regime on NEE is more pronounced, particularly at the boreal site.

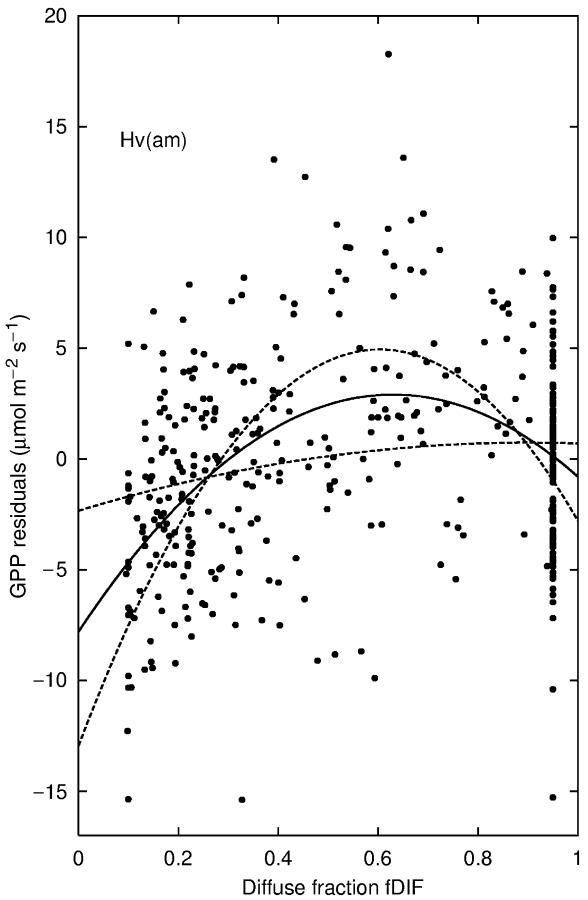

Fig. 4 An empirical fit between gross photosynthetic product (GPP) residuals, after accounting for SW and canopy temperature, and the fraction of diffuse sky radiance (fDIF). The solid line indicates the best fit while the dashed lines demonstrate permissible fits within the errors. Measurements (•) relate to Harvard during the morning. Note that this figure does not show the complete relationship between GPP and fDIF as we have already fitted GPP for SW and fDIF itself depends on SW. This plot typifies all three sites – maximum GPP residual usually occurs for a diffuse fraction between 0.6 and 0.7.

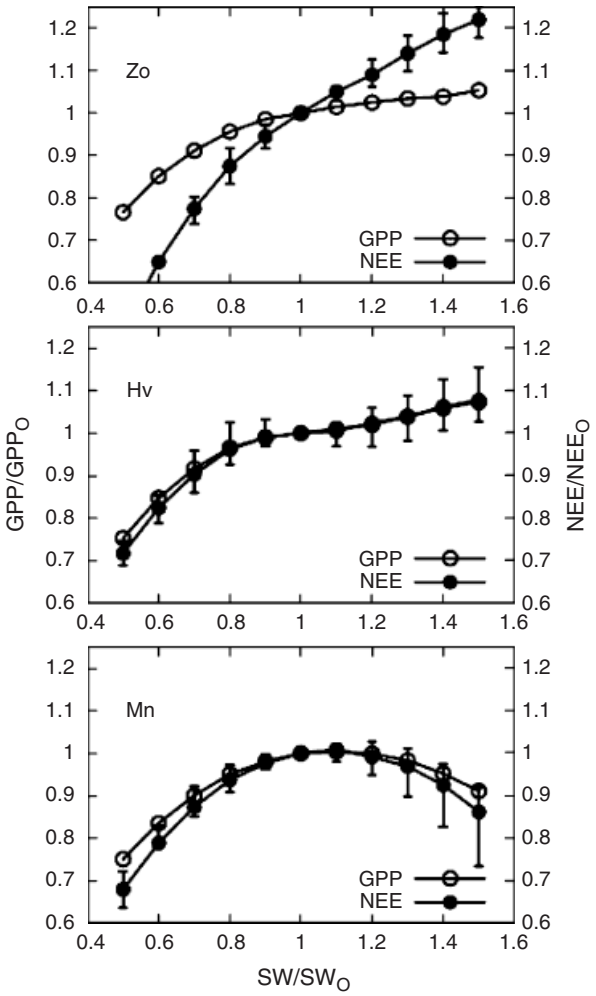

Fig. 5 Change in gross photosynthetic product (GPP) and net ecosystem exchange (NEE) predicted for Manaus (bottom), Harvard (middle) and Zotino (top) under decreased/increased insolation. GPP_o is the measured mean for the (current) mean shortwave radiation (SW_o). GPP and NEE are, respectively, the mean gross and net values predicted for a modified shortwave regime (SW). Uncertainties are only given for NEE as errors in GPP are similar. Note that for increased SW at Harvard the symbols for GPP are eclipsed by those representing NEE.

Discussion

Is canopy LUE enhanced under diffuse sunlight ?

The observations indicate an LUE enhancement of 6–33% with the greatest increase occurring in dense foliage (Manaus). While subject to considerable theoretical conjecture in the past (e.g. Farquhar & Roderick, 2003), our simulations show unequivocally that the observed LUE enhancement under diffuse sunlight (Fig. 1) can be attributed to increased sharing of the radiation-load across the canopy foliage. Leaf productivity is linear with photosynthetically active radiation

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Table 3 Measured (left) and simulated (right) ratios of LUE

	Measured			Simulated		
LUE ratio	Zotino	Harvard	Manaus	Zotino	Harvard	Manaus
fDIF (am)	1.06 ± 0.01	1.28 ± 0.06	1.30 ± 0.03	1.12	1.22	1.18
fDIF (pm)	1.18 ± 0.02	1.15 ± 0.02	1.33 ± 0.03	1.26	1.15	1.26
am/pm	1.24 ± 0.02	0.91 ± 0.03	1.30 ± 0.03	1.19	1.02	1.12

The simulated values are calculated using the sunfleck/Ball–Berry model but recalibrating V_{cmax} for Harvard (see text). The ratios 'fDIF (am)' and 'fDIF (pm)' compare the LUE under diffuse sunlight (fDIF $\geq$0.5) with that prevailing under direct sunlight (fDIF $<$0.5) for the morning and afternoon periods, respectively. The ratio 'am/pm' compares LUE before and after noon combining both direct and diffuse measurements.
LUE, light-use efficiency.

(PAR) irradiance $\leq$350 μmol m^{-2} s^{-1} but, at higher light-exposure, the response begins to saturate. When sunflecks are present (direct sunlight) a large dispersion in leaf irradiance is established at any given height in the canopy. A significant fraction of the foliage is either light saturated (sunlit) or not receiving sufficient light (deep shade). In contrast, the dispersion in leaf irradiance is relatively small under diffuse sunlight allowing canopy photosynthesis to be more efficient.

In the past, environmental variables that might change in concert with fDIF (temperature, VPD) have been invoked as factors increasing canopy LUE under diffuse sunlight (Gu *et al*., 2002; Lloyd *et al*., 2002). However, our simulations indicate that these environmental changes are of second order. Only at Zotino do lower systematic temperatures in the canopy account for a significant (1/3) part of the increase under diffuse sunlight. Owing to their oblique angle of incidence with the canopy ceiling, diffuse sky photons are preferentially absorbed near the crown (Alton *et al*., 2005). While Rubisco-limited assimilation rates are highest in the top foliage, interpretation with our model indicates that the average vertical light profiles under diffuse and direct radiance are, nevertheless, very similar. It is the dispersion in leaf irradiance, and not the small difference in mean light profile, which increases canopy LUE under diffuse sunlight.

Pooling measurements of GPP regardless of diffuse fraction results in a canopy response that saturates at high sky radiance due to bias towards direct sunlight at $>$1000 μmol m^{-2} s^{-1} (Fig. 3). This may explain the apparent success of so-called Big Leaf models where the canopy is expected to respond as linearly scaled version of a flat, top leaf (Baker *et al*., 2003; Denning *et al*., 2003).

The 6–33% enhancement in canopy LUE is well below that reported for crops (110%; Choudbury, 2001), New Zealand beech (50%; Hollinger *et al*., 1994) and a number of broadleaf and needleleaf woodlands studied by Gu *et al*. (110–180%; 2002). For low LAI systems (grassland and shrubs) the net carbon exchange and, therefore, possibly GPP, is shown to be approximately neutral with respect to the diffuse fraction (Niyogi *et al*., 2004; Letts *et al*., 2005). However, apart from the Boreal stand at Zotino (LAI = 2), our sites are characterized by moderate to high foliage density (LAI = 4.5–5.5). We note that the LUE reported by Choudbury for diffuse (cloudy) conditions pertains to a lower sky radiance than that under direct (sunny) conditions which might explain the large increase in LUE he reports (d(GPP)/d(SW) increases as SW $\rightarrow$ 0). To infer the behaviour under cloud, Hollinger *et al*. compare GPP for only 1 or 2 adjacent days; thus their analysis of diffuse light is less extensive than the present investigation. It is somewhat surprising, however, that Gu *et al*. (2002) infer much higher LUE enhancements than we do as these authors adopt an empirical model. This is a technique, which resembles the method we use in 'Inference of GPP and NEE under changing SW'. We note that the parameters inferred by Gu *et al*., which determine the canopy photosynthetic response to light (α and β), vary dramatically from one 15-day period to the next and such large fluctuations are difficult to explain through changes physiology, phenology or, indeed, soil moisture stress. Additionally, these authors, by extrapolating with their empirical model, compare canopy LUE under pure diffuse sunlight with that inferred for pure direct sunlight. The current study compares LUE for *predominantly* direct sunlight (fDIF $<$0.5) and predominantly diffuse sunlight (fDIF $\geq$0.5). Thus, substituting fDIF = 0.25 and 0.75 into Eqn (5) of Gu *et al*., yields an LUE enhancement of only 60%, for example, for the mixed temperate forest studied by Gu *et al*., (comparison made for a sky radiance of 1000 μmol m^{-2} s^{-1}). This is still higher than the enhancement we measure for Harvard, our own mixed temperate site (15–28%), but less than the 160% enhancement estimated by Gu *et al*., for conditions of pure diffuse and pure direct sunlight. In a future study, it would be instructive to expand our analysis to the sites treated by Gu *et al*.

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Table 4 Model performance for GPP and LE

	ΔGPP (%)			ΔLE (%)		
Model	Zotino	Harvard	Manaus	Zotino	Harvard	Manaus
ST + COX	27	20	45	69	37	60
ST + BB	18	19	33	33	15	40
ST + SPA	17	21	17	31	19	44
SF + COX	15	27	15	57	17	43
SF + BB	13	32	14	28	25	39
SF + SPA	13	33	23	30	19	46

Submodels of stomatal conductance and canopy photosynthesis follow the designations in Fig. 2. ΔGPP (ΔLE) denotes the root mean square difference between model and measurement expressed as a percentage of the mean measured GPP (LE). As in Fig. 2, the comparison is made independently for each site under conditions of both direct and diffuse sunlight and during both morning and afternoon periods.
GPP, gross photosynthetic product; LE, latent heat.

Are canopy GPP and NEE enhanced under diffuse sunlight?

The modest enhancement in LUE that we record under diffuse sunlight is insufficient to increase canopy productivity under increased cloudiness. Contrary to the prediction made by some authors (Niyogi *et al.*, 2004), Fig. 5 indicates that forest productivity is likely to fall under decreasing insolation. Moreover, the reduction is more pronounced for NEE. While ecosystem respiration is slight suppressed under dimming (due to lower temperatures) both GPP and NEE are influenced primarily by SW. As the absolute values associated with NEE are smaller than those describing GPP the impact of SW-attenuation is greatest for net production.

Gu *et al.* (2003) claim a ~20% increase in NEE, compared with the mean, during cloudless days at one of our sites (Harvard) for the growing season following the Pinatubo volcanic eruption (summer 1992). This is attributed to increased diffuse sky radiance from atmospheric aerosols. Both the direction and magnitude of the purported change stands in stark contrast to our own results for Harvard. One explanation may lie in the nature of the diffusing medium. Aerosols scatter preferentially in the forward direction and tend, therefore, to be more conservative with respect to total downwelling shortwave radiation compared with cloud water droplets (Farquhar & Roderick, 2003). Lucht *et al.* (2002) identify surface temperature, and its impact on both microbial soil respiration and the length of the growing season, as a dominant factor in observed and simulated NEE for the northern boreal zone. Our empirical fits to both the daytime and nighttime fluxes at Zotino indicate that temperature and respiration are second order effects compared with total sky radiance. In future studies of global GPP under diffuse sunlight (Alton *et al.*, 2007a), we wish to take account of the growing season and its temperature-dependent duration.

Arguably, the most remarkable aspect of Fig. 5 is the apparent stability in GPP and NEE with respect to modest changes in SW. This behaviour is reminiscent of crop yields which are shown, in artificial shading experiments, to be undiminished for reductions in SW of <20% (Evans, 1993). Alton *et al.* (2007a) find that the total SW received during the growing season fluctuates by <10% from 1 year to the next for the majority (88%) of global landpoints (1°×1°). Globally, insolation fell by 5–10% over the latter half of the 20th century although reductions of 15–30% are recorded regionally (Stanhill & Cohen, 2001; Liepert, 2002). According to Fig. 5, all three forest biomes treated in this study appear to be fairly well adapted to the average sunshine they receive and the impact on carbon sequestration would be <5% for an attenuation of <10% in SW. The most sensitive site is the boreal stand, Zotino, where NEE is predicted to fall by 9 ± 4% for a 15% reduction in SW.

Conclusions

We infer the GPP and LUE for three forest canopies under predominantly diffuse and direct sunlight for both morning and afternoon periods. These stands, which represent quite different biomes, are the following: Zotino, Siberia (Boreal needleleaf site, LAI ~2), Harvard, USA (temperate broadleaf, LAI ~4.5) and Manaus, Amazonia (tropical broadleaf, LAI ~5.5). We interpret the observations using the land-surface scheme JULES. The standard scheme is modified to allow for sunfleck penetration and an explicit range of leaf orientations. Within real canopies, leaf pores are known to close near mid-day (e.g. Jones, 1992). There-

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fore, we implement within JULES two sophisticated algorithms for stomatal conductance: the Ball–Berry (Collatz *et al.*, 1991) and SPA (Williams *et al.*, 1996) submodels. The latter, in particular, takes account of water-use efficiency during photosynthesis. Empirical relations are developed between observed GPP and the environmental variables SW, temperature and diffuse fraction. We predict the change in GPP at each of the three sites when total downwelling shortwave radiation undergoes a systematic increase or decrease. Furthermore, empirical relations established between ecosystem respiration and temperature, based on night-time fluxes, allow us to judge the impact on NEE.

Our main conclusions can be summarized as follows:

(1) An increase in canopy LUE is observed under diffuse sky radiance for all three sites. The enhancement is greatest for dense foliage ($33 \pm 3\%$ at Manaus) and least for the sparse canopy Zotino (6–18%). These values are significantly less than the corresponding enhancement inferred previously for both crops (110%; Choudbury, 2001) and moderately dense temperate woodland (50–180%; Hollinger *et al.*, 1994; Gu *et al.*, 2002).

(2) Once sunflecks and leaf orientation are explicitly incorporated into the land-surface scheme, our simulations reproduce fairly well the overall level of canopy GPP, its enhancement with respect to diffuse sunlight and the mean 15% reduction in productivity observed during the afternoon due to stomatal closure. For example, using physiological site data to parameterize JULES, the simulation incorporating Ball–Berry conductance reproduces observed GPP within 14% (r.m.s.) for both the boreal and tropical site. The corresponding simulation for the temperate site produces 10% (r.m.s.) agreement between predicted and measured GPP but only if we increase the Rubiso-limited rate in the top leaves by 100% with respect to its *a priori* value (from 45 to $90\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$).

(3) Our simulations suggest that the LUE enhancement under diffuse sunlight is attributable to the dispersion in leaf irradiance. The dispersion is more pronounced, for any given height within the canopy, when sunflecks are present. Thus, under direct sunlight, a sizeable fraction of the foliage is either light saturated or not receiving enough sunlight to photosynthesize efficiently.

(4) Although previously invoked as important (Gu *et al.*, 2002; Lloyd *et al.*, 2002) our simulations indicate that concomitant changes in canopy temperature and VPD are generally too small to enhance canopy LUE significantly under diffuse sunlight.

(5) Pooling measurements of GPP, regardless of the fraction of diffuse sunlight, results in a canopy response that saturates at high sky radiance producing a so-called Big Leaf effect (Baker *et al.*, 2003; Denning *et al.*, 2003). This is due to a bias towards measurements taken under direct sunlight when sky radiance exceeds $1000\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$.

(6) Although the fraction of diffuse sky radiance increases with cloudiness, the LUE enhancement we infer under diffuse sunlight is insufficient to increase NEE when SW is reduced. Indeed, for the most light-sensitive site (Zotino in the boreal forest), NEE is predicted to fall by $9 \pm 4\%$ for a 15% attenuation in SW. For the temperate site, Harvard, NEE is actually seen to increase by 20% under diffuse light in the wake of the Pinatubo volcanic eruption (Gu *et al.*, 2003). Some of the difference between this result and our own findings for the site, may lie in the nature of the scatterers; aerosols are more conservative with respect to the total quantity of downwelling shortwave radiation compared to clouds.

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