Michael L. Roderick · Graham D. Farquhar Sandra L. Berry · Ian R. Noble

On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation

Received: 11 May 2001 / Accepted: 1 June 2001 / Published online: 28 July 2001 © Springer-Verlag 2001

Abstract The volume of shade within vegetation canopies is reduced by more than an order of magnitude on cloudy and/or very hazy days compared to clear sunny days because of an increase in the diffuse fraction of the solar radiance. Here we show that vegetation is directly sensitive to changes in the diffuse fraction and we conclude that the productivity and structure of vegetation is strongly influenced by clouds and other atmospheric particles. We also propose that the unexpected decline in atmospheric $[CO_2]$ which was observed following the Mt. Pinatubo eruption was in part caused by increased vegetation uptake following an anomalous enhancement of the diffuse fraction by volcanic aerosols that would have reduced the volume of shade within vegetation canopies. These results have important implications for both understanding and modelling the productivity and structure of terrestrial vegetation as well as the global carbon cycle and the climate system.

Keywords Global carbon cycle · Diffuse radiation · Global change · Light use efficiency · Mt. Pinatubo

Introduction

Models which attempt to predict broad-scale variations in the productivity and/or structure of vegetation as a function of climate and other environmental factors have not generally considered the effects of clouds and other atmospheric particles. Instead, such models describe the weather and climate using factors like solar radiation, rainfall, evaporation and temperature, which have generally been assumed to exert a dominant influence over the productivity and structure of vegetation. However, measurements, particularly from forest ecosystems, have consistently shown that the efficiency of canopy gas exchange increases with, and is very sensitive to, the diffuse component of the incoming solar radiance (Hollinger et al. 1994, 1998). These observations suggest that models which ignore the diffuse component of solar radiance, such as the so-called big-leaf models, will not correctly predict changes in CO_2 uptake as a consequence of changes in diffuse radiance (De Pury and Farquhar 1997). That is important because the diffuse fraction of the solar radiance incident at the earth's surface has increased substantially in many regions as a consequence of increases in both cloudiness and the concentration of aerosols in the atmosphere (Suraqui et al. 1974; Abakumova et al. 1996).

The basic concept that canopy photosynthesis models must separately account for diffuse and beam radiance has long been realised by canopy modellers (Sinclair et al. 1976; Goudriaan 1977). However, the broader ecological and earth science communities have not yet appreciated the fundamental importance of the diffuse component of global solar irradiance. This may in part be caused by the apparently complex mathematics that is often used to describe the propagation of beam and diffuse radiance within vegetation canopies and through the atmosphere. While that mathematical complexity is often necessary for many purposes, the fundamental biological significance of diffuse radiance is related to shadows and this can be easily understood from casual observations. For example, when light is mostly diffuse, such as on cloudy days, there are minimal shadows. In contrast, when the solar disk is clearly visible, the shadows are well-defined and occupy a much larger volume because most of the radiance is coming from a single direction. A second basic fact that has not yet been fully exploited in climate-vegetation models is that the fraction of the global solar irradiance that is diffuse is negatively correlated with the fractional transmission of solar radiance through the atmosphere (Liu and Jordan 1960; Spitters et al. 1986; Roderick 1999). Thus, there is a robust relationship between the diffuse and global solar irradiance at the top of vegetation canopies.

M.L. Roderick (☞) · G.D. Farquhar · S.L. Berry · I.R. Noble CRC for Greenhouse Accounting, Research School of Biological Sciences, Institute of Advanced Studies, Australian National University, Canberra ACT 0200, Australia e-mail: michael.roderick@anu.edu.au Tel.: +61-2-61254020, Fax: +61-2-61255095

The aim of this paper is to show that variations in the diffuse fraction of solar radiation are an important, but largely ignored factor in understanding global scale variations in vegetation productivity and structure. To do that we initially use semi-quantitative arguments to show why the diffuse fraction is very important in determining the rates of canopy gas exchange. We then combine estimates of the sensitivity of canopy photosynthesis to the diffuse fraction, with the direct relation between the diffuse and global solar irradiance noted above, to derive a simplified version of the widely used light use efficiency model. The application of this new formulation is demonstrated by estimating the productivity over Australia using satellite and solar irradiance data. Following that, we apply the theory by showing that the unexpected decrease in atmospheric CO₂ that was observed following the Mt. Pinatubo volcanic eruption was most likely caused by an increased uptake of CO_2 by the vegetation. The increased uptake would have been a consequence of a reduction in the volume of shade within vegetation canopies that resulted from the anomalous nature of the increase in the diffuse fraction following the eruption.

The importance of diffuse radiance

Canopy shade and the diffuse fraction

The shadow cast by an object has a three-dimensional structure that is determined by the optical properties of the object and the geometry of the incoming radiance. Individual leaves typically absorb about 80% of the incident visible solar radiance (Monteith and Unsworth 1990) so that the (visible) component which is scattered by the leaves is relatively small. Because of that, the three-dimensional structure of shadows within a canopy, which can be described in terms of the volumes of umbra (full shade), sunflecks (full sun) and penumbra (part sunpart shade) (Horn 1971), is largely determined by the geometry of the incoming solar radiance. When the solar disk is totally obscured, such as commonly occurs on cloudy days, vegetation canopies at the surface are located within the shadows cast by clouds and the irradiance is predominantly diffuse. Consequently, the length of the umbra under each leaf is very short and there is only a very small volume of shade within vegetation canopies (Fig. 1B). In contrast, when the solar disk is clearly visible, the length of the umbra under each leaf is much longer because most of the solar radiance is coming from a single direction (Fig. 1C). Estimating the volume of penumbra on sunny days is a very difficult practical problem because it mostly depends on the spatial arrangement of the leaves (Smith et al. 1989; Ross and Mottus 2000) which is highly variable. Despite that, it is easy to see from Fig. 1 that the volume of shade within a vegetation canopy will be at least an order of magnitude larger on a sunny day compared to a cloudy day.

It follows from the above discussion that the volume of shade within a vegetation canopy must largely depend



Fig. 1A-C A simplified method for estimating the reduction in solar irradiance caused by shadows. A Radiance coming from the upper hemisphere is intercepted by an opaque horizontal circular object of diameter D, centred at A and there is a reduction in the irradiance at $B(R_{\rm B})$ located a distance X below A. The relative loss of irradiance at B, defined as $R_{\rm B}/R_{\rm A}$ is denoted S. **B** S is plotted as a function of X/D for overcast days using two different radiance distributions; isotropic distribution (full line) in which the radiance is assumed to be the same in all directions and the standard overcast sky (dashed line) in which the radiance at the zenith is assumed to be 2.2 times the radiance at the horizon. Calculations to define these curves are described in the Appendix. Note that S is very similar for both distributions and when X/D is ≈ 2 , $R_{\rm B}$ is about 95% of R_{Λ} and there is virtually no shade. C Relatively simple analytical expressions like those used above cannot be derived for sunny days. However, on sunny days most of the radiance is coming directly from the sun and the calculation can be greatly simplified without too much error by assuming that all of the radiance is coming from the solar disk. Accordingly, the semi-diameter of the sun is $\approx 16'$ so the length of the umbra is $\approx 107D \cos \beta$ where β is the angle between the sun and the surface normal, and $S \approx \max\{0, 1-107D\cos \beta/X\}$. This formula is used to plot S as a function of X/D for a sunny day at three different values of $\cos \beta$ (0.1, 0.5, 1.0). Note that even if the umbra was only half as long as the above calculations suggest (Horn 1971), the volume of shade within a vegetation canopy is still at least an order of magnitude larger for a sunny sky compared to a cloudy sky

on the relative magnitude of the beam (R_b) and diffuse (R_d) solar irradiance at the top of a vegetation canopy where:

$$R_{\rm s} = R_{\rm b} + R_{\rm d} \tag{1}$$

and R_s is the global solar irradiance. Thus when the solar disk is not obstructed by clouds or other atmospheric



Fig. 2 Relationship between the diffuse fraction (R_d/R_s) and the atmospheric transmission (R_s/R_o) where R_d , R_s and R_o are the diffuse, global and top of the atmosphere solar irradiance using daily (D, *full line*) and monthly (M, y=1.11-1.31x) totals (Roderick 1999). The relation shown for daily data is for 40° latitude but there are only minor differences for other latitudes and the daily and monthly curves shown here typically account for at least 90% of the observed variation (Roderick 1999). The daily and monthly curves have a different form and slope because of differences in the inter- and intra-day distribution of cloud over a month. See Roderick (1999) for a theoretical treatment. Note that the relationship for annual data is virtually identical to the relation given for monthly data (Roderick 1999)

particles, the beam fraction, $R_{\rm b}/R_{\rm s}$, approaches unity and the diffuse fraction, R_d/R_s , must approach zero. In contrast, when the solar disk is totally obscured by clouds and/or very thick haze, $R_{\rm d}/R_{\rm s}$ approaches unity and $R_{\rm b}/R_{\rm s}$ approaches zero. These limits set the bounds on variation in the diffuse fraction. In that context, it has long been known that the diffuse fraction is negatively correlated with the atmospheric transmission, R_s/R_o where R_o is the global solar irradiance at the top of the atmosphere (Liu and Jordan 1960). More recently, it has been shown that the parameters of that relationship are more or less globally invariant (but see later for exceptions following volcanic eruptions) (Fig. 2). It follows that relative to the solar irradiance at the top of the atmosphere, high levels of solar irradiance at the top of vegetation canopies must be nearly all beam radiance, while low levels must be nearly all diffuse radiance.

Canopy photosynthesis and the diffuse fraction

Canopy scale photosynthesis depends amongst other things on the spatial distribution of irradiance in relation to the biochemical capacity (e.g. Rubisco and other enzymes) for photosynthesis. Models that account for these factors as well as the saturating response of leaf scale photosynthesis to the instantaneous irradiance at the leaf show that canopy scale photosynthesis is very sensitive to the diffuse fraction (De Pury and Farquhar 1997). One way to examine the direct effect of the diffuse irradiance on canopy photosynthesis is to use the so-called lightuse efficiency model (Monteith 1972) where the daily net assimilation rate of the canopy (A, mol CO₂ m⁻² day⁻¹) is given by: 23

where $e \pmod{CO_2 \mod^{-1} \text{PAR}}$ is commonly known as the efficiency of the canopy, f is the fraction of photosynthetically active radiation (PAR) absorbed by the canopy, C is a more or less constant factor (c. 2.3 mol PAR MJ⁻¹) used to convert from global solar irradiance to quanta in the PAR part of the spectrum and R_s is the daily global solar irradiance at the top of the canopy. The effect of the diffuse fraction on e is more easily assessed by rewriting Eq. 2 as:

$$A = efC\frac{R_{\rm s}}{R_{\rm o}}R_{\rm o} \tag{3}$$

Thus, as R_s/R_o declines, there is typically less irradiance on individual leaves at the top of the canopy relative to that at the top of the atmosphere. However, the decline in R_s/R_o is accompanied by an increase in the diffuse fraction (Fig. 2) so that there will also be concurrent reduction in the volume of shade within the canopy. Further, because the photosynthetic rate of individual leaves usually saturates at high irradiance, it follows that individual leaves in low irradiance will have a higher *e*, and the reduction in the volume of shade within the canopy means that the canopy as a whole will also be more efficient in low irradiance. On that basis, we expect that *e* should generally increase as R_s/R_o decreases.

The above prediction is consistent with measurements above crop (Murata 1981; Sinclair et al. 1992; Rochette et al. 1996) and forest canopies (Price and Black 1990; Hollinger et al. 1994, 1998; Fan et al. 1995; Baldocchi et al. 1997) which show that e does increase as the irradiance at the top of the canopy declines. In many of these studies, the observed increase in e was attributed to increases in the diffuse fraction (Hollinger et al. 1994). That proposition has been confirmed by modelling studies of both crop and forest canopies that have found that e increases more or less linearly with the diffuse fraction (Norman and Arkebauer 1991; Choudhury 2000, 2001a, b).

As a further qualitative test of the above theoretical framework, we note that some forests have a leaf area index (L, defined as the total projected leaf area per unit ground area) as high as 7-10, or sometimes even higher (Anderson 1981). These values are extraordinary because both measurements (Ross et al. 1998; Ross and Mottus 2000) as well as estimates from relatively simple models indicate that on sunny days, most of the leaves in such canopies are in deep shade, presumably with marginal or negative carbon balances (Fig. 3). However, forests with a large L are often located in cloudy climates and the large values of L could be sustained by a reduction in the volume of shade within the canopy resulting from a higher diffuse fraction, as suggested by H. Horn (Horn 1971). If that were true, then we would expect forests with large L to have higher rates of CO_2 uptake on cloudy days than on sunny days. This accords with measurements over a dense forest canopy $(L\approx7)$ in New Zealand (Hollinger et al. 1994).



Fig. 3 Sunlit leaf area index (L_s) as a function of leaf area index (L) at three different solar zenith angles (z). The calculation is based on a simplified formula that has been recommended for general use in forest studies (Landsberg and Gower 1997); $L_s=(1-e^{-Lk} \sec z)$ (k sec z) where k is the canopy extinction coefficient. Values of k typically vary from 0.2 (i.e. near vertical leaves) to 1.1 (i.e. near horizontal leaves) but 0.5 has been recommended as a general value suitable for most forest canopies (Landsberg and Gower 1997) and was used to prepare the curves. The important conclusion is that L_s saturates at relatively small values of L and decreases as z increases. That general conclusion also holds for other values of k

Estimating productivity using the diffuse fraction

Formulation of a simplified light use efficiency model

The above analyses suggest that it is possible to develop an (approximate) generic function relating *e* with the diffuse fraction and to use that relation in an integrated form of Eqs. 2 and 3 to estimate the annual gross and net productivity of plant communities. To do that, we can express the annual net production (*N*, mol CO₂ m⁻² year⁻¹) of a plant community as the difference between gross photosynthesis (P_G , mol CO₂ m⁻² year⁻¹) and autotrophic respiration (P_R , mol CO₂ m⁻² year⁻¹):

$$N = P_{\rm G} - P_{\rm R} \tag{4}$$

 $P_{\rm R}$ is usually found to be 30–70% of $P_{\rm G}$ and observations suggest that 45% is close to a typical average value (Landsberg and Gower 1997) which is consistent with theoretical expectations (Dewar 2000). The gross photosynthesis is given by:

$$P_{\rm G} = e'f'C'\frac{R_{\rm s}'}{R_{\rm o}'}R_{\rm o}' \tag{5}$$

where the superscripts denote that we are using annual totals or averages as appropriate. Both R_s'/R_o' and e' can be expressed as functions of the diffuse fraction. For annual (and monthly) totals, we have (see Fig. 2):

$$\frac{R'_{\rm d}}{R'_{\rm s}} \approx 1.11 - 1.31 \frac{R'_{\rm s}}{R'_{\rm o}} \tag{6}$$

Choudhury (2001a) modelled the CO_2 uptake for a wide variety of different crop and (native) forest canopies (n=57) spanning a large range of different climatic zones. His summary suggests that e' was on average about 0.015 and 0.036 under sunny and overcast conditions, respectively. Assuming that the diffuse fraction is



Fig. 4 Variation in $e'(R_s'/R_o')$ as a function of the annual diffuse fraction as predicted from Eq. 8. Note that Eq. 8 is in part dependent on Eq. 7, and the parameters of Eq. 7 do vary between different vegetation canopies (Choudhury 2001a). Consequently, the predicted maximum will also vary for different vegetation canopies. (See the main text for further discussion of this important point)

13% and 100% on sunny and overcast days respectively (Roderick 1999), those data can be used to derive the following relation:

$$e' \approx 0.024 \frac{R'_{\rm d}}{R'_{\rm s}} + 0.012$$
 (7)

By using Eqs. 6 and 7, it is straightforward to write a single expression for the product, $e'(R_s'/R_o')$, as a sole function of either R_s'/R_o' or R_d'/R_s' depending on which is more convenient for the purpose at hand. In terms of the diffuse fraction, that function is:

$$e'\left(R'_{\rm s}/R'_{\rm o}\right) \approx 0.010 + 0.011 \frac{R'_{\rm d}}{R'_{\rm s}} - 0.018 \left(\frac{R'_{\rm d}}{R'_{\rm s}}\right)^2$$
 (8)

and by substitution into Eq. 5, we have:

$$P_{\rm G} \approx f' C' R'_{\rm o} \left(0.010 + 0.011 \frac{R'_{\rm d}}{R'_{\rm s}} - 0.018 \left(\frac{R'_{\rm d}}{R'_{\rm s}} \right)^2 \right) \tag{9}$$

for the gross annual productivity of a plant community. The quadratic function in Eqs. 8 and 9 predicts that at fixed values of f', C' and R_o' , the gross productivity would have a maximum value at a diffuse fraction of about 31% (Fig. 4). In the context of this paper, the precise value of the maximum is not important because there is variation in Eq. 7, and hence Eqs. 8 and 9, between different plant communities (Choudhury 2001a). For example, the measurements from New Zealand forests which were cited earlier (Hollinger et al. 1994) show that the maximum would occur at a much higher diffuse fraction, because the uptake of CO_2 was higher on cloudy days. Nevertheless, it is important to note here that the quadratic function predicts that a broad optimum will occur and this is consistent with observations (Gu et al. 1999).

Estimating continental scale annual productivity: a case study using Australia

Equation 9 is convenient for practical applications because (ignoring orbital perturbations) R_0' is only a func-



Fig. 5 Top four panels include the estimate of gross annual productivity for the period 1982–1990 ($P_{\rm G}$) and the data used to make that estimate (per Eq. 9). *The lower four panels* are ancillary climate data that are included to highlight the inter-relationships between the radiation and water balance and the vegetation cover. (Note that the annual rainfall is greater than 1.5 m in the 'white' areas on the rainfall image and that the pan evaporation is for a Class A pan.) The 'Rainfall – Pan Evaporation' image was computed as the difference between the respective images. The *upper left* and *lower right* corners of each image are at 110°E, 10°S and 155°E, 45°S respectively

tion of latitude and C' is reasonably constant (*c*. 2.3 mol PAR MJ⁻¹), leaving only the annual diffuse fraction, R_d'/R_s' and f', the fraction of the incident annual PAR absorbed by the vegetation, to be estimated. The diffuse fraction can be estimated from measurements of global solar irradiance (per Fig. 2) and f' can be estimated using satellite observations.

To demonstrate this approach, we estimated the average f' for 1982–1990 using 9 years of monthly satellite images following the method of Roderick et al. (1999) as modified by Berry and Roderick (2001). The average annual global solar irradiance, and the other average annual climatic data (Fig. 5), were computed using monthly averages from the ESOCLIM database available from the Centre of Resource and Environmental Studies at the Australian National University. The average annual diffuse fraction was calculated by estimating the diffuse irradiance for each month, using the method of Roderick (1999) and then summing the diffuse and global solar irradiance for each month to calculate the ratio of the annual values.

Using these data, and Eq. 9, we estimated the annual average gross production for Australia for the period 1982–1990 as 66 mol C m⁻² year⁻¹ corresponding to about 5.9 GtC year-1 for the whole country (Fig. 5). Assuming that autotrophic respiration was 45% of the gross production, the corresponding average net production would be about 36 mol C m⁻² year⁻¹ or about 3.2 GtC year⁻¹ over the whole country. From sensitivity analysis (results not shown) we found that our estimate of gross (and net) production would be most sensitive to errors in estimating f' over the partially vegetated surfaces that cover most of Australia. Our estimates of e' based on Eq. 7 were generally consistent with estimates for Australian forests made using other means (Landsberg and Hingston 1996) but we expect that Eq. 7 could be improved for specific vegetation types and environmental conditions (Choudhury 2001a), especially during droughts. Note that in cloudy environments such as tropical rainforests, the variation in e' would generally be larger than the variation in f'. Our estimate of c. 3.2 GtC year-1 for the average annual net primary production of Australia is higher than, but still of the same order as, estimates made using a variety of other approaches, e.g. c. 2.8 GtC year⁻¹ (Gifford et al. 1992), c. 2.7 GtC year⁻¹ (Pittock and Nix 1986), c. 2.0 GtC year-1 (Field et al. 1998; DeFries et al. 1999), c. 1.6 GtC year-1 (Kirschbaum 1999). However, here we emphasise the underlying relationships and methods that are used in subsequent analysis, rather than the absolute accuracy of the results, given that we have not addressed the effects of, for example, water stress on e'.

Mt. Pinatubo – the effect of perturbations in the diffuse-global relationship

The data in Fig. 5 highlight the interrelationships between the water balance (rainfall, pan evaporation) and the radiation balance (global solar irradiance, diffuse fraction). In particular, as cloud cover increases, rainfall and the diffuse fraction typically increase, and the atmospheric transmission of solar radiance declines as does the pan evaporation. These interrelationships are at the heart of the light use efficiency model because it is ultimately based on the (reasonable) assumption that the interception of light by leaves will be accompanied by the uptake of water and nutrients necessary for photosynthesis and transpiration (Roderick et al. 2000). Nevertheless, that does not mean that diffuse radiance, and hence the diffuse fraction, is only important because it is correlated with changes in the radiation and water balance. On the contrary, the earlier theoretical analysis predicted, and the existing data showed, that canopy photosynthesis is sensitive to changes in the diffuse fraction. One way to explicitly test the direct effect of diffuse irradiance on canopy photosynthesis would be to conduct experiments in which the diffuse fraction was varied using artificial means, independently from the global solar irradiance. Plot-scale agricultural experiments of this sort have been conducted, and the results showed that plant productivity increases dramatically when the diffuse fraction is artificially increased while the global solar irradiance is held constant (Healey et al. 1998). While that is important confirmation of the significance of diffuse radiance, it is important to note that in nature, these various combinations do not usually occur (at the top of vegetation canopies) because increases in the diffuse fraction occur concurrently with decreases in atmospheric transmission (Fig. 2). However, there is (at least) one spectacular exception.

Following volcanic eruptions the solar irradiance at the surface usually remains more or less constant but there is a large increase in the diffuse fraction because the volcanic aerosols predominantly forward scatter the incoming solar radiance (Garrison 1995). Thus, for a period of time following a volcanic eruption there is a greater amount of diffuse irradiance at any given global solar irradiance than predicted by the relationship in Fig. 2. Of particular interest here is the Mt. Pinatubo (120°E, 15°N) eruption which occurred in June 1991 at the height on the northern hemisphere growing season, because there was a distinct change in atmospheric [CO₂] (Sarmiento 1993) that lasted for about 2 years after that eruption (Keeling and Whorf 1999). The decline is unique in the atmospheric $[CO_2]$ (Keeling) measurements and surprised many scientists because it also coincided with an El Niño event and previous and subsequent such events have been associated with increases in atmospheric [CO₂]. Initial analysis of this anomaly concluded that the effect was probably a terrestrial one (Sarmiento 1993). Subsequent work has suggested a combined terrestrial-oceanic sink (Keeling et al. 1996) or an oceanic sink because of fertilisation by iron ejected in the eruption (Watson 1997) and/or changes in wind patterns over the Pacific ocean (Murray et al. 1994). Here we propose an additional/alternative mechanism, based on the perturbation in the diffuse-global relationship (Fig. 2) that would lead to a terrestrial sink.

Following the Mt. Pinatubo eruption the solar irradiance at the surface typically declined by a few percent (Molineaux and Ineichen 1996). This reduction was most pronounced in the latter half of 1991 and in 1992 and had begun to disappear by the end of 1993 (Michalsky et al. 1994; Molineaux and Ineichen 1996; Adeyefa et al. 2000). There was also a large anomalous increase in the diffuse fraction (Michalsky et al. 1994; Molineaux and Ineichen 1996; Adeyefa et al. 2000) during the same period that accords with the time scale of the observed atmospheric CO_2 anomaly. Thus, there would have been a reduction in the volume of shade within vegetation canopies as a result of the anomalous increase in the diffuse fraction. Because this occurred without a large reduction in the amount of global solar irradiance, the combination of events should have resulted in an increased uptake of CO_2 by vegetation worldwide.

While we have little doubt about the direction of change following Pinatubo, the key issue here is to establish whether the expected increase in CO_2 uptake by vegetation would have been of sufficient magnitude to explain a significant part of the observed atmospheric anomaly. To do that, we attempt a simple analysis by estimating the perturbation in net production (d*N*) resulting from the increased diffuse fraction as:

$$\frac{\mathrm{d}N}{N} = \frac{\mathrm{d}P_{\mathrm{G}} - \mathrm{d}P_{\mathrm{R}}}{P_{\mathrm{G}} - P_{\mathrm{R}}} \tag{10}$$

By expressing the autotrophic respiration as a fraction (α) of gross production:

$$P_{\rm R} = \alpha P_{\rm G} \tag{11a}$$

and for the perturbation in those quantities:

$$dP_{\rm R} = \beta \, dP_{\rm G} \tag{11b}$$

we can rewrite Eq. 10 as:

$$\frac{\mathrm{d}N}{N} = \frac{(1-\beta)\mathrm{d}P_{\mathrm{G}}}{(1-\alpha)P_{\mathrm{G}}} \tag{12}$$

We make the assumption that C' and f' remained constant after the eruption. Based on those assumptions, Eq. 12 can be rewritten as:

$$\frac{\mathrm{d}N}{N} = \left(\frac{(1-\beta)}{(1-\alpha)}\right) \left(\frac{\mathrm{d}e'}{e'} + \frac{\mathrm{d}R'_{\mathrm{s}}}{R'_{\mathrm{s}}}\right) \tag{13}$$

By differentiating Eq. 7, we have:

$$de' \approx 0.024 d(R_d'/R_s')$$
 (14)

Note that Eq. 7 was derived for conditions where the diffuse fraction would have followed the usual pattern as depicted in Fig. 2. The extensive calculations of Choudhury (2001a) need to be repeated for the conditions discussed here, and the slope (0.024) may need to be altered. In the absence of such calculations we assume that Eq. 14 is still a useful approximation.

Measurements of global and diffuse solar irradiance in New Zealand in March 1992, just after the Pinatubo eruption, showed a much higher diffuse fraction than expected (Kelliher et al. 1996), and are generally consistent with the widespread distribution of volcanic aerosols after the Pinatubo eruption (Minnis et al. 1993). Using data for Geneva (Switzerland, 46°N) and Albany (N.Y., USA, 43°N) (Molineaux and Ineichen 1996) we estimate that $d(R_d'/R_s')$ was 0.08 and 0.10 respectively when averaged over the year following the Mt. Pinatubo eruption. Adopting 0.09, we get:

$$\frac{\mathrm{d}e'}{e'} \approx \frac{(0.024)(0.09)}{0.024 \left(R'_{\mathrm{d}}/R'_{\mathrm{s}}\right) + 0.012} \tag{15}$$

If $R'_{\rm d}/R'_{\rm s}$ is assumed to be in the range 0.2–0.6 (Roderick 1999), then de'/e' would be between 0.13 and 0.08, say $de'/e'\approx 0.10$. Following volcanic eruptions, there is typically a small reduction in global solar irradiance $(R'_{\rm s})$ and here we assume 3% (Garrison 1995; Olmo et al. 1999). Assuming that global N is about 60 GtC year⁻¹ (Field et al. 1998), we can rewrite Eq. 13 using the above estimates as:

$$dN \approx \frac{(1-\beta)}{(1-\alpha)} (0.10 - 0.03) (60) \approx \frac{(1-\beta)}{(1-\alpha)} (4.2)$$
(16)

in units of GtC year⁻¹. Thus, assuming that there was no change in the fraction of autotrophic respiration, we estimate that dN would be about 4.2 GtC year⁻¹. Even if we make the (unlikely) assumption that the average autotrophic respiration increased from 45 to 65% of gross productivity, the estimate of dN is still of the same order (*c*. 2.7 GtC year⁻¹).

To estimate the effect of this change in net production on the atmospheric $[CO_2]$, we also need to consider the decomposition of the increment as well as changes in heterotrophic (the so-called soil) respiration. To consider decomposition of the increment, we assume that the net carbon fixed by woody plants is incorporated in longlived structures (e.g. woody stems) while the additional carbon fixed by herbaceous plants is decomposed and returns to the atmosphere. Assuming that approximately 60% of the global net production is attributed to woody plants (Potter and Klooster 1998), we can reduce our estimate of 4.2 GtC year⁻¹ to 2.5 GtC year⁻¹. (Note that while it is the case that some of the primary production of woody plants is allocated to leaves, which in temperate conditions are often lost within a few months, we have been conservative by treating the response in terms of net primary productivity. For example, in practice, the autotrophic respiration, $P_{\rm R}$, that diminishes $P_{\rm G}$ to N will not occur instantaneously as assumed here. Also, as noted above, the increase in the diffuse fraction persisted for at least two years and will have been promoting $P_{\rm G}$ over that period. This may explain the persistence of the CO_2 anomaly.) Soil respiration has traditionally been assumed to increase with temperature. Observations show that the average global surface air temperature decreased by about 0.1–0.2°C in the year following the Mt. Pinatubo eruption (Keeling et al. 1995), but this change would not be sufficient to significantly alter the order of magnitude of the above estimate.

While the above calculations are approximate, the estimate of the 'Pinatubo pertubation' on atmospheric CO_2 in the year following the eruption is a reduction of about 2.5 GtC which equates to about 1.2 ppmv CO_2 in the atmosphere and is of the same order as the observed effect (Sarmiento 1993). It is important to note that while the parameters we have used seem to have given a high estimate of Australian annual net primary production, the estimate of the Mt. Pinatubo effect is not generally sensitive to the assumed values of the parameters because the calculations are based on the proportional change in the parameter values. One caveat identified earlier is that further calculations of the dependence of e' on the diffuse fraction need to be made for conditions of extreme haze. Further, we acknowledge that there were probably many other subtle effects of the eruption on the climate and biosphere, including those noted by Watson (1997) and Murray et al. (1994). Nevertheless, we conclude that a decrease in the volume of shade caused by an anomalous increase in the diffuse fraction as a consequence of the scattering properties of volcanic aerosols is a major reason for the atmospheric CO₂ anomaly that was observed after the Mt. Pinatubo eruption.

Discussion

In most existing global scale climate-vegetation models, many of the gross effects of clouds are indirectly included via changes in variables like the global solar irradiance, or via the reduction in the vapour pressure deficit which is usually observed under cloudy conditions (Hammer and Wright 1994; Gu et al. 1999). While these indirect effects are important, clouds and other atmospheric particles also have an important direct effect on vegetation productivity and structure because changes in the diffuse fraction, resulting from variations in both cloudiness and aerosol concentrations, lead to large changes in the volume of shade within vegetation canopies. This direct effect can be readily incorporated into models because there is a robust relationship linking the diffuse fraction with the fractional transmission of solar radiance through the atmosphere (Fig. 2).

These latter results are very important in the context of global climate change, because there is now substantial evidence that the solar irradiance incident at the surface has declined substantially over the last 50 years (Stanhill and Cohen 2001). To put those observations in perspective, the radiative forcing at the surface as a consequence of the increase in CO_2 and other greenhouse gases since the start of the industrial era is believed to be about 1-3 W m⁻², while increases in aerosols are suspected to have decreased the radiative forcing by about the same amount (Hansen et al. 1998, 2000). These estimated changes are small by comparison with the *observed* changes in global solar irradiance. For example, Stanhill and Cohen (2001) estimate that since 1950, the global solar irradiance has decreased on average by about 25 W m⁻². According to the diffuse-global relationship (Fig. 2), that should have resulted in substantial increases in the diffuse fraction. Although estimates of diffuse irradiance are relatively scarce, observations made over the former Soviet Union are consistent with the predicted increase in the diffuse fraction (Fig. 6).

Because the diffuse radiance is very important in determining canopy photosynthesis, and because the globally observed trends in the diffuse fraction over the last 50 years are large, it is important that climate-vegetation models, including global scale carbon balance models,



Fig. 6 Observed increases in the annual diffuse fraction at three sites (1, 2, 3) located in the former Soviet Union (Abakumova et al. 1996). Dotted line (y=1.11-1.31x) is the estimated relation for annual data (see Fig. 2). The base of each arrow signifies the observed relation in 1960 while the tip of the arrowhead is the observed relation in 1985 for sites 1 and 2, and 1990 is used for site 3. Sites are; 1 (Odessa, 46°24' N, 30°48' E), 2 (Toropets, 56°30' N, 31°48' E), 3 (Moscow, 55°42' N, 37°30' E). Data for the nine other sites reported in Abakumova et al. (1996) also follow the same trend reported here

be modified to include this important direct effect on vegetation productivity and structure.

We conclude that atmospheric scattering has important effects on the global carbon cycle and we support the recent call by Broecker (2000) for intense study of a possibly pivotal role of atmospheric dust in the global climate system.

Acknowledgements We thank Stephen Roxburgh, Frank Kelliher and two anonymous referees for helpful comments on the manuscript.

Appendix

Mathematical expressions for shadows

The irradiance of a surface receiving radiance from the upper hemisphere can be computed by integrating the intercepted radiance over the visible hemisphere. In the most general case, the radiance is a function of both azimuth and zenith angles. However, under overcast skies it is usually assumed that the radiance (I) is only a function of the zenith angle (z) and that dependence is usually expressed as (Monteith and Unsworth 1990):

$$I(z) = \frac{I(0)(1+b\cos z)}{(1+b)}$$
(A1)

where (1+b) is the ratio of the radiance at the zenith, I(0)to that at the horizon, $I(\pi/2)$. With reference to Fig. 1A, the irradiance at A, denoted R_A , is (Monteith and Unsworth 1990):

$$R_{\rm A} = \pi \int_{0}^{\pi/2} I(z) \sin z \cos z dz \qquad (A2)$$
$$R_{\rm B} = \pi \int_{\alpha}^{\pi/2} I(z) \sin z \cos z dz \qquad (A3)$$

where:

$$\tan \alpha = \frac{D}{2X} \tag{A4}$$

Equation A3 is evaluated as:

$$R_{\rm B} = \frac{2\pi I(0)}{(1+b)} \left(\frac{\cos 2\alpha - \cos \pi}{4} + \frac{b}{3} (\cos^3 \alpha - \cos^3 \pi/2) \right)$$
(A5)
which reduces to:

$$R_{\rm B} = \frac{2\pi I(0)}{(1+b)} \left(\frac{\cos 2\alpha + 1}{4} + \frac{b}{3} (\cos^3 \alpha) \right)$$
(A6)

The integral of Eq. A2 can be derived from Eq. A6 by replacing α with zero throughout and is:

$$R_{\rm A} = \frac{2\pi I(0)}{(1+b)} \left(\frac{2}{4} + \frac{b}{3}\right) \tag{A7}$$

The reduction in irradiance at B, relative to that at A, denoted S, is given by:

$$S = \frac{R_{\rm B}}{R_{\rm A}} \tag{A8}$$

For an isotropic distribution of radiance, b equals zero, and from Eqs. A6, A7 it follows that:

$$S_i = \frac{\cos 2\alpha + 1}{2} \tag{A9}$$

For the standard overcast sky, b equals 1.2 (Monteith and Unsworth 1990) and it can be shown that:

$$S_{\rm sos} = \frac{1}{0.9} \left(\frac{\cos 2\alpha + 1}{4} + 0.4 \cos^3 \alpha \right)$$
(A10)

Equations. A4, A9 and A10 have been used to prepare Fig. 1B in the main text.

References

- Abakumova GM, Feigelson EM, Russak V, Stadnik VV (1996) Evaluation of long-term changes in radiation, cloudiness, and surface temperature on the territory of the former Soviet Union. JClim 9:1319-1327
- Adeyefa ZD, Holmgren B, Adedokun JA (2000) Spectral solar irradiance in northern Scandinavia before and after Pinatubo. Atmosfera 13:133-146
- Anderson MC (1981) The geometry of leaf distribution in some south-eastern Australian forests. Agric Meteorol 25:195-205
- Baldocchi DD, Vogel CA, Hall B (1997) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric For Meteorol 83:147-170
- Berry SL, Roderick ML (2001) Estimating mixtures of leaf functional types using continental-scale satellite and climatic data. Global Ecol Biogeogr 10(in press)
- Broecker WS (2000) Abrupt climate change: causal constraints provided by the paleoclimate record. Earth-Sci Rev 51:137-154
- Choudhury BJ (2000) A sensitivity analysis of the radiation use efficiency for gross photosynthesis and net carbon accumulation by wheat. Agric For Meteorol 101:217-234
- Choudhury BJ (2001a) Estimating gross photosynthesis using satellite and ancillary data: Approach and preliminary results. Remote Sensing Environ 75:1–21
- Choudhury BJ (2001b) Modeling radiation- and carbon-use efficiencies of maize, sorghum and rice. Agric For Meteorol 106: 317-330

- De Pury DGG, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ 20:537–557
- DeFries RS, Field CB, Fung I, Collatz GC, Bounoua L (1999) Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. Global Biogeochem Cycles 13:803–815
- Dewar R (2000) A model of the coupling between respiration, active processes and passive transport. Ann Bot 86:279–286
- Fan S-M, Goulden ML, Munger JW, Daube BC, Bakwin PS, Wofsy SC, Amthor JS, Fitzjarrald DR, Moore KE, Moore TR (1995) Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole ecosystem exchange measurements by eddy correlation. Oecologia 102:443–452
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: Integrating terrestrial and oceanic components. Science 281:237–239
- Garrison J (1995) An evaluation of the effect of volcanic eruption on the solar radiation at six Canadian stations. Solar Energy 55:513–525
- Gifford RM, Cheney NP, Noble JC, Russell JS, Wellington AB, Zammit C (1992) Australian land use, primary production of vegetation and carbon pools in relation to atmospheric carbon dioxide concentration. In: Gifford RM, Barson MM (eds) Australia's renewable resources sustainability and global change. Bureau of Rural Resources and CSIRO Division of Plant Industry, Canberra, pp 151–187
- Goudriaan J (1977) Crop micrometeorology: a simulation study. PUDOC, Wageningen
- Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. J Geophys Res 104:31421–31434
- Hammer GL, Wright GC (1994) A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. Aust J Agric Res 45:575–589
- Hansen JE, Sato M, Lacis A, Ruedy R, Tegen I, Mathews E (1998) Climate forcings in the industrial era. Proc Natl Acad Sci USA 95:12753–12758
- Hansen JE, Sato M, Ruedy R, Lacis A, Oinas V (2000) Global warming in the twenty-first century: an alternative scenario. Proc Ntl Acad Sci USA 97:9875–9880
- Healey KD, Rickert KG, Hammer GL, Bange MP (1998) Radiation use efficiency increases when the diffuse component of incident radiation is enhanced under shade. Aust J Agric Res 49:665–672
- Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. Ecology 75:134–150
- Hollinger DY, Kelliher FM, Schulze E-D, Bauer G, Arneth A, Byers JN, Hunt JE, McSeveny TM, Kobak KI, Milukova I, Sogatchev A, Tatarinov F, Varlargin A, Ziegler W, Vygodskaya NN (1998) Forest-atmosphere carbon dioxide exchange in eastern Siberia. Agric For Meteorol 90:291–306
- Horn HS (1971) The adaptive geometry of trees. Princeton University Press, Princeton
- Keeling ČD, Whorf TP (1999) Atmospheric CO₂ records from sites in the SIO air sampling network. In: Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge
- Keeling CD, Whorf TP, Wahlen M, van der Pilcht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375:666–670
- Keeling RF, Piper SC, Heinmann M (1996) Global and hemispheric CO₂ sinks deduced from changes in atmospheric CO₂. Nature 381:218–221
- Kelliher FM, Owens IF, Sturman AP, Byers JN, Hunt JE, McSeveny TM (1996) Radiation and ablation on the névé of Franz Josef Glacier. J Hydrol (Dunedin) 35:131–150

- Kirschbaum MUF (1999) The effect of climate change on forest growth in Australia. In: Howden SM, Gorman JT (eds) Impacts of global change on Australian temperate forests. BRS Working Paper Series No. 99/08, Canberra, pp 62–68
- Landsberg JJ, Gower ST (1997) Applications of physiological ecology to forest management. Academic Press, San Diego
- Landsberg JJ, Hingston FJ (1996) Evaluating a simple radiation/dry matter conversion model using data from *Eucalyptus* globulus plantations in Western Australia. Tree Physiol 16: 801–808
- Liu BYH, Jordan RC (1960) The interrelationship and characteristic distribution of direct, diffuse and total solar radiation. Solar Energy 4:1–19
- Michalsky JJ, Perez R, Seals R, Ineichen P (1994) Degradation of solar concentrator performance in the aftermath of Mt Pinatubo. Solar Energy 52:205–213
- Minnis P, Harrison EF, Stowe LL, Gibson GG, Denn FM, Doelling DR, Smith WL Jr (1993) Radiative climate forcing by the Mount Pinatubo eruption. Science 259:1411–1415
- Molineaux B, Ineichen P (1996) Impact of Pinatubo aerosols on the seasonal trends of global, direct and diffuse irradiance in two northern mid-latitude sites. Solar Energy 58:91–101
- Monteith JL (1972) Solar radiation and productivity in tropical ecosystems. J Appl Ecol 9:747–766
- Monteith JL, Unsworth M (1990) Principles of environmental physics. Edward Arnold, London
- Murata Y (1981) Dependence of potential productivity and efficiency for solar energy utilization on leaf photosynthetic capacity in crop species. Jpn J Crop Sci 50:223–232
- Murray JW, Barber RT, Roman MR, Bacon MP, Feely RA (1994) Physical and biological controls on carbon cycling in the equatorial pacific. Science 266:58–65
- Norman JM, Arkebauer TJ (1991) Predicting canopy light-use efficiency from leaf characteristics. In: Hanks J, Ritchie JT (eds) Modelling Plant and Soil Systems, Agronomy Monograph No. 31. ASA-CSSA-SSSA, Madison, pp 125–143
- Olmo FJ, Tovar J, Alados-Arboledas L, Okulov O, Ohvril HO (1999) A comparison of ground level solar radiative effects of recent volcanic eruptions. Atmos Environ 33:4589–4596
- Pittock AB, Nix HA (1986) The effect of changing climate on Australian biomass production – a preliminary study. Clim Change 8:243–255
- Potter CS, Klooster SA (1998) Dynamic global vegetation modelling for prediction of plant types and biogenic trace gas fluxes. Global Ecol Biogeogr 8:473–488
- Price DT, Black TĂ (1990) Effects of short-term variation in weather on diurnal canopy CO₂ flux and evapo-transpiration of a juvenile Douglas-fir stand. Agric For Meteorol 50:139– 158
- Rochette P, Desjardins RL, Pattey E, Lessard R (1996) Instantaneous measurement of radiation and water use efficiencies of a maize crop. Agron J 88:627–635
- Roderick ML (1999) Estimating the diffuse component from daily and monthly measurements of global radiation. Agric For Meteorol 95:169–185
- Roderick ML, Noble IR, Cridland SW (1999) Estimating woody and herbaceous vegetation cover from time series satellite observations. Global Ecol Biogeogr 8:501–508
- Roderick ML, Berry SL, Noble IR (2000) A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. Funct Ecol 14:423–437
- Ross J, Mottus M (2000) Statistical treatment of sunfleck length inside the willow coppice. Agric For Meteorol 104:215–231
- Ross J, Sulev M, Saarelaid P (1998) Statistical treatment of the PAR variability and its application to willow coppice. Agric For Meteorol 91:1–21
- Sarmiento JL (1993) Atmospheric CO₂ stalled. Nature 365:697–698
- Sinclair TR, Murphy CE, Knoerr KR (1976) Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. J Appl Ecol 13:813–829

- Sinclair TR, Shiraiwa T, Hammer GL (1992) Variation in crop radiation use efficiency in response to increased proportion of diffuse radiation. Crop Sci 32:1281–1284
- Smith WK, Knapp AK, Reiners WA (1989) Penumbral effects on sunlight penetration in plant communities. Ecology 70:1603– 1609
- Spitters CJT, Toussaint HAJM, Goudriaan J (1986) Separating the diffuse and direct component of global radiation and its implication for modelling canopy photosynthesis. I. Components of incoming radiation. Agric For Meteorol 38:217–229
- Stanhill G, Cohen S (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. Agric For Meteorol 107:255–278
- ricultural consequences. Agric For Meteorol 107:255–278 Suraqui S, Tabor H, Klein WH, Goldberg B (1974) Solar radiation changes at Mt. St. Katherine after forty years. Solar Energy 16:155–158
- Watson AJ (1997) Volcanic iron, CO₂, ocean productivity and climate. Nature 385:587–588