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Estimation of daytime ecosystem respiration to determine gross primary production of a mountain meadow

Georg Wohlfahrt *, Michael Bahn, Alois Haslwanter,
Christian Newesely, Alexander Cernusca

Institut für Botanik, Universität Innsbruck, Sternwartestr. 15, 6020 Innsbruck, Austria

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Abstract

Gross primary production (F_{GPP}) may be calculated from net ecosystem CO_2 exchange (F_{NEE}), measured, for example, by means of the eddy covariance method, provided an estimate of daytime ecosystem respiration is available. The latter is now often estimated by extrapolating functional relationships between nighttime F_{NEE}, when F_{GPP} is zero, and temperature to daytime conditions. The present paper deals with one problem associated with this approach, namely the reduction of leaf respiration in light relative to darkness, which causes an overestimation of daytime ecosystem respiration, and hence F_{GPP}. The overestimation of F_{GPP} is quantified for a mountain meadow in the Austrian Alps using a coupled model of the reduction of leaf dark respiration as a function of light intensity and within-canopy radiative transfer. For the two study years analysed in the present paper, model simulations suggest a reduction of F_{GPP} by 11–13% and 13–17%, for a low and a high estimate of the maximum leaf-level reduction of dark respiration, respectively. This reduction is shown to be most sensitive to the ratio between F_{GPP} and total ecosystem respiration, as well as to the ratio between leaf and total ecosystem respiration. The largest factors of uncertainty in this modelling approach are the cause for and the actual level of the reduction of leaf dark respiration in light. The significance of the present findings for estimating F_{GPP} of other sites is discussed.

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Keywords: Eddy covariance; Grassland; Model; Plant area index; Radiative transfer; Soil respiration

1. Introduction

Recently, a global network of micrometeorological flux measurement sites, the so-called FLUXNET project, has been originated in order to meet the emerging need for long-term studies of the biosphere-atmosphere exchange of CO_2, water vapour and energy (Baldocchi et al., 2001). As for net ecosystem CO_2 exchange (F_{NEE}), most of the currently 250+ registered sites use the eddy covariance method (Baldocchi et al., 1988; Aubinet et al., 2000; Baldocchi, 2003) to directly measure F_{NEE} on a half-hourly to hourly basis. Inevitable gaps in the data record are filled using appropriate algorithms (Falge

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* Corresponding author. Tel.: +43 512 507 5917;
fax: +43 512 507 2975.
E-mail address: georg.wohlfahrt@uibk.ac.at (G. Wohlfahrt).

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Nomenclature

a	minimum value of R_{Ld}/R_{Ln} (dimensionless)
b	Q_{PPFD} where R_{Ld}/R_{Ln} reaches half of the maximum reduction (μmol m^{-2} s^{-1})
E_a	energy of activation for soil respiration (J mol^{-1})
F_{dif}	fraction of diffuse Q_{PPFD} (fraction)
F_{GPP}	gross primary production (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
F_{GPP}^{*}	gross primary production corrected for reduction of leaf dark respiration in light (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
F_{NEE}	net ecosystem CO_2 exchange (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
F_{NEP}	net ecosystem production (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
L	plant area index (m^2 m^{-2})
LAI	leaf area index (m^2 m^{-2})
PAI	plant area index (m^2 m^{-2})
Q_{PPFD}	total photosynthetically active radiation (μmol m^{-2} s^{-1})
$Q_{PPFD,dir}$	direct Q_{PPFD} (μmol m^{-2} s^{-1})
$Q_{PPFD,dif}$	diffuse Q_{PPFD} (μmol m^{-2} s^{-1})
R	universal gas constant (8.314 J mol^{-1} K^{-1})
R_{Cd}	canopy leaf respiration in light (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_{Cn}	canopy leaf respiration in darkness (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_{eco}	ecosystem respiration (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_{eco}^{*}	ecosystem respiration corrected for reduction of leaf dark respiration in light (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_{Ld}	leaf respiration in light (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_{Ln}	leaf respiration in darkness (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_{res}	residual (non-leaf) respiration (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
R_s	soil respiration (μmol m^{-2} s^{-1}, g C m^{-2} day^{-1})
$R_{s,Tref}$	soil respiration at reference temperature (μmol m^{-2} s^{-1})
T_{ref}	reference temperature (283.16 K)
T_s	soil temperature at 0.05 m depth (K)

Greek symbols

β	sun's elevation (°)
μ	leaf angle distribution (fraction)
ε	leaf and soil optical properties (fraction)
τ	sunlit/shaded leaf area fraction (fraction)

et al., 2001), whereupon net ecosystem production ($F_{NEP} = -F_{NEE}$) may be calculated by summing up the gap-filled F_{NEE} data over longer (e.g. yearly) intervals. F_{NEP} is related to the gross primary production (F_{GPP}) via

$$F_{NEP} = F_{GPP} - R_{eco}, \tag{1}$$

where R_{eco} represents the total (i.e. above- and belowground) ecosystem respiration. In principle, F_{GPP} may thus be calculated from F_{NEP} provided that R_{eco} is quantified. Estimates of R_{eco} may be derived from a combination of chamber respiration measurements on the various ecosystem components (soil, boles, stems, leaves, etc.) and some logic to scale these measurements to the ecosystem level (Goulden et al., 1996; Lavigne et al., 1997; Law et al., 1999; Granier et al., 2000; Bolstad et al., 2004; Wohlfahrt et al., 2005). As an alternative to this admittedly difficult and laborious task, it has become popular to extrapolate eddy covariance measurements during nighttime, when F_{GPP} is zero, to estimate daytime R_{eco} using functional relationships with some reference temperature and possibly some measure of soil water availability (Granier et al., 2000; Valentini et al., 2000; Barford et al., 2001; Janssens et al., 2001).

The latter approach, however, has a major limitation, since it is well established (Brooks and Farquhar, 1985; Pärnik and Keerberg, 1995; Villar et al., 1995; Atkin et al., 1997, 1998, 2000; Schultz, 2003), that leaf respiration in the light (R_{Ld}[1]) is reduced relative to the darkness (R_{Ln}[1]), resulting in an overestimation of F_{GPP}

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[1] Subscript L stands for leaf and subscripts d and n refer to day and night, respectively.

(Amthor and Baldocchi, 2001). Assessing the consequences of the leaf-level reduction of respiration at the canopy level is complicated by the fact, that the absorbed radiation, and thus the reduction of respiration, varies spatially within the canopy depending on the amount and spatial organisation of phytoelements, the amount and proportion of incident direct and diffuse radiation, and solar elevation (Ross, 1981). In addition, the bias in F_{GPP} depends critically on the ratio of R_{eco} to F_{GPP}, i.e. the ecosystem source/sink strength, as well as the ratio of leaf to residual (soil, bole and stem) respiration, which in turn depends on the amount of leaf area and the plant and soil respiratory intensity (Janssens et al., 2001). These complex interactions, which usually require a model to be mastered, are probably the cause for the lack of a realistic assessment of the overestimation of F_{GPP} using daytime respiration extrapolated from nighttime R_{eco} measurements. The only quantitative estimate of the reduction of F_{GPP} available to date is by Janssens et al. (2001) for the forests investigated within the Euroflux project. These authors assert a 15% reduction, which has been recently adopted for a Pacific Douglas fir forest by Morgenstern et al. (2004), but do not elaborate on how this figure was derived.

Aim of the present paper is to quantify the overestimation of daytime ecosystem respiration, and hence of F_{GPP}, derived from extrapolating nighttime R_{eco} measurements using a model of radiative transfer coupled to a model of the reduction of leaf dark respiration in the light. In a first step, the model will be used to study the sensitivity of the reduction of canopy-level leaf respiration to various influence factors. In a next step the model will then be applied to assess the magnitude of the overestimation of F_{GPP} of a mountain meadow in the Austrian Alps using two years worth of data on F_{NEE}, measured by means of the eddy covariance method, as well as on soil respiration and the seasonal development of the plant area index (PAI). Finally, the implications of the present findings for estimating F_{GPP} of other sites will be discussed.

2. Material and methods

2.1. Site description

Investigations were carried out at a meadow in the vicinity of the village Neustift (47°07′N, 11°19′E) in the Stubai Valley (Austria). The study site is situated at an elevation of 970 m a.s.l. in the middle of the flat valley bottom. The fetch is homogenous up to 300 m to the East and 900 m to the West of the instrument tower, the dominant day and nighttime wind directions, respectively. The average annual temperature is 6.3 °C, average annual precipitation amounts to 850 mm. The snow-free (vegetation) period usually extends from mid March to the end of November, in the study year 2001 from 16th March–23rd November and in 2002 from 8th March–28th November. The meadow is cut between two and three times a year, during 2001 on 20th June, 13th August and 22nd October and 2002 on 11th June, 2nd August and 30th September.

The vegetation has been classified as a Pastinaco-Arrhenatheretum and consists mainly of a few dominant graminoid (Dactylis glomerata, Festuca pratensis, Phleum pratensis Trisetum flavescens) and forb (Ranunculus acris, Taraxaxum officinale, Trifolium repens, Trifolium pratense, Carum carvi) species. The soil has been classified as a Fluvisol (FAO classification) and is approximately 1 m deep. Below a thin (0.001 m) organic layer, an A horizon, with an organic volume fraction of approximately 14%, extends down to 0.02 m, followed by the B horizon, which is best described as a (sandy) loam. Roots reach down to 0.5 m, but 80% of them are concentrated in the upper 0.13 m of the soil.

2.2. Eddy covariance

Net ecosystem CO_2 exchange was measured using the eddy covariance method (Baldocchi et al., 1988; Baldocchi, 2003) using the same instrumentation as and following the procedures of the Euroflux project (Aubinet et al., 2000) since 1st March 2001 and continues as of this writing. Briefly, the three wind components and the speed of sound were measured by a three-dimensional sonic anemometer (R3A, Gill Instruments, Lymington, UK). CO_2 mole fractions were measured by a closed-path infra-red gas analyser (Li-6262, Li-Cor, Lincoln, NE, USA). Air was pumped from the intake, a distance of 0.1 m from the centre of the sensor volume of the sonic anemometer mounted at 3 m above ground, through a 4 m Teflon tube of 0.004 m inner diameter through a filter (Acro 50, Gelman, Ann Arbor, MI, USA) to the infra-red gas analyser at a flow rate 9 l min^{-1} (pump model N035ANE, KNF Neuberger, Freiburg, Germany). The infra-red gas analyser was operated in the absolute mode, flushing the reference cell with dry N_2 from a gas cylinder at 100 ml min^{-1}. Raw voltage signals of the CO_2 mole fraction were output at 5 Hz to the analogue input of the sonic, where they were synchronised with the sonic signals, which were measured at 20 Hz. All raw data were saved to the hard disc of a PC for post-processing using the Edisol software (University of Edinburgh).

Half-hourly mean eddy fluxes were calculated as the covariance between the vertical wind speed and the CO_2 mixing ratio using the post-processing software Edire (University of Edinburgh): means and turbulent departures therefrom were calculated by Reynolds (block) averaging. The tube-induced time delay of the CO_2 signal was determined by optimising the correlation coefficient with the vertical wind velocity (McMillen, 1988). A three-axis co-ordinate rotation was performed aligning the co-ordinate system's vector basis with the mean wind streamlines (Kaimal and Finnigan, 1994). Finally, frequency response corrections were applied to raw eddy fluxes accounting for low-pass (sensor separation, dynamic frequency sensor response, scalar and vector path averaging, frequency response mismatch, and the attenuation of concentration fluctuations down the sampling tube) and high-pass filtering following Moore (1986) and Aubinet et al. (2000). Experimentally derived frequency response correction factors, according to Aubinet et al. (2000, 2001), were used to calibrate and assess the validity of the theoretical low-pass filtering correction method, as detailed in Wohlfahrt et al. (2005). Net ecosystem CO_2 exchange was calculated as the sum of the corrected vertical eddy term and the storage flux, the latter being estimated from the time-rate-of-change of the CO_2 mixing ratio at the reference height, which in a previous comparison with a profiling system was found to be sufficiently accurate. In general, the storage flux ranged between ± 1.0 $\mu\text{mol m}^{-2}\,\text{s}^{-1}$. Negative flux densities represent transport towards the surface, positive values the reverse.

Half-hourly CO_2 flux data were rigorously screened for validity by removal of time periods with (i) the CO_2 signal outside the specified range, (ii) the IRGA internal pressure standard deviation to mean ratio exceeding specified limits (due to calibration or pump malfunction), (iii) the third rotation angle exceeding $\pm 10^\circ$ (McMillen, 1988), and (iv) the deviation from the integral turbulence or stationarity test exceeding 30% (Foken and Wichura, 1996). This procedure, together with data gaps due to instrument malfunction or breakdown, reduced data coverage to 40% during the 24-month study period. In order to derive continuous time series of F_{NEE}, the following gap filling procedure was employed: Gaps less than two hours were filled by linear interpolation. Larger gaps were filled by means of functional relationships between F_{NEE} and temperature and photosynthetically active radiation (Q_{PPFD}) during nighttime and daytime, respectively. To this end, daytime F_{NEE} data during the vegetation period were sorted into weekly blocks and related to incident Q_{PPFD} using a Michaelis-Menten-type function, which was then used to calculate missing F_{NEE} values based on measured Q_{PPFD}. Nighttime data gaps during the vegetation period were filled by an Arrhenius relationship between nighttime F_{NEE} and temperature, after filtering out measurements during periods of low turbulence (friction velocity < 0.1 m s^{-1}; Wohlfahrt et al., 2005). Nighttime R_{eco} calculated this way agreed within 35% with (i) R_{eco} measured using ecosystem chambers, (ii) R_{eco} derived from daytime eddy covariance light response curves, (iii) up-scaled leaf and soil chamber respiration measurements, as well as (iv) ensemble average nighttime eddy covariance measurements (Wohlfahrt et al., 2005). Gaps in the F_{NEE} time series during snow-covered periods were filled using an Arrhenius relationship between F_{NEE} and soil temperature at 0.05 m depth for both day and night.

2.3. Auxiliary data

Incoming total and diffuse photosynthetically active radiation (Q_{PPFD}) was measured by means of a heated quantum sensor (BF2H, Delta-T, Burwell, UK). Data were recorded by a data logger

The plant area index (PAI; m^2 plant area per m^2 ground area) was assessed in a destructive fashion by stratified clipping (Monsi and Saeki, 1953) of square plots of 0.25 m^2 at regular intervals throughout the vegetation periods of 2001 and 2002. Thickness of the harvested layers ranged between 0.05 and 0.1 m, depending on plant area density. Silhouette plant areas were determined by the means of an area meter (LI-3100, Li-Cor, Lincoln, NE, USA). Continuous time series of the PAI were derived by linear interpolation between the harvesting dates.

Soil respiration, R_s (μmol m^{-2} s^{-1}), was measured continuously using a steady-state system described in Cernusca and Decker (1989) and an infra-red gas analyser (CIRAS-Sc, PP-Systems, Hitchin, UK). Soil respiration rates were related to soil temperature measured inside the chamber at 0.05 m depth using an Arrhenius relationship,

$$R_s = R_{s,Tref} \exp\left[\frac{E_a}{RT_{ref}}\left(1 - \frac{T_{ref}}{T_s}\right)\right] \quad (2)$$

where $R_{s,Tref}$ is the soil respiration rate (μmol m^{-2} s^{-1}) at the reference temperature (T_{ref}, 283.16 K), T_s the absolute soil temperature (K), R the universal gas constant (8.314 J mol^{-1} K^{-1}) and E_a an activation energy (J mol^{-1}). $R_{s,Tref}$ and E_a were determined to be 3.34 μmol m^{-2} s^{-1} and 33537 J mol^{-1}, respectively, in good agreement with soil respiration parameters calculated inversely from nighttime eddy covariance measurements (Wohlfahrt et al., 2005). Residuals were independent of soil moisture (at 0.05 m depth) and season, allowing to neglect effects of soil water availability and seasonality on soil respiration parameters. Continuous time series of soil respiration were constructed using Eq. (2) and half-hourly measurements of soil temperature at 0.05 m depth.

2.4. Model

Steady-state reduction of leaf dark respiration in the light, R_{Ld}/R_{Ln}, is modelled using an inverted Michaelis–Menten-type relationship of the form

$$\frac{R_{Ld}}{R_{Ln}} = 1 - \frac{(1-a)Q_{PPFD}}{b + Q_{PPFD}}, \quad (3)$$

where a (dimensionless) represents the minimum value of R_{Ld}/R_{Ln} (i.e. the maximum reduction) and b (μmol m^{-2} s^{-1}) is the Q_{PPFD} where R_{Ld}/R_{Ln} reaches half of the maximum reduction. Given the lack of data specific for the plant species present at the study site and the large variability in the response of R_{Ld}/R_{Ln} evident from Fig. 1, two contrasting scenarios are considered for the purpose of the present study: Scenario I is characterised by a relatively modest maximum reduction of 50% (a = 0.5), which is reached at a relatively low light intensity (b = 2 μmol m^{-2} s^{-1}). Scenario II, in contrast, represents the upper end observed in literature with a maximum reduction of 85% (a = 0.15), which is gradually reached at comparably high light intensities (b = 25 μmol m^{-2} s^{-1}). Since reports on the role of leaf temperature in determining R_{Ld}/R_{Ln} are contradictory (Brooks and Farquhar, 1985; Atkin et al., 1998, 2000), Eq. (3) neglects any interactive effects between Q_{PPFD} and leaf temperature, thereby avoiding any complications arising from the need to solve the leaf energy balance.

Radiative transfer and thus the distribution of Q_{PPFD} within the canopy is computed based on the

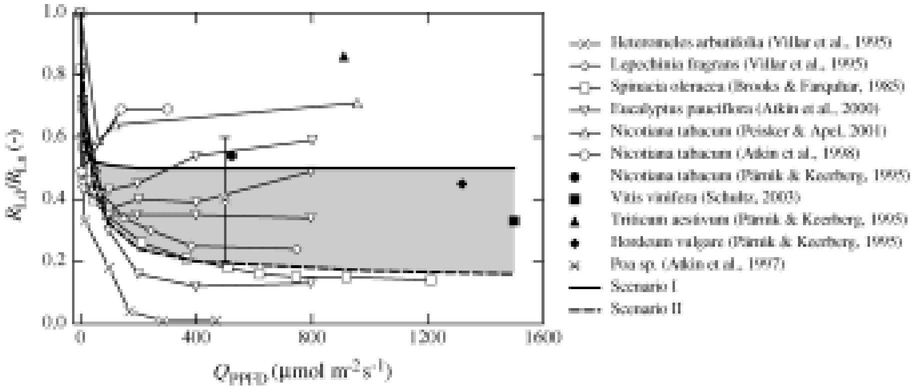

Fig. 1. Reduction of leaf-level respiration in light relative to darkness (R_{Ld}/R_{Ln}) as a function of incident photosynthetically active radiation (Q_{PPFD}) from several published studies and for two scenarios assumed in the context of the present paper. The shaded area refers to the difference between Scenario I and II.

model by Goudriaan (1977) as summarised in Wohlfahrt et al. (2000, 2001a), for which we refer for further details. Briefly, the model treats the canopy as a horizontally homogeneous, plane-parallel turbid medium in which multiple scattering occurs on the elements of turbidity (phytoelements). The canopy is divided into sufficiently small, statistically independent layers, within which self-shading may be considered negligible and phytoelements to be distributed at random and symmetrically with respect to the azimuth. Hemispherical reflection and transmission of radiation are assumed to be lambertian. The model recognises the bi-modal distribution of light within the canopy, shaded leaves receiving diffuse radiation only (sky diffuse and scattered beam radiation), sunlit leaves receiving both beam and diffuse radiation. Penumbral effects were assumed negligible as grassland canopies are short and phytoelements relatively large (Baldocchi, 1993). The model of radiative transfer, which has been successfully validated for mountain grasslands at several occassions (Wohlfahrt et al., 2000, 2001a,b), requires eight input parameters: latitude and longitude of the site, longitude of the closest standard meridian (required to calculate the sun's elevation), the leaf angle distribution (as nine classes of ten degrees each; assumed invariant with canopy height), the PAI and the soil and leaf reflection and leaf transmission cofficients for Q_{PPFD}. The latter three are treated as constant within the context of this paper, with values of 0.15, 0.12 and 0.06, respectively (Wohlfahrt et al., 2001a).

The corrected F_{GPP}, referred to as $F_{GPP}{}^{*}$ in the following, is then calculated by multiplying the canopy leaf respiration in darkness, $R_{Cn} = R_{eco} - R_{res}$, by a correction function, $f = R_{Cd}/R_{Cn}$, i.e.

$$\begin{aligned} F^{*}_{GPP} &= -F_{NEE} + R^{*}_{eco} \\ &= -F_{NEE} + R_{res} + R_{Cn}\, f \\ &\qquad \times (Q_{PPFD,dif}, Q_{PPFD,dir}, \beta, L, \mu, \varepsilon, a, b), \end{aligned} \tag{4}$$

where R_{res} stands for the residual (non-leaf) respiration, in the case of the investigated mountain meadow approximately equivalent to soil respiration, $R_{eco}{}^{*}$ for the corrected total ecosystem respiration, and R_{Cd} for the canopy leaf respiration in light. $Q_{PPFD,dif}$ and $Q_{PPFD,dir}$ refer to the incident diffuse and direct Q_{PPFD}, L to the PAI, β to the sun's elevation, μ to the leaf angle distribution, ε to the leaf and soil optical properties, and a and b to the parameters of Eq. (3) described above. The correction function, $f = R_{Cd}/R_{Cn}$, is calculated as

$$\frac{R_{Cd}}{R_{Cn}} = \frac{1}{\sum_{l=1}^{n} L(l)} \sum_{l=1}^{n} L(l) \sum_{s=1}^{2} \left[\frac{R_{Ld}}{R_{Ln}}(l, s)\, \tau(l, s) \right], \tag{5}$$

where the index l refers to the number of canopy layers (1 to n) and s to sunlit (s = 1) and shaded (s = 2) phytoelement areas, represented by the corresponding aera fraction, τ.

3. Results

For a given leaf-level response of R_{Ld}/R_{Ln} to Q_{PPFD} (i.e. parameters a and b in Eq. (3)), the distribution of radiation within the canopy critically affects the canopy-level reduction of respiration, as shown in Fig. 2. Governed by the leaf-level response (Fig. 1), the canopy-level reduction increases with Q_{PPFD} availability (Fig. 2). Beyond a certain amount of leaf area however, the maximum canopy-level reduction (50 and 85% for Scenario I and II, respectively) is not reached even at the highest light intensities (Figs. 2A and B), since a part of the leaf area in the lower canopy region receives insufficient radiation to attain the maximum level of reduction. The directional composition of incident radiation, i.e. the fraction of beam and diffuse radiation, also plays a critical role, diffuse radiation being distributed more evenly within the canopy than beam radiation, resulting in a comparatively larger reduction (Figs. 2C and D). The leaf angle distribution also affects the canopy-level reduction of leaf respiration, steeper leaves (e.g. erectophile leaf angle distribution; De Wit, 1965) allowing more radiation to penetrate into the lower canopy layers, causing a more complete reduction of respiration (Fig. 2E). The most sensitive parameters, however, are the ones which determine the response of R_{Ld}/R_{Ln} to Q_{PPFD}, i.e. parameters a and b in Eq. (3): The canopy-level response to Q_{PPFD} shown in Fig. 2F mirrors the differences in the maximum leaf-level reduction of respiration, which is 50 and 85% for Scenario I and II, respectively (Fig. 1). Since Scenario II is characterised by a comparably gradual convergence to the max-

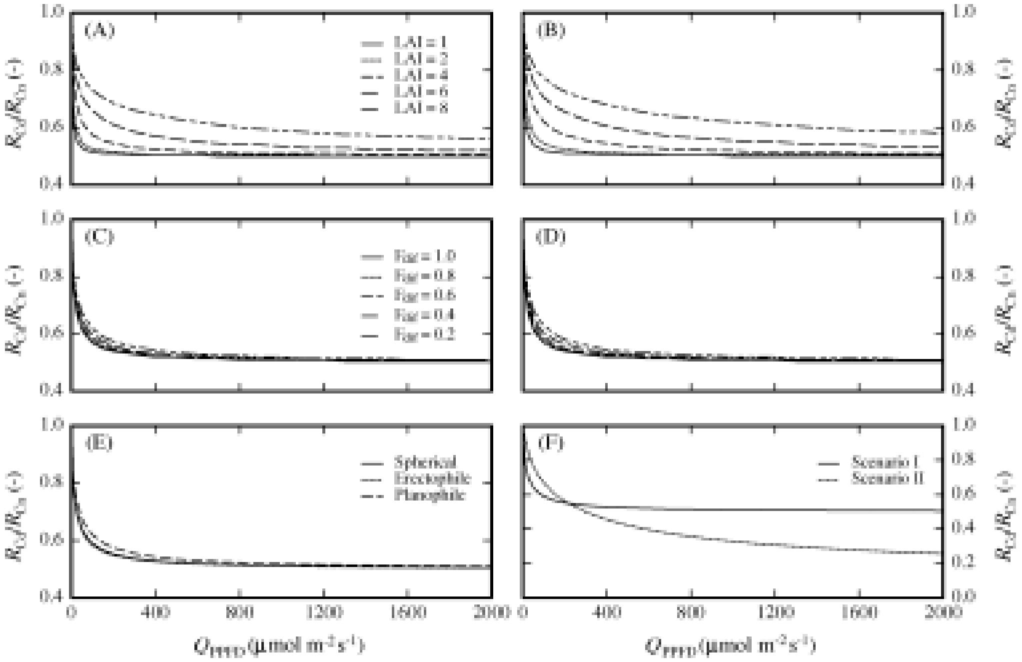

Fig. 2. Reduction of canopy-level respiration in light relative to darkness (R_{Cd}/R_{Cn}) as a function of incident photosynthetically active radiation (Q_{PPFD}) for various leaf area indices (LAI, A and B), fractions of diffuse radiation (F_{dif}, C and D), leaf angle distributions (after De Wit, 1965; E), and Scenario I and II (F). Scenario I is assumed for all simulations except for F a spherical leaf angle distribution is assumed for all simulations except for (E). The LAI is 4 m^{-2} m^{-2} in (C and F). The fraction of diffuse radiation is 0.2 in (A and E and F), 0.8 in B. The sun angle is 65° in A–C and E and F, and 25° in D.

imum reduction level (Fig. 1), the maximum canopy-level reduction, in contrast to Scenario I, is though never reached (Fig. 2F).

Under field conditions, the consequences of the reduction of leaf respiration in light for the estimation of F_{GPP} depend on a complex interplay between the factors which determine daytime canopy respiration per se (as described above) and the ratios of R_{eco} to F_{GPP} and leaf to residual (in our case soil) respiration. Overall, correcting for the reduction of leaf respiration in light reduces F_{GPP} of the investigated mountain meadow by 11% (2001) and 13% (2002) in case of Scenario I, and 13% (2001) and 17% (2002) in case of Scenario II (Table 1). On a daily basis the overestimation of F_{GPP} amounts to up to 3.4 and 4.6 g C m^{-2} day^{-1} for Scenario I and II, respectively (Fig. 3). The overestimation of F_{GPP} is larger during 2002 than 2001 because more carbon is lost during this year (Table 1), and because the ratio of soil to total ecosystem respiration is lower in 2002 (0.55 versus 0.62, Table 1, Fig. 3), while the average daytime canopy-level reduction of respiration in light relative to darkness is similar in both years (Fig. 3). The overriding importance of the ratio between soil and total ecosystem respiration for determining the overestimation of F_{GPP} is illustrated in Fig. 4, which shows that the overestimation of F_{GPP} increases exponentially as the ratio between soil and total ecosystem respiration decreases (i.e. as the fractional contribution of above-ground respiration increases), with the canopy-level reduction of respiration in light exhibiting only a modulating influence. The exponential nature of this relationship is due to an exponential increase of R_{eco} with a decreasing ratio between soil and total ecosystem respiration (data not shown).

A worst case scenario in terms of overestimating F_{GPP} may be derived by assuming canopy leaf respiration to be reduced to the maximum level at any time during daylight hours: this reduces F_{GPP}, as compared to the calculations which account for the effects of within-canopy light climate, by a further 1%

Table 1
Comparison of annual sums of net ecosystem CO_2 exchange (F_{NEE}), soil respiration (R_s), gross primary production (F_{GPP}) and total ecosystem respiration (R_{eco}) with (marked with an asterisk) and without correction for the effects of the reduction of leaf dark respiration in the light

		Without correction		Scenario I				Scenario II		
	F_{NEE}	R_s	F_{GPP}	R_{eco}	F_{GPP}^*	R_{eco}^*	F_{GPP}^*/F_{GPP}	F_{GPP}^*	R_{eco}^*	F_{GPP}^*/F_{GPP}
2001	−6	1081	1757	1751	1568	1562	0.89	1522	1516	0.87
2002	−5	1020	1867	1862	1620	1615	0.87	1545	1539	0.83

Scenario I and II refer to a low and high level of reduction of leaf respiration, respectively (see text and Fig. 1 for details). Units are g C m^{-2} a^{-1}, except for F_{GPP}^*/F_{GPP} which is dimensionless.

during both 2001 and 2002 in case of Scenario I, and by further 7% for Scenario II (data not shown). The larger potential reduction in case of Scenario II is again due to the more asymptotic approach of the maximum leaf-level reduction of respiration (Fig. 1), which prevents the maximum canopy level reduction to be reached (Fig. 2F).

4. Discussion

F_{GPP} is a key parameter in any carbon cycle study, reflecting the amount of autotrophic carbon uptake available for ecosystem growth and respiratory processes (Boysen-Jensen, 1932). Currently, global estimates of F_{GPP} are being produced operationally at

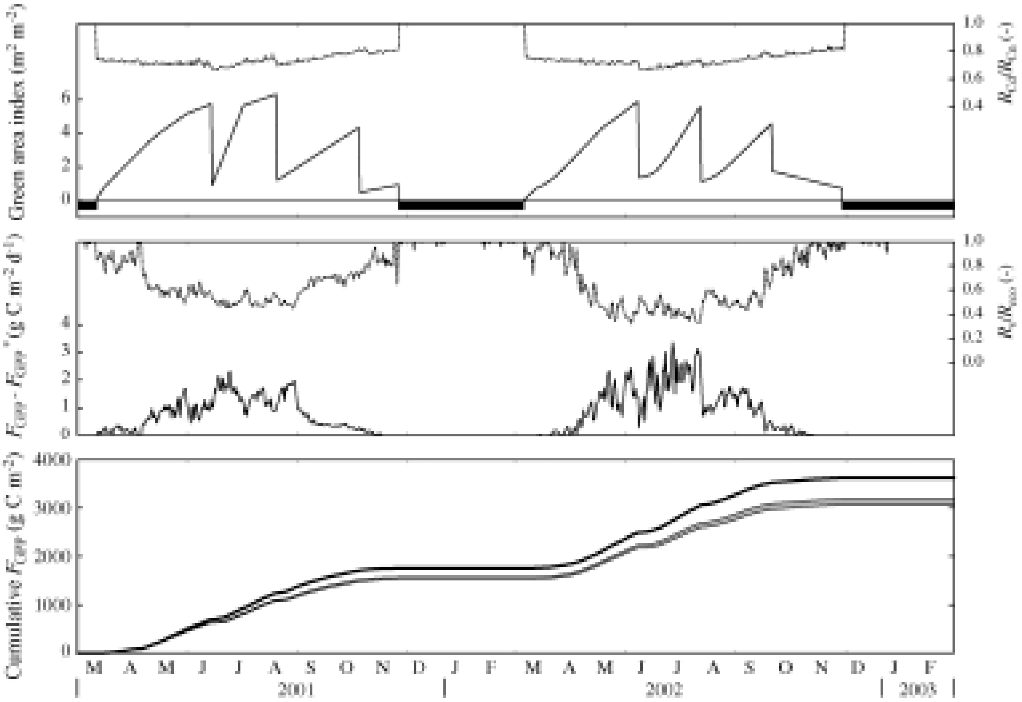

Fig. 3. Time course of the reduction of average daytime canopy-level respiration in light relative to darkness (R_{Cd}/R_{Cn}; dotted line; assuming Scenario I) and the green area index (solid line; upper panel), of the daily averaged ratio between soil and total ecosystem respiration (R_s/R_{eco}; dotted line) and the daily difference between uncorrected (F_{GPP}) and corrected (F_{GPP}^*; assuming Scenario I) gross primary production (solid line; middle panel), and of the cumulative uncorrected (bold line) and corrected F_{GPP} (thin lines; lower panel). Black bars in the upper panel indicate snow cover duration. The shaded area in the lower panel refers to the difference in corrected F_{GPP} between Scenario I and II. A spherical leaf angle distribution is assumed for all simulations, following the findings by Wohlfahrt et al. (2001b).

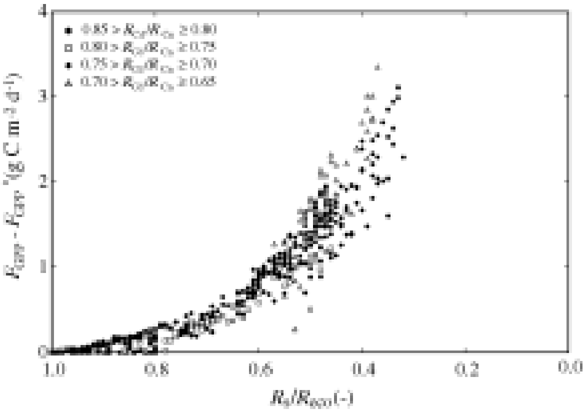

Fig. 4. Overestimation of daily F_{GPP} (F_{GPP}–F_{GPP}*; assuming Scenario I) as a function of the daily ratio between soil and total ecosystem respiration (R_s/R_{eco}). Symbols refer to four classes of average daytime canopy-level reduction of leaf dark respiration in light.

a 1 km spatial resolution based on data of the Moderate Imaging Spectroradiometer (MODIS) sensor on board the NASA TERRA and AQUA satellite platforms (Running et al., 2000). Unfortunately though, ground truth for this product cannot be provided by direct measurements (Larcher, 1995), but must be estimated on the basis of additional information. With the increasing availability of continuous multi-year records of net ecosystem CO_2 exchange (F_{NEE}) through various national and international projects (e.g. Fluxnet), estimates of F_{GPP} are now becoming available for a large number of sites in various biomes of the earth (e.g. Falge et al., 2002). These data not only provide an unprecedented possibility to extend our knowledge about the global variation of F_{GPP}, but also to validate/calibrate the parameters of the F_{GPP} algorithms used with MODIS or other satellite sensors (Turner et al., 2003; Aalto et al., 2004; Xiao et al., 2004a, b). The usual way of inferring F_{GPP} from net ecosystem production ($F_{NEP} = -F_{NEE}$) is by adding total daytime ecosystem respiration, which is modelled using functional relationships between temperature (and possibly some measure of soil water availability) and nighttime total ecosystem respiration (R_{eco}; Valentini et al., 2000; Janssens et al., 2001; Falge et al., 2002). The acknowledged problem with this approach is that leaf respiration in light is reduced relative to darkness (Hoefnagel et al., 1998), resulting in an overestimation of daytime canopy respiration and consequently F_{GPP} (Amthor and Baldocchi, 2001; Janssens et al., 2001; Morgenstern et al., 2004).

One of the largest factors of uncertainty in our assessment of the reduction of daytime canopy respiration are the extent of and the cause for the reduction of leaf respiration in the light. The reduction of leaf respiration in light, according to Atkin et al. (1997), varies between 23 and 84% (see also Fig. 1). Currently it is unclear whether these differences are real and reflective of differences between species, growth conditions, developmental stage, etc. (Atkin et al., 2000), or whether these disparate estimates represent experimental artefacts related to the difficulties in accurately measuring CO_2 evolution in light (Peisker and Apel, 2001). Consequently, it does not come as a surprise that the exact mechanisms responsible for the observed reduction of leaf respiration in light are still subject to debate (Hoefnagel et al., 1998). Some authors advocate the inhibition of some component process of non-photorespiratory CO_2 release by light (e.g. Atkin et al., 1998), whilst newer studies suggest the photosynthetic re-fixation of respired CO_2 to be the dominant process (Pinelli and Loreto, 2003). If the latter is true, i.e. the reduction is to some extent only apparent, the overestimation of F_{GPP} would be less than suggested by the data in Fig. 1. Given these uncertainties we have assumed two scenarios in the present study, a low and a high level of reduction, which yielded between 2 and 4% differing F_{GPP} estimates (Table 1). While this uncertainty is considerably less than the leaf-level difference between the two scenarios (50 and 85% reduction) and also small as compared to the accuracy commonly attributed to eddy covariance measurements (Goulden et al., 1996), it nevertheless represents 15–30% of the calculated overall reduction in F_{GPP} (Table 1). Further studies aiming at revealing the mechanisms responsible for the reduction of leaf dark respiration in light, in particular under field conditions, and thus the causes for the observed differences are thus clearly desirable and will in the future help to reduce uncertainties in daytime canopy respiration estimates.

But there are also other uncertainties associated with the current approach of estimating daytime ecosystem respiration from nighttime measurements. One relates to the fact that daytime temperatures are usually higher than nighttime temperatures and that functional relationships between nighttime temperature and R_{eco}, when applied during daytime, are therefore likely to be at the upper end or even outside the range they have been parameterised for (Janssens et al., 2001). Another source of uncertainty is due to the dependence of respiration on the substrate pool size, reflected for example in comparatively lower nighttime leaf respiration rates following reduced carbon uptakes during the previous day (Whitehead et al., 2004) or a decline in leaf respiration during the course of the night (Larcher, 1995), which is neglected by entirely abiotic-driven respiration algorithms (Dewar et al., 1999; Whitehead et al., 2004). In order to further consolidate the accuracy of F_{GPP} estimates, the consequences of both these issues for estimating daytime canopy respiration need to be addressed in the future.

It also should be stressed that the correct partitioning between leaf and residual (soil, bole and stem) respiration is crucial for estimating the reduction of daytime canopy respiration, no matter whether canopy (leaf) respiration, as in the present paper, is inferred as the residual between R_{eco} and soil, and where applicable bole, respiration, or up-scaled from leaf respiration measurements (Goulden et al., 1996; Lavigne et al., 1997; Law et al., 1999; Granier et al., 2000; Bolstad et al., 2004; Wohlfahrt et al., 2005).

The canopy-level reduction of leaf dark respiration in light is the result of the combined effects of the leaf-level reduction of dark respiration as a function of light intensity and the distribution of radiation within the canopy, which depends on well-known interactions between the directionality of radiation and the amount and spatial organisation of phytoelements (De Wit, 1965; Goudriaan, 1977; Ross, 1981). The more radiation is available to the leaves in the various canopy layers, the closer the canopy will approach the maximum level of reduction. Accordingly, low leaf area indices, steep leaf angles and a high proportion of diffuse radiation promote the reduction of leaf canopy respiration to its maximum level and vice versa (Fig. 2). This has some important practical consequences for estimating daytime canopy respiration: Since the maximum canopy-level reduction is reached at fairly low Q_{PPFD} levels for low leaf area indices (up to 2 $m^2\ m^{-2}$; Fig. 2), daytime canopy respiration of these canopies might, to a first order, be assumed completely reduced, considerably simplifying the correction of F_{GPP}. Conversely, daytime canopy respiration is much more difficult to quantify without a detailed model for ecosystems with large leaf area indices (Fig. 2), which in addition are often characterised by a comparably high ratio of leaf to total ecosystem respiration and thus particularly sensitive to the reduction of canopy respiration in light (Fig. 4).

For the two years of data presented, the modelled reduction of F_{GPP} of the investigated mountain meadow varies between 11–13% and 13–17% for Scenario I and II, respectively (Table 1), which is in good correspondence with the 15% reduction asserted by Janssens et al. (2001) for the forests investigated within the Euroflux project. Given the complex interactions between multiple biotic and abiotic influence factors, though it should be clear that extrapolating results of this grassland to other sites is, at best, difficult. However, we can use these results and the insights from the sensitivity analysis to qualitatively predict overall patterns:

(i) Comparatively large reductions in F_{GPP} may be expected for ecosystems which exhibit year-round carbon assimilation, such as many temperate coniferous, maritime, Mediterranean and tropical forests, as opposed to ecosystems where carbon uptake is seasonally suspended, such as temperate deciduous/boreal forests or temperate/cold grasslands, as in this study (Falge et al., 2002).

(ii) Comparatively large reductions in F_{GPP} may be expected also for ecosystems characterised by high ratios of leaf to total ecosystem respiration, such as temperate/cold grasslands, where leaf respiration often contributes around 50% to R_{eco} (Lohila et al., 2003). Conversely, corrections to F_{GPP} will be quantitatively less important for ecosystems with low ratios between leaf respiration and R_{eco}, such as many forest or savanna ecosystems, where soil respiration makes up 60–80% of R_{eco} and additional 2–20% are attributable to woody respiration (Lavigne et al., 1997; Law et al., 1999; Malhi et al., 1999; Granier et al., 2000; Janssens et al., 2001; Chen et al., 2003; Bolstad et al., 2004).

(iii) Comparatively small reductions in F_{GPP} are to be expected for ecosystems characterised by large leaf area indices, as self-shading prevents these to reaching the maximum level of reduction even at high light intensities, as opposed to canopies with low leaf area indices, where the maximum reduction is reached already at low Q_{PPFD} levels (Fig. 2). However, in comparison with (i) and (ii), effects of canopy structure (including also the spatial distribution of phytoelements) are quantitatively of minor importance given the uncertainties associated with the leaf-level reduction of respiration.

Provided available data permit the partitioning of R_{eco} into canopy leaf and residual respiration, an upper, worst-case estimate of the reduction of F_{GPP} may be derived by assuming canopy respiration to be at a maximum level of reduction of around 80% (i.e. Scenario II) at any time during daylight hours. In particular for canopies characterised by low leaf area indices and leaves which reach the maximum reduction at low light intensities (similar to Scenario I), this estimate will be relatively close to the value one would obtain by means of a more detailed radiative transfer model.

5. Conclusion

The overestimation of gross primary production resulting from neglecting the reduction of leaf respiration in light relative to darkness has been quantified for a mountain meadow in the Austrian Alps using a coupled model of the reduction of leaf dark respiration as a function of light intensity and within-canopy radiative transfer. For the two study years analysed in the present paper, model simulations suggest a reduction of gross primary production by 11–13% and 13–17%, for a low and a high estimate of the maximum leaf-level reduction of dark respiration, respectively. This reduction was shown to be most sensitive to the ratio between gross primary production and total ecosystem respiration, as well as to the ratio between leaf and total ecosystem respiration. The largest factors of uncertainty in this modelling approach are the cause for and the actual level of the reduction of leaf dark respiration in light. Given recent evidence that the observed reduction of leaf dark respiration in light is to some extent only apparent, respired CO_2 being re-fixed within the leaf, this study is likely to provide an upper bound on the reduction of gross primary production.

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References

Aalto, T., Ciais, Ph., Chevillard, A., Moulin, C., 2004. Optimal determination of the parameters controlling biospheric CO_2 fluxes over Europe using eddy covariance fluxes and satellite NDVI measurements. Tellus 56B, 93–104.

Amthor, J.S., Baldocchi, D.D., 2001. Terrestrial higher plant respiration and net primary productivity. In: Roy, J., Saugier, B., Mooney, H.A. (Eds.), Terrestrial Global Productivity. Academic Press, San Diego, pp. 33–59.

Atkin, O.K., Westbeek, M.H.M., Cambridge, M.L., Lambers, H., Pons, T.L., 1997. Leaf respiration in light and darkness. Plant Physiol. 113, 961–965.

Atkin, O.K., Evans, J.R., Siebke, K., 1998. Relationship between the inhibition of leaf respiration by light and enhancement of leaf dark respiration following light treatment. Aust. J. Plant Physiol. 25, 437–443.

Atkin, O.K., Evans, J.R., Ball, M.C., Lambers, H., Pons, T.L., 2000. Leaf respiration of snow gum in the light and dark. Interactions between temperature and irradiance. Plant Physiol. 122, 915–923.

Aubinet, M., Grelle, A., Ibrom, A., Rannik, Ü., Moncrieff, J., Foken, T., Kowalski, A.S., Martin, P.H., Berbigier, P., Bernhofer, Ch., Clement, R., Elbers, J., Granier, A., Grünwarld, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual net carbon and water exchange of forest: the EUROFLUX methodology. Adv. Ecol. Res. 30, 113–175.

Aubinet, M., Chermanne, B., Vandenhaute, M., Longdoz, B., Yernaux, M., Laitat, E., 2001. Long term carbon dioxide exchange above a mixed forest in the Belgian Ardennes. Agric. For. Meteorol. 108, 293–315.

Baldocchi, D.D., 1993. Scaling water vapor and carbon dioxide exchange from leaves to canopy: rules and tools.. In: Ehleringer, J.R., Field, C.B. (Eds.), Scaling Physiological Processes: Leaf to Globe. Academic Press, San Diego, pp. 77–116.

Baldocchi, D.D., 2003. Assessing ecosystem carbon balance: problems and prospects of the eddy covariance technique. Global Change Biol. 9, 478–492.

Baldocchi, D.D., Hicks, B.B., Meyers, T.P., 1988. Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. Ecology 69, 1331–1340.

Baldocchi, D.D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, Ch., Davis, K., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, J.W., Oechel, W., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. Bull. Am. Meteorol. Soc. 82, 2415–2435.

Barford, C.C., Wofsy, S.C., Goulden, M.L., Munger, J.W., Hammond Pyle, E., Urbanski, S.P., Hutyra, L., Saleska, S.R., Fitzjarrald, D., Moore, K., 2001. Factors controlling long and short term sequestration of atmospheric CO_2 in a mid-latitude forest. Science 294, 1688–1691.

Bolstad, P.V., Davis, K.J., Martin, J., Cook, B.D., Wang, W., 2004. Component and whole-system respiration fluxes in northern deciduous forests. Tree Physiol. 24, 493–504.

Boysen-Jensen, P., 1932. Die Stoffproduktion der Pflanzen. Fischer, Jena.

Brooks, A., Farquhar, G.D., 1985. Effect of temperature on the CO_2/O_2 specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in light. Planta 165, 397–406.

Cernusca, A., Decker, P., 1989. Vergleichende Atmungsmessungen an Graslandökosystemen. In: Cernusca, A. (Ed.), Struktur und Funktion von Graslandökosystemen in Nationalpark Hohe Tauern. Universitätsverlag Wagner, Innsbruck, pp. 405–417.

Chen, X., Hutley, L.B., Eamus, D., 2003. Carbon balance of a tropical savanna of northern Australia. Oecologia 137, 405–416.

Dewar, R.C., Medlyn, B.E., McMurtrie, R.E., 1999. Acclimation of the respiration/photosynthesis ratio to temperature: insights from a model. Global Change Biol. 5, 615–622.

De Wit, C.T., 1965. Photosynthesis of leaf canopies. Agricultural Research Reports No. 663, Pudoc, Wageningen, 57 pp.

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, Ch., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jenson, N.-O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B., Meyers, T., Moncrieff, J., Moors, E.J., Munger, W., Pilegaard, K., Rannik, Ü., Rebmann, C., Sukyer, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agric. For. Meteorol. 107, 43–69.

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

Foken, Th., Wichura, B., 1996. Tools for quality assessment of surface-based flux measurements. Agric. For. Meteorol. 78, 83–105.

Goudriaan, J., 1977. Crop Micrometeorology: A Simulation Study. Pudoc, Wageningen, p. 249.

Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and critical evaluation of accuracy. Global Change Biol. 2, 169–182.

Granier, A., Ceschia, E., Damesin, C., Dufrêne, E., Epron, D., Gross, P., Lebaube, S., Le Dantec, V., Le Goff, N., Lemoine, D., Lucot, E., Ottorini, J.M., Pontailler, J.Y., Saugier, B., 2000. The carbon balance of a young Beech forest. Funct. Ecol. 14, 312–325.

Hoefnagel, M.H.N., Atkin, O.K., Wiskich, J.T., 1998. Interdependence between chloroplasts and mitochondria in the light and the dark. Biochim. Biophys. Act. 1366, 235–255.

Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Guomundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, Ch., Jensen, O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Global Change Biol. 7, 269–278.

Kaimal, J.C., Finnigan, J.J., 1994. Atmospheric Boundary Layer Flows. Oxford University Press, Oxford, 289.

Larcher, W., 1995. Physiological Plant Ecology. Springer, New York.

Lavigne, M.B., Ryan, M.G., Anderson, D.E., Baldocchi, D.D., Crill, P.M., Fitzjarrald, D.R., Goulden, M.L., Gower, S.T., Massheder, J.M., McCaughey, J.H., Rayment, M., Striegl, R.G., 1997. Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. J. Geophys. Res. 102/D24, 28977–28985.

Law, B.E., Ryan, M.G., Anthoni, P.M., 1999. Seasonal and annual respiration of a ponderosa pine ecosystem. Global Change Biol. 5, 169–182.

Lohila, A., Aurela, M., Regina, K., Laurila, T., 2003. Soil and total ecosystem respiration in agricultural fields: effect of soil and crop type. Plant Soil 251, 303–317.

Malhi, Y., Baldocchi, D.D., Jarvis, P.G., 1999. The carbon balance of tropical, temperate and boreal forests. Plant Cell Environ. 22, 715–740.

McMillen, R.T., 1988. An eddy correlation system with extended applicability to non-simple terrain. Boundary-Layer Meteorol. 43, 231–245.

Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jpn. J. Bot. 14, 22–52.

Moore, C.J., 1986. Frequency response corrections for eddy correlation systems. Boundary-Layer Meteorol. 37, 17–35.

Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Drewitt, G.B., Cai, T., Nesic, Z., Spittlehouse, D.L., Livingston, N.J., 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. Agric. For. Meteorol. 123, 201–219.

Pärnik, T., Keerberg, O., 1995. Decarboxylation of primary and end products of photosynthesis at different oxygen concentrations. J. Exp. Plant Physiol. 46, 1439–1447.

Peisker, M., Apel, H., 2001. Inhibition by light of CO_2 evolution from dark respiration: comparison of two gas exchange methods. Photosynth. Res. 70, 291–298.

Pinelli, P., Loreto, F., 2003. (CO_2)–C^{12} emission from different metabolic pathways measured in illuminated and darkened C_3 and C_4 leaves at low, atmospheric and elevated CO_2 concentration. J. Exp. Bot. 54, 1761–1769.

Ross, J., 1981. The Radiation Regime and Architecture of Plant Stands. Junk Publishers, The Hague, 391.

Running, S.W., Thornton, P.E., Nemani, R., Glassy, J.M., 2000. Global terrestrial gross and net primary productivity from the Earth observing system. In: Sala, O.E., Jackson, R.B., Mooney, H.A., Howarth, R.W. (Eds.), Methods in Ecosystem Science. Springer, New York, pp. 44–57.

Schultz, H.R., 2003. Extension of a Farquhar model for limitations of leaf photosynthesis induced by light environment, phenology and leaf age in grapevines (Vitis vinifera L. cvv White Riesling and Zinfandel). Funct. Plant Biol. 30, 673–687.

Turner, D.P., Ritts, W.D., Cohen, W.B., Gower, S.T., Zhao, M., Running, S.W., Wofsy, S.C., Urbanski, S., dunn, A.L., Munger, J.W., 2003. Scaling gross primary production (GPP) over boreal and deciduous forest landscapes in support of MODIS GPP product validation. Remote Sens. Environ. 88, 256–270.

Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.-D., Rebman, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404, 861–865.

Villar, R., Held, A.A., Merino, J., 1995. Dark leaf respiration in light and darkness of an evergreen and a deciduous plant species. Plant Physiol. 107, 421–427.

Whitehead, D., Griffin, K.L., Turnbull, M.H., Tissue, D.T., Engel, V.C., Brown, K.J., Schuster, W.S.F., Walcroft, A.S., 2004. Response of total night-time respiration to differences in total daily photosynthesis for leaves in a Quercus rubra L. canopy: implications for modelling canopy CO_2 exchange. Global Change Biol. 10, 925–938.

Wohlfahrt, G., Bahn, M., Tappeiner, U., Cernusca, A., 2000. A model of whole plant gas exchange: model algorithms, parameterisation and validation for five herbaceous species from three mountain grassland sites differing in land use. Ecol. Model. 125, 173–201.

Wohlfahrt, G., Bahn, M., Tappeiner, U., Cernusca, A., 2001a. A multi-component, multi-species model of vegetation-atmosphere CO_2 and energy exchange for mountain grasslands. Agric. For. Meteorol. 106, 261–287.

Wohlfahrt, G., Sapinsky, S., Tappeiner, U., Cernusca, A., 2001b. Estimation of plant area index of grasslands from measurements of canopy radiation profiles. Agric. For. Meteorol. 109, 1–12.

Wohlfahrt, G., Anfang, Ch., Bahn, M., Haslwanter, A., Newesely, Ch., Schmitt, M., Drösler, M., Pfadenhauer, J., Cernusca, A., 2005. Quantifying ecosystem respiration of a meadow using eddy covariance, chambers and modelling. Agric. For. Meteorol. 128, 141–162.

Xiao, X.M., Hollinger, D., Aber, J., Goltz, M., Davidson, E.A., Zhang, Q.Y., Moore, B., 2004a. Satellite-based modeling of gross primary production in an evergreen needleleaf forest. Remote Sens. Environ. 89, 519–534.

Xiao, X.M., Zhang, Q., Braswell, B., Urbanski, S., Boles, S., Wofsy, S., Moore, B. III, Ojima, D., 2004b. Modelling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data. Remote Sens. Environ., in press.