



## Disentangling leaf area and environmental effects on the response of the net ecosystem CO<sub>2</sub> exchange to diffuse radiation

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[1] There is an ongoing discussion about why the net ecosystem CO<sub>2</sub> exchange (NEE) of some ecosystems is less sensitive to diffuse radiation than others and about the role other environmental factors play in determining the response of NEE to diffuse radiation. Using a six-year data set from a temperate mountain grassland in Austria we show that differences between ecosystems may be reconciled based on their green area index (GAI; square meter green plant area per square meter ground area) - the sensitivity to diffuse radiation increasing with GAI. Our data suggest diffuse radiation to have a negligible influence on NEE below a GAI of 2 m<sup>2</sup> m<sup>-2</sup>. Changes in air/soil temperature and air humidity concurrent with the fraction of diffuse radiation were found to amplify the sensitivity of the investigated temperate mountain grassland ecosystem to diffuse radiation. **Citation:** Wohlfahrt, G., A. Hammerle, A. Haslwanger, M. Bahn, U. Tappeiner, and A. Cernusca (2008), Disentangling leaf area and environmental effects on the response of the net ecosystem CO<sub>2</sub> exchange to diffuse radiation, *Geophys. Res. Lett.*, 35, L16805, doi:10.1029/2008GL035090.

### 1. Introduction

[2] Atmospheric carbon dioxide (CO<sub>2</sub>) is responsible for around 60 % of anthropogenic global warming [Intergovernmental Panel on Climate Change, 2007]. Each year, the terrestrial biosphere absorbs on average about one third of the 7 Pg carbon released to the atmosphere through fossil fuel burning [Canadell et al., 2007]. Projecting whether terrestrial ecosystems will continue to provide a negative feedback to climate change requires understanding and quantifying the interactions and feedbacks between the carbon cycle and its major drivers, that is climate and land use [Heimann and Reichstein, 2008].

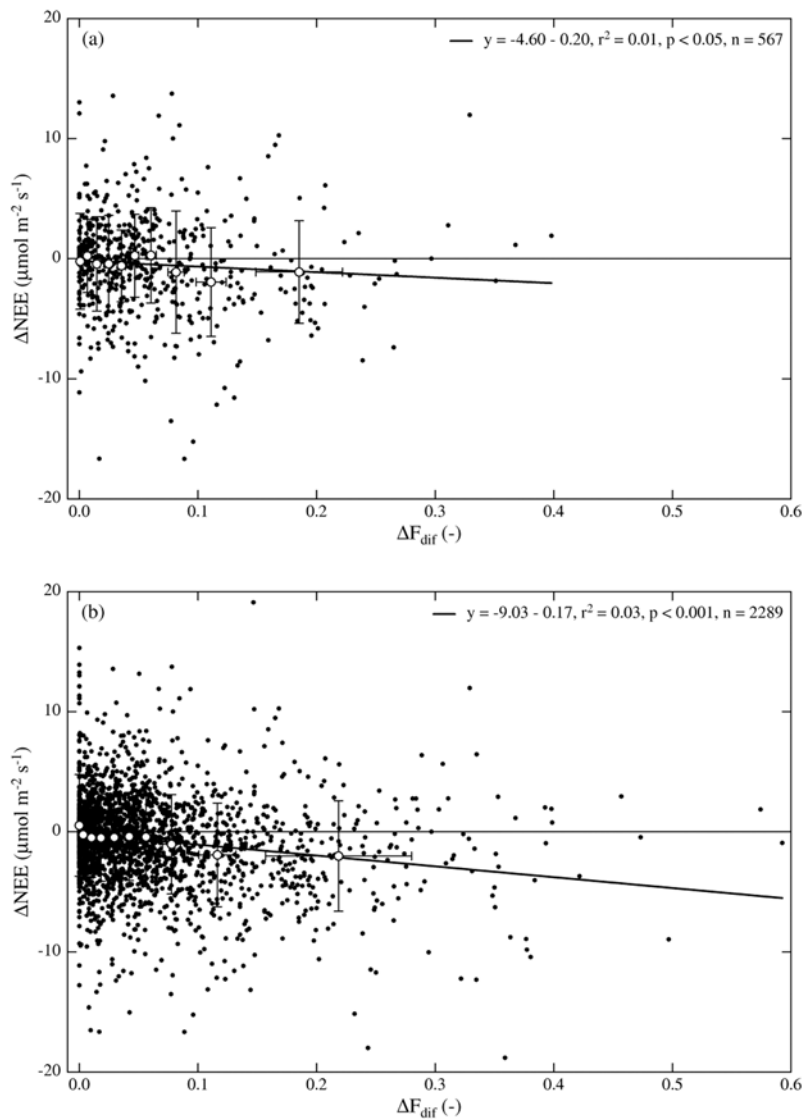
[3] A number of recent studies suggest that the net ecosystem CO<sub>2</sub> exchange (NEE), especially of forests, is sensitive to changes in the fraction of incoming diffuse (F<sub>dif</sub>) photosynthetically active radiation (PAR), ecosystems taking up more CO<sub>2</sub> when, at similar levels of total PAR, F<sub>dif</sub> is higher [Gu et al., 1999, 2002, 2003; Freedman et al., 2001; Niyogi et al., 2004; Alton et al., 2005, 2007; Misson et al., 2007; Rodriguez and Sadras, 2007; Urban et al., 2007; Knohl and Baldocchi, 2008; Min and Wang, 2008]. Thereby, the terrestrial biosphere may have contributed to the slowdown of the rise in temperature between 1960–1990

[Wild et al., 2007], a period during which increases in aerosol load and cloud formation have caused a decrease in total and an increase in diffuse radiation incident at the earth's surface [Stanhill and Cohen, 2001; Wild et al., 2005]. With the reversing of this trend after 1990 [Wild et al., 2005], this negative feedback on climate change may be expected to weaken.

[4] While the response of canopy photosynthesis to changes in diffuse radiation may be well explained based on the leaf-level photosynthesis-light relationship [see Brodersen et al., 2008] and within-canopy radiative transfer [Roderick et al., 2001; Knohl and Baldocchi, 2008], there is an ongoing discussion about why some ecosystems are less sensitive to diffuse radiation than others, and about the role that other environmental factors, especially air temperature and humidity, which co-vary with F<sub>dif</sub>, play in determining the response of NEE to diffuse radiation. Based on comparative experimental [Niyogi et al., 2004; Alton et al., 2007] and simulation studies [Roderick et al., 2001; Knohl and Baldocchi, 2008], it has been suggested that the response of NEE to diffuse radiation increases with the area of photosynthetically active plant matter (so-called green area index; GAI; square meter green plant area per square meter ground area) and that this is why forests appear more sensitive to diffuse radiation than some grasslands [Niyogi et al., 2004] or ecosystems with open canopies [Alton et al., 2005, 2007]. With regard to the role of air temperature and humidity in modulating the response of NEE to diffuse radiation, some studies suggest these effects to be more important than diffuse radiation itself [Steiner and Chameides, 2005], others report interactive effects with diffuse radiation [Gu et al., 1999, 2002, 2003; Freedman et al., 2001; Urban et al., 2007; Min and Wang, 2008], while yet others find these factors to play a minor role [Alton et al., 2007; Knohl and Baldocchi, 2008].

[5] The objectives of the present paper are (1) to examine the relative importance of concurrent changes in air temperature and humidity for the response of NEE to diffuse radiation and (2) to provide direct experimental evidence in support of simulation studies suggesting that the sensitivity of NEE to diffuse radiation increases with GAI. To this end, we analyse a six year data set from a temperate mountain grassland [Wohlfahrt et al., 2008] which, because the grassland is cut three times a year and thus undergoes multiple growing phases, provides a wide range of GAIs. In order to disentangle the various factors confounding the response of NEE to diffuse radiation we employ a novel method of data analysis which

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**Figure 1.** Sensitivity of NEE to diffuse radiation for (a) all data pairs which have been acquired under identical meteorological conditions except for  $F_{\text{dif}}$  and (b) the same as Figure 1a but with the limitation to identical air/soil temperature and air humidity removed. Small grey symbols refer to half-hourly data pairs, large white symbols to bin-averages (equal number of observations in each bin; error bars refer to one standard deviation), and lines to linear regressions through the half-hourly data (regression statistics are given in the upper right corner of each panel).

allows us to study the role of GAI and air/soil temperature/humidity in isolation.

## 2. Data and Methods

[6] The study site is a temperate mountain grassland (Neustift, 47°07'N, 11°19'E) in the Western part of the Austrian Alps. A detailed description of the study site in terms of soil, vegetation and climate is given by *Hammerle et al.* [2008]. The NEE was measured using the eddy covariance method [*Aubinet et al.*, 2000]. Details on eddy covariance instrumentation and calculation protocols, as well as supporting environmental and GAI measurements are given by *Wohlfahrt et al.* [2008]. Incident total and diffuse photosynthetically active radiation, from which  $F_{\text{dif}}$  was derived, were measured with a heated quantum sensor (BF2H, Delta-T, UK). In order to analyze how GAI or air

temperature/humidity affect the response of NEE to diffuse radiation, the influence of all other potentially confounding factors has to be minimized and to this end we have adapted an approach devised by *Hollinger and Richardson* [2005] for quantifying the random uncertainty of eddy covariance flux measurements. This approach involved calculating half-hourly pairs of data from the same time of the day on the respective subsequent day under identical meteorological conditions, except for  $F_{\text{dif}}$ . By restricting our analysis to data pairs from the same time of day on subsequent days we minimized the influence of endogenous (diurnal) and phenological changes in NEE (ecosystem structural, optical, and physiological properties [*Knohl and Baldocchi*, 2008]), as well as solar elevation. Identical meteorological conditions were defined as differing by less than 5 % in total PAR, soil temperature, air temperature and humidity, wind speed and soil water content. Only data from the snow-free

(vegetation) period were used and data pairs with precipitation were excluded. For the purpose of exploring the confounding effects of air temperature and humidity, the restriction of the data pairs to the same temperature and humidity was removed; for analyzing the role of GAI data were stratified into GAI classes. In the following, data pairs are presented in terms of the difference ( $\Delta$ ) in NEE and  $F_{\text{dif}}$ , with the convention that NEE and  $F_{\text{dif}}$  of the day with the smaller  $F_{\text{dif}}$  are subtracted from that with the larger  $F_{\text{dif}}$  ( $\Delta F_{\text{dif}}$  is always positive by this definition and a negative  $\Delta\text{NEE}$  indicates that NEE was more negative when  $F_{\text{dif}}$  was larger). In order to quantify the sensitivity of NEE to diffuse radiation we plot  $\Delta\text{NEE}$  as a function of  $\Delta F_{\text{dif}}$  and use the sign and magnitude of the slope as a measure of the direction and strength of the sensitivity. Statistical analysis was conducted with the SPSS statistics software package (SPSS 15.0, SPSS Inc., Chicago, USA).

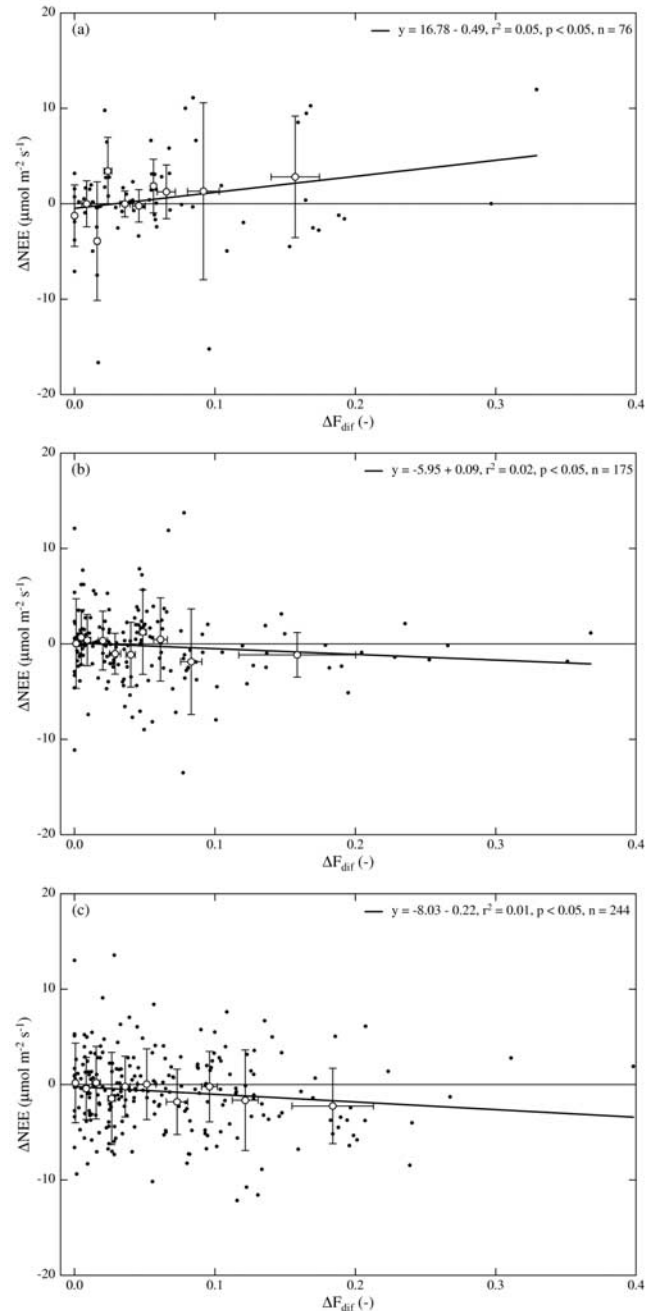
### 3. Results

[7] NEE from the same time of day on the respective subsequent day and under identical environmental conditions, except for  $F_{\text{dif}}$ , was significantly more negative when  $F_{\text{dif}}$  was larger (paired T-test,  $p = 0.005$ ). As shown in Figure 1a, NEE decreased (i.e., more net uptake of CO<sub>2</sub>) by around  $0.46 \mu\text{mol m}^{-2} \text{s}^{-1}$  for a 10% increase in  $\Delta F_{\text{dif}}$ .  $\Delta\text{NEE}$  and  $\Delta F_{\text{dif}}$  were independent of the residual variation (i.e., <5%) in environmental drivers of data pairs (data not shown). When the restriction to identical air temperature and humidity was removed (Figure 1b), the sensitivity of NEE to diffuse radiation doubled ( $0.90 \mu\text{mol m}^{-2} \text{s}^{-1}$  decrease in NEE for a 10% increase in  $\Delta F_{\text{dif}}$ ). In order to put the results of Figure 1 into perspective – the average midday NEE of our site amounts to  $-10.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ . At GAIs between  $0\text{--}2 \text{ m}^2 \text{ m}^{-2}$ , NEE pairs were not significantly different ( $p = 0.324$ ) and  $\Delta\text{NEE}$  even showed an increase with increasing  $\Delta F_{\text{dif}}$  (Figure 2a). At intermediate ( $2\text{--}4 \text{ m}^2 \text{ m}^{-2}$ ) GAIs, NEE pairs were still not statistically significantly different ( $p = 0.445$ ), but  $\Delta\text{NEE}$  decreased with increasing  $\Delta F_{\text{dif}}$  (Figure 2b). At high ( $4\text{--}6 \text{ m}^2 \text{ m}^{-2}$ ) GAIs, finally, NEE pairs were statistically significantly different ( $p = 0.004$ ), and the sensitivity to diffuse radiation was increased by 35% as compared to intermediate GAIs (Figure 2c).

### 4. Discussion and Conclusion

[8] The objectives of the present paper were to quantify the role of GAI and concurrent changes in air/soil temperature and air humidity in determining the response of NEE to diffuse radiation. To this end we have applied a novel method of analysis to a six year data set from a temperate mountain grassland.

[9] Our study shows that NEE decreases by  $0.46 \mu\text{mol m}^{-2} \text{s}^{-1}$  for a 10 % increase in  $F_{\text{dif}}$  (Figure 1a), when all other environmental parameters are held constant. This may appear like a small change (4.5 % of average midday NEE), but if applied to all daylight hours during the vegetation period, the site would be gaining an additional  $73 \text{ gC m}^{-2}$  annually, i.e., would turn from a source of  $18 \text{ gC m}^{-2}$  [Wohlfahrt et al., 2008] to a sink.



**Figure 2.** Sensitivity of NEE to diffuse radiation for all data pairs which have been acquired under identical meteorological conditions except for  $F_{\text{dif}}$ . Data have been stratified into GAI classes of (a)  $0\text{--}2 \text{ m}^2 \text{ m}^{-2}$ , (b)  $2\text{--}4 \text{ m}^2 \text{ m}^{-2}$ , and (c)  $4\text{--}6 \text{ m}^2 \text{ m}^{-2}$ . Symbols are the same as in Figure 1.

[10] The observed increases in canopy carbon gain under diffuse radiation may be explained based on well-established theory of the saturation-type response of photosynthesis to PAR and the bi-modal distribution of PAR within the plant canopy [Roderick et al., 2001; Knohl and Baldocchi, 2008]: Sunlit leaves, that is leaves illuminated by both diffuse and direct radiation, are usually saturated

with radiation (provided the intensity of incident radiation is high enough to allow for saturation). Shaded leaves, which receive only sky diffuse and scattered (diffused) beam radiation, in contrast are often light-limited. Total canopy photosynthesis increases with  $F_{\text{dif}}$  because photosynthesis of shaded leaves, which experience higher light intensities under these conditions, increases, while the photosynthesis of sunlit light-saturated leaves remains approximately unchanged (as long as their light intensity does not fall below the saturation level). Any factor modifying the response of photosynthesis to PAR or the within-canopy light climate will affect the response to diffuse radiation, including: solar elevation [Gu *et al.*, 1999], the intensity of total PAR [Gu *et al.*, 2002], the spatial and angular distribution of leaves and their optical properties [Alton *et al.*, 2007; Knohl and Baldocchi, 2008], the curvature of the leaf-level photosynthesis-light relationship [Letts *et al.*, 2005; Brodersen *et al.*, 2008] and finally GAI [Niyogi *et al.*, 2004; Letts *et al.*, 2005; Alton *et al.*, 2007; Knohl and Baldocchi, 2008]. Previous assessments of the role of GAI in modulating the response of canopy photosynthesis to diffuse radiation were either based on theoretical considerations [Roderick *et al.*, 2001], numerical simulation analysis [Knohl and Baldocchi, 2008], or on studies comparing canopies with differing GAIs [Niyogi *et al.*, 2004; Alton *et al.*, 2007]. The salient effect of differences in GAI is changes in the fraction of shaded leaf area, which increases approximately exponentially with GAI [Goudriaan, 1977]. Consequently, a larger fraction of the leaf area profits from the redistribution of radiation towards shaded leaves under diffuse sky conditions in tall canopies with large GAI, while small enhancements are to be expected for small or open canopies with low GAI [Niyogi *et al.*, 2004; Letts *et al.*, 2005; Alton *et al.*, 2005, 2007]. Because of between-site differences in structural and/or physiological canopy attributes as well as other environmental factors, the results of the previous comparative studies may be confounded by factors other than GAI. The present study overcomes this deficiency in two ways: First, by analysing data in a fashion which minimizes all confounding factors, and second, by studying an ecosystem which, because it is cut three times per year and thus undergoes multiple growing cycles during each vegetation period, provides a wide range of GAIs to specifically address this question (provided the other structural and/or physiological canopy attributes affecting the diffuse radiation response do not change significantly with GAI). Based on these data (Figure 2) we are able to confirm previous modelling and experimental studies suggesting that the sensitivity of NEE to diffuse radiation increases with GAI. Our finding that NEE is not sensitive to diffuse radiation for  $\text{GAI} < 2 \text{ m}^2 \text{ m}^{-2}$  corresponds well with the earlier assessment of Goudriaan [1977], who argued that for accurate modelling of canopy photosynthesis it is not necessary to distinguish sunlit/shaded leaf area below this threshold. It follows that we may expect biomes with LAIs  $< 2 \text{ m}^2 \text{ m}^{-2}$  (e.g., deserts, shrublands, tundra, and some grasslands and boreal forests [Asner *et al.*, 2003]), to exhibit little sensitivity to diffuse radiation.

[11] Whether observed increases in canopy carbon gain under diffuse sky conditions are to be attributed largely to

the redistribution of radiation to shaded leaves [Alton *et al.*, 2007; Knohl and Baldocchi, 2008], whether there are interactions with air temperature and humidity which amplify this effect [Gu *et al.*, 1999, 2002, 2003; Freedman *et al.*, 2001; Urban *et al.*, 2007; Min and Wang, 2008] or whether the latter two are even more important than diffuse radiation *per se* [Steiner and Chameides, 2005] is controversial. Our study shows that, all other potential influence factors being held constant, NEE is significantly more negative under diffuse radiation, but also that NEE is twice as sensitive to diffuse radiation when air/soil temperature and air humidity are allowed to co-vary with  $F_{\text{dif}}$  (Figure 1), lending support to the above-cited studies showing that concurrent variations in air temperature and humidity amplify the diffuse radiation effect. Typically, air temperatures are lower and relative humidity higher, resulting in a lower vapour pressure deficit (VPD), under more overcast sky conditions [Gu *et al.*, 1999]. Lower air/soil temperatures are known to reduce ecosystem respiration [Wohlfahrt *et al.*, 2005] and thus increase NEE. In case leaf temperatures are beyond the optimum for photosynthesis, lower air temperatures may also contribute to an increase in NEE by increasing photosynthesis [Steiner and Chameides, 2005]. Conversely, if leaf temperatures are suboptimal, decreases in air temperature may though also reduce photosynthesis. Decreases in VPD are known to result in increased stomatal conductance and hence to some extent in photosynthesis. While our study conclusively shows that concurrent changes in air/soil temperature and air humidity amplify the effect of diffuse radiation on the NEE of the investigated temperate mountain grassland, we caution of generalizing this finding to other ecosystems and/or climates. Firstly, because it is well established that ecosystems differ in the way their NEE responds to changes in air/soil temperature and VPD, for example because of plant species- or site-specific differences in the temperature sensitivity of soil respiration [Reichstein *et al.*, 2003], the shape of the temperature-photosynthesis relationship [Medlyn *et al.*, 2002] or the response of stomatal conductance to VPD [Tardieu and Simonneau, 1998]. Second, because other factors may strongly modify or even override the sensitivity to diffuse radiation and the way it is modulated by air/soil temperature and air humidity. For example under conditions of low water availability, soil respiration may be governed by substrate availability rather than temperature [Davidson and Janssens, 2006], or low leaf water potentials may induce stomatal closure and thus limit diffusion of CO<sub>2</sub> into the leaves irrespective of temperature and VPD.

[12] To summarize, our study confirms that the sensitivity to diffuse radiation increases with GAI. Below a GAI of  $2 \text{ m}^2 \text{ m}^{-2}$  diffuse radiation is suggested to have a negligible direct influence on NEE. Concurrent changes in air temperature and humidity were found to amplify the sensitivity of the investigated mountain grassland ecosystem to diffuse radiation.

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