Effect of variations of PAR on CO₂ exchange estimation for Scots pine

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Abstract

A set-up with 161 photosynthetically active radiation (PAR) sensors was used to investigate spatio-temporal variations of irradiance for five horizontal arrays within a Scots pine canopy. The measured PAR was converted to CO₂ exchange using of a shoot-scale photosynthetic response curve and the vertical distribution of the needle area. The net ecosystem exchange was simultaneously measured by the eddy covariance technique. The effect of spatial and temporal averaging of the PAR values and the number of sensors were analysed under different conditions as regards cloudiness and the shading by the foliage. In 1/2 h CO₂ exchange values for the entire canopy, a maximum overestimation of 30% resulted from a spatial averaging over horizontal arrays of 2–5 m and occurred under clear-sky conditions and significant foliage shading. Under partly cloudy conditions, the largest overestimation occurred for a case of little shading and the inaccuracy resulting from 1/2 h temporal averaging exceeded that of spatial averaging. ©2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Photosynthesis depends on various environmental factors, with solar radiation changing most temporally and spatially. The PAR may vary a lot already above canopies, and the foliage itself generates a complicated non-stationary pattern of direct, diffuse and scattered radiation (see e.g., Hutchison and Matt, 1977;

Ross, 1981; Caldwell and Pearcy, 1994). Since the light response curve of photosynthesis is curvilinear, the application of averaged PAR measurements will give biased results for estimates of the exchange of CO₂. The magnitude of the error is dependent both on the shape of the light response (degree of curvature) and the PAR distribution within the period (variation of radiation) (Smolander, 1984). In principle, all information concerning spatio-temporal properties of light is valuable and therefore any averaging should be avoided in the measuring procedure, although in practice this cannot be fully achieved.

The purpose of the study was to estimate the spatio-temporal variations of PAR in relation to canopy CO₂ exchange and, to estimate how the number of measuring points and the spatial and temporal averaging of readings influence the calculations of

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canopy photosynthesis. The measured PAR is converted into CO₂ exchange by means of a photosynthetic response curve and the vertical leaf area index (LAI) distribution. The response curve was parameterised based on shoot cuvette measurements. The formulation of the response curve includes the optimal regulation of stomatal conductance since it has been shown to agree well with observations (e.g., Berninger et al., 1996). Generally the CO₂-fixing capacity of a canopy depends on the nitrogen concentration of foliage, the vertical distribution of photosynthetic capacity and the leaf area and the amount of absorbed PAR. We consider here only the significance of PAR and assume a constant photosynthetic capacity with canopy depth, an assumption which was shown to be satisfactory by Dang et al. (1997). The aim of the paper is not to focus on scaling from shoot to canopy measurements; the results are presented in terms of CO₂ exchange for convenience and because of it being a more practical quantity, and the shoot cuvettes are used only for the parameterisation of photosynthesis, formulae. However, since scaling can have a large impact on predictions of actual canopy photosynthesis, the overall validity of the chosen procedure should be confirmed. This was done by comparing the estimated CO₂ exchange to that measured by the eddy covariance (EC) technique.

The different spatio-temporal averaging procedures for four different radiation conditions, according to the degree of foliage shading and cloud cover, were analysed. Overcast conditions were not analysed since the diffuse light is much more uniform. The 1/2 h canopy CO₂ exchange estimates were calculated using different averaging rules and the results were compared.

2. Materials and experimental methods

2.1. General site description

The data were collected at the SMEAR II field measurement station (Station for Measuring Forest Ecosystem-Atmosphere Relations), which is located in Hyytiälä, southern Finland (61°51'N, 24°17'E, 181 m asl) (see Vesala et al., 1998). The 34-year-old Scots pine (*Pinus sylvestris* L.) dominated stand is homogeneous for about 200 m in all directions from the measurement site, extending to the north for about 1.2 km

(60° sector). Under unstable atmospheric conditions the fetch is adequate in all directions (the upwind distance contributing 80% to the flux in the very unstable case (the Monin–Obukhov length being –10) is about 100 m (Rannik, 1998)). The terrain is subject to modest height variation. The height of the dominant trees in the stand is 13 m, its zero plane displacement is about 6 m and roughness length is 0.8 m. The mean diameter at breast height is 13 cm and the total (all-sided) needle area index is 9. The wood biomass is 47 t per ha and the tree density is 2500 per ha. The nitrogen content per total needle area varies from 0.67 to 1.2 g m⁻² increasing with the height and the nitrogen (mass) concentration is between 1.0 and 1.4%. The dominant stand contains only 1% of species other than Scots pine: downy birch (*Betula pubescens*), grey alder (*Alnus incana*) and aspen (*Populus tremula*). The ground vegetation consists of heather (*Calluna vulgaris*), lingonberry (*Vaccinium vitis-idaea*) and blueberry (*V. myrtillus*). The dominating moss species is *Dicranum undulatum*. The annual mean temperature is 3°C and precipitation is 700 mm. The parent material of the soil is coarse, silty, glacial till and the soil is a haplic podzol.

2.2. PAR measurements and determination of LAI

The PAR measuring system consisted of 168 calibrated photosensors divided into measuring units of 24 sensors controlled by a computer-based central unit. The use of stationary sensors, in contrast to traversing sensors, makes the separation of spatial and temporal information and its conversion into terms of photosynthesis easier (see Baldocchi and Collineau, 1994) although mobile sampling has its own advantages (see e.g., Brown, 1973; Péch, 1986). In this study, the readings of 161 sensors were used, which is less than the over 400 sensors needed to estimate the instantaneous field of direct radiation in a coniferous forest within a standard error of 7 W m⁻² presented by Reifsnyder et al. (1971). The sensors were installed on five cross-booms supported by a 12 m tall pole (Fig. 1). The sensors were silicon diodes with IR filters (VTB 9412B, EG & G Vactec Optoelectronics, St. Louis, MO). The spectral range of sensitivity is 330–720 nm with a maximum at 580 nm. The applicability of silicon diodes for PAR measurements was investigated

Fig. 1. Experimental set-up to measure PAR. It consists of 161 PAR sensors (each of area 1.6 mm^2) installed on five booms at different heights within the canopy but with the same orientation. The lengths of the booms are 2, 4 and 5 m.

by Chartier et al. (1989). Integration over space by the sensor is small since the active cross-sectional measurement area is 1.6 mm^2 . The sensor diameter should be considerably smaller than the characteristic leaf width in order to measure penumbras properly (see e.g. Palmroth et al., 1999). Each diode is installed on a PVC-plastic mount in an attempt to keep the departure of the sensor from the horizontal position below 1° . The units of 24 sensors are capable of registration of the values of incident PAR in 40 ms and the whole set-up in 280 ms. Data analysed in this investigation were collected every 7–12 s. Smolander (1984) reports for Scots pine that the temporal lag autocorrelation coefficient reaches 0.6 after 200 s, decreasing linearly with time lag.

Five booms were attached to the pole (Fig. 1), of which the longest was 5 m (2.5 m for both sides) and two of them were 4 m and 2 m each. The sensors were

placed systematically on both sides of the pole in the way that the ordinary separation between the adjacent sensors was 0.1 m. Norman and Jarvis (1975) showed that the size of most sunflecks in a dense coniferous canopy ($\text{LAI} = 6$) are less than 0.3 m, and according to Smolander (1984) the spatial autocorrelation function of light in Scots pine exhibits zero correlations at separations exceeding 0.2 m (5 min averaging periods). The middle boom did not contain any sensors close to the pole. In addition, 1.3 m above the highest boom (at 12 m) there were four sensors to detect PAR values above the canopy. Here we will examine the data from 16 and 17 July 1997, clear-sky and partly cloudy periods, respectively.

The pole was erected in the middle of the stand and the sensor array was laid out in a northwest-southeast direction. Fig. 2 shows the trees surrounding the set-up within a distance of 10 m. The vertical distribution of

Fig. 2. The distribution of individual trees within the circle of radius 10 m. One of the booms (length of 5 m) is visible between the origin and the tree number 15. The size of the circles represents the relative stem diameter at breast height. The diameters vary from 0.1 to 0.22 m and the heights of the trees from 9.8 to 14.5 m.

the needle mass (area) was determined at the time of the maximum needle mass, in late August 1997. The determination was based on the ideas of the pipe model theory (Shinozaki et al., 1964), i.e. on the relationship between foliage area (mass) and stem cross-sectional area. The regressions (needle mass to branch area, branch area sum to stem area and needle mass to stem area) and the specific needle area were determined from six cut-down trees and were then used for calculating the stand level estimates. In this study, five LAI sections were used, the values of which from bottom were 1.8, 1.4, 1.4, 1.2 and $3.2 \text{ m}^2 \text{ (needles) m}^{-2}$ (ground). The values represent the foliage sections from 0.3 m below and above the booms, the lower part of the lowest section including all the needles below the boom and the upper part of the highest section in-

cluding all the needles above the boom (see Fig. 1). The total needle mass was 6200 kg/ha and $\text{LAI } 9 \text{ m}^2 \text{ (needles) m}^{-2}$ (ground).

2.3. Measurements of CO_2 exchange for shoots and the ecosystem

Shoot-scale gas exchange measurements were carried out by means of several (up to eight) cylindrical trap-type cuvettes, each enclosing a shoot installed through the cuvette base. In this study, the measurements from one cuvette were used to represent the average level of the exchange rate. The measurement is based on the detection of the gas concentration change in the cuvettes after they are alternately closed for 70 s. The gas concentration is recorded every 5 s.

The cuvettes are open for the remaining time, providing an environment close to the ambient one for the shoots. The suitability of the set-up for the determination of exchanged amounts of CO₂ was assessed by Aalto (1998) and Hari et al. (1999a). The cuvettes are made of acrylic-plastic (volume of 3.5 dm³) or a combination of quartz glass and acrylic (1 dm³). Care should be taken in the choice of suitable materials but according to our calibrations acrylic-plastic can be used in the type of measurements described above (Hari et al., 1999a). When a cuvette is closed, the airflow to the gas analyser is compensated by the ambient air (plastic cuvette) or from a pipeline regulated by a mass flow controller (glass cuvette), which keeps the total pressure unchanged. The air in the cuvette is kept well-mixed using a small fan. The air temperature in the cuvettes was measured using a shielded copper-constantan thermocouple. Heated pipelines made of stainless steel or Teflon fed air samples to a gas analyser. Adjacent to the shoot, PAR was measured with a reference sensor (LI-190SA, Licor Inc., Lincoln, NE).

At 23 m, being 10 m above the forest canopy, an eddy covariance (EC) system was installed to measure the net ecosystem CO₂ exchange. The method is based on the average of the instantaneous product of vertical velocity (w) and the gas concentration (c) (see e.g. Kaimal and Finnigan, 1994; Aubinet et al., 1999). The vertical flux is given by

$$F = \overline{w'c'} \quad (1)$$

where the primes denote instantaneous departures from the mean velocity and overbar represents a mean over a given period.

The set-up included an ultrasonic anemometer (Solent 1012R2, Gill Instruments Ltd., Lymington, UK) and a closed-path infrared gas analyser (LI-COR 6262, Licor Inc., Lincoln, NE). The distance of the anemometer from the mast was 3.5 m and a 7 m long heated Teflon (PTFE) tube (inner diameter of 4 mm) is used to sample air from near the anemometer (tube inlet fixed below the sensing head of the anemometer, about 15 cm from the centre) to the gas analyser. The flow rate of 6.3 dm³ min⁻¹ was used to produce turbulent flow. In addition to a membrane filter (1 µm PTFE) at the gas analyzer inlet there was a sintered brass filter at the inlet of the gas sample line to remove particles larger than 50 µm. Pure, dry nitrogen is used

as the reference gas for the gas analyser. The fluctuating components were extracted from the turbulent records by linear detrending (see e.g., Rannik and Vesala, 1999). After an averaging period, the delay time for CO₂ was obtained by determining the maximum unrotated vertical covariance. Finally, the flux was corrected for the imperfect frequency response of the system (damping of fluctuations in sampling line, frequency response of the gas analyser) according to Moore (1986), by using the model co-spectra of atmospheric surface layer turbulence (Kaimal et al., 1972). A more detailed description of the set-up operation is given by Rannik (1998).

3. Theory and modelling

3.1. Description of CO₂ exchange for shoots and the ecosystem

Measurements of the light climate inside a canopy were used in the analysis of photosynthetic productivity and utilized in the comparison of scaled-up shoot-scale CO₂ assimilation to that measured for the ecosystem. Therefore, the relationship between the photosynthesis rate and independent variables, such as light, temperature, humidity and CO₂ that vary in time and space, were required. Photosynthesis is also known to respond differently to a given stimulus as a result of differences in age, physiology, species, and acclimation to the local environment. In this study we focus on the importance of the time-space dynamics of radiation and apply a rectangular hyperbola for the relationship between PAR and gross photosynthesis.

The rate of carbon dioxide exchange (net photosynthesis) (A in µmol m⁻² s⁻¹) is formulated by means of stomatal conductance (g_s in mol m⁻² s⁻¹), the ambient carbon dioxide concentration (C in µmol mol⁻¹), PAR (Q_p in µmol m⁻² s⁻¹) and dark respiration (r in µmol m⁻² s⁻¹). The following expression has been shown to agree well with the detected rates (see e.g., Mäkelä et al., 1996; Berninger et al., 1996; Hari et al., 1999b) offering the required non-linear transform from PAR to photosynthesis:

$$A = \frac{\alpha f(Q_p)(g_s C + r)}{g_s + \alpha f(Q_p)} - r \quad (2)$$

where α is the carboxylation efficiency and the hyperbolic PAR dependence is

$$f(Q_p) = \frac{Q_p}{Q_p + \gamma} \quad (3)$$

and the respiration rate is

$$r = r_0 2^{T_C/10} \quad (4)$$

In Eq. (3) r_0 is an empirical parameter and T_C is the needle temperature in °C. The existence of r in the numerator of the first term in Eq. (2) can be interpreted as the immediate assimilation of the carbon produced by respiration. Its numerical effect is small and hence it is ignored in the subsequent analysis. In the Eqs. (2) and (3) α and γ are also empirical parameters which can be deduced from the measurements of the shoot CO_2 exchange as well as the parameter r_0 . For estimation of the conductance (g_s), the information on the transpiration rate is required. We also include the optimum control of gas exchange according to Mäkelä et al. (1996) in the evaluation of the conductance. The optimum regulation model is based on the assumption that stomata are expected to function so as to maximize the rate of photosynthesis minus transpiration costs. Consequently, the conductance is given by (Mäkelä et al., 1996)

$$g_s = \alpha \left(\sqrt{\frac{C}{1.6\lambda(e_i - e_a)} - 1} \right) f(Q_p) \quad (5)$$

where e_i and e_a are the sub-stomatal and ambient water vapour concentrations ($\mu\text{mol mol}^{-1}$), respectively. The sub-stomatal concentration corresponds to that of a RH of 100% at the needle temperature. λ ($\text{mol}(\text{CO}_2)/\text{mol}(\text{water})$) is an empirical parameter, cost of transpiration, which is a measure of intrinsic water use efficiency. The factor of 1.6 is the ratio of binary diffusivity of water vapour in the air to that of CO_2 . In practice the discriminant may be negative and in these cases it is set to zero. In addition, there is a maximum stomatal conductance ($g_{s,0}$) determined by the morphological properties of stomata (in practice it is estimated from shoot measurements) and if g_s exceeds $g_{s,0}$ it is set to $g_{s,0}$.

Finally, the preceding expressions are applied for the entire canopy using the measured values of the ambient variables. Assuming the canopy is horizontally homogeneous, the mean exchange rate per unit ground area is

$$A = \sum_{k=1}^V \sum_{j=1}^T \sum_{i=1}^H L_k A \frac{(Q_{p,ijk}, C_j, T_{C,j}, e_{a,j})}{HT} \quad (6)$$

where i refers to horizontal measurements and H is the number of sensors, j refers to measurements at different times and T is the number of measurement times during a time interval and k refers to vertical measurements and V is the number of the vertical sections. L_k is the leaf area index at level k . All the quantities except PAR driving the photosynthesis are assumed to be constant throughout the canopy. On unstable days the canopy air is well-mixed and setting the temperature and the gas concentrations to be constant is not a critical assumption in the numerical analysis.

To obtain an estimate of the net ecosystem exchange A_{NEE} the contribution of soil respiration must be included, that is

$$A_{\text{NEE}} = A - r_{s,0} 2^{r_{s,1} T_{s,C}/10} \quad (7)$$

where $r_{s,0}$ and $r_{s,1}$ are empirical parameters and $T_{s,C}$ is the soil temperature in °C. The influence of the soil water content is ignored here.

4. Results

We present experimental results on the radiation environment of the Scots pine canopy and using these data, the differences between various spatial and temporal averaging procedures for canopy net photosynthesis are compared under clear-sky and partly cloudy conditions. Finally, canopy photosynthesis estimates are compared to those obtained by EC measurements.

The calculation of the photosynthetic uptake requires the values of the empirical parameters appearing in the Eqs. (2)–(5). The parameters were evaluated based on the continuous shoot chamber measurements carried out for one of the uppermost shoots and the following values were obtained: $\alpha = 0.035 \text{ mol m}^{-2} \text{ s}^{-1}$ (at 101 kPa and 293 K), $\gamma = 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, $r_0 = 0.068 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and $\lambda = 5.9 \times 10^{-3}$. The stomatal conductance g_s is restricted to be larger than zero and smaller than $0.02 \text{ mol m}^{-2} \text{ s}^{-1}$. The parameter values were found to be same for the 2 days examined in this study. Finally, the parameters $r_{s,0}$ and $r_{s,1}$ describing soil (and understorey) respiration

were estimated to be 0.74 and $1.37 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, based on the night-time EC fluxes (including data with PAR smaller than $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the friction velocity larger than 0.2 m s^{-1}), from which the estimated canopy biomass respiration (based on cuvette measurements) was subtracted. The soil temperature at a depth of 2–5 cm was used for the regression. The separate analysis showed also that the maximum photosynthetic rate and γ varied across the canopy by over 10% and the dark respiration rate by over 30%, all decreasing with the decreasing height (Sari Palmroth, unpublished results). Since the main emphasis of this study is to examine the appearance of spatio-temporal variability of PAR converted into the terms of canopy CO_2 uptake by means of the simple photosynthesis model, but not making rigorous scaling, the vertical variations of the empirical parameters were omitted. The inclusion of the decreasing respiration rate would increase the CO_2 uptake rate but the overall results on the sensitivity of uptake estimates to averaging of PAR would remain practically the same.

In Eq. (6) the gas concentrations and temperature at a height of 8 m were used. In the following analysis, the basic calculation of the carbon dioxide exchange is done using the maximum number of PAR sensors on each level for H and the maximum number of successive readings of PAR within the considered time interval (1/2 h here) for T . V is 5 and LAI values are those given in Section 2.2. In addition, estimates are calculated by applying more inaccurate spatial or temporal averaging. In these cases, the values of PAR, gas concentrations and temperatures are already averaged and H and T are consequently altered.

4.1. Frequency distributions of PAR

Here we present some illustrative frequency histograms on PAR distributions at different heights in the canopy. Fig. 3 shows data obtained by 161 sensors (see Fig. 1) between 11:00–11:30 hours and 14:14–14:44 hours (16 July 1997), when the sky was clear. The fraction of direct light (large PAR values) decreases with decreasing height due to the shading by the foliage. High flux density contributions are from sunflecks and low ones from shade patches of

diffuse and scattered radiation. The peak at low values is considered to represent umbra, which is an area inside the plant canopy in which the sun's disk is fully covered by phytoelements (see e.g., Ross et al., 1998). The moderate values correspond to penumbra, an area in which the sun's disk is partly covered by any phytoelements. The uppermost level does not show any umbra in the morning by contrast to afternoon, indicating the little shading by the foliage between 11:00–11:30 hours and the significant one between 14:14–14:44 hours as a result of the different azimuth angle of the sun (the mean solar elevation angle varied from $46^\circ 30'$ to $48^\circ 13'$ and from $43^\circ 9'$ to $45^\circ 37'$ for the morning and afternoon periods, respectively) and the position of adjacent trees. The data in Fig. 3 were collected over 1/2 h and if similar histograms were plotted using instantaneous measurements they would naturally show a lot of variation between each other. Under partly cloudy conditions the time period of 1/2 h may be too short to obtain representative enough statistical characteristics, but the period could not be lengthened since the conditions just before as well as after the selected period were substantially different.

4.2. Spatial and temporal averaging

The effects of different averaging methods for PAR to estimate the 1/2 h canopy CO_2 exchange are studied at two different shading conditions during clear-sky and partly cloudy periods. The shading was low between 11:00–11:30 hours and significant between 14:14–14:44 hours (see Fig. 3). On 16 July the sky was clear (duration of sunshine was 100%) whereas on 17 July the sky was partly cloudy during the same morning and afternoon 1/2 h periods (duration of sunshine was 57% for both periods). On 16 July the mean value of PAR and its standard deviation were 1520 and $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ (morning) and 1470 and $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ (afternoon) whereas on 17 July they were 1020 and $670 \mu\text{mol m}^{-2} \text{s}^{-1}$ (morning) and 1200 and $430 \mu\text{mol m}^{-2} \text{s}^{-1}$ (afternoon), measured by Li-Cor LI-190 SA above the canopy. As a combination of two classes of shading and cloudiness, we obtain four classes of different irradiation environments concerning the degree of spatio-temporal variation resulting from the foliage

Fig. 3. Frequency of PAR values (normalised to unity) collected during a 1/2 h clear-sky period (16 July 1997) at different heights. (a): Data for 11:00–11:30 hours with little shading by the foliage. (b): Data for 14:14–14:44 hours with significant shading by the foliage.

itself and the cloud cover. These are the factors which give rise to biased photosynthesis estimates when averaging.

Fig. 4 shows the calculated CO_2 exchange for the whole canopy using all the individual readings of PAR sensors as well as employing three different averaging methods. Related to the latter ones, the readings of the PAR sensors are averaged for each array, or the readings are averaged over 2 or 30 min. In the first approach, no temporal averaging is made whereas two others do not include any spatial averaging. Fig. 4 shows also the results from the analysis where two sensors were selected at each of five levels and all the combinations were examined.

For all sensors in use, the greatest overestimation (averaging like that done here never produces underestimation) occurs in the case of spatial averaging

under clear-sky conditions when shading is significant (Case 2, Fig. 4b), being 29% compared to the value without averaging. Spatial averaging tends to give a larger error than 1/2 h averaging in the case of a cloudless sky (Case 4, Fig. 4a and b) whereas under partly cloudy conditions the error for 1/2 h averaging (Case 4, Fig. 4c and d) exceeds that of spatial averaging. In the partly cloudy case, the greatest overestimation occurs for the little shading being 24% (Case 4, Fig. 4c). The relative error resulting from 2 min averaging is less than 5% (all Cases 3). We calculated also the exchange estimates using the PAR readings every 2 min without any averaging. The results were very close to those obtained for 2 min averaging. The variability of the calculated exchange rates is very large when the readings of only 10 sensors were used (all Cases 5–7), being a maximum under shaded clear-sky conditions (Fig. 4b). This is

Fig. 4. The significance of various averaging procedures for the estimates of the 1/2h canopy CO₂ exchange. The four all-sensor cases refer to calculations based on (1) each PAR sensor, (2) horizontal averaging, (3) 2-min averaging and (4) 1/2-h averaging. In the other cases only 10 sensors (two at each level) are used and the largest and smallest exchange rates among the all possible combinations of the sensors are indicated. (a): Clear-sky and little shading by the foliage. (b): Clear-sky and significant shading. (c): Partly cloudy and little shading. (d): Partly cloudy and significant shading.

the same condition for which the spatial averaging produced the greatest error in the all-sensor analysis. We calculated also the largest and smallest exchange rates by increasing the number of the sensors by steps of five (added one to each level). The minimum and maximum values were about 90 and 110% of the all-sensor value when the number of sensors was 140–150.

Above we have examined the entire canopy. This tends to decrease deviations and more variability can be observed if a single level (weighted by corresponding LAI) is examined, especially the lowest ones which do not contribute a lot to the whole canopy photosynthesis but where the variation of PAR is large. Overestimation of more than 30% were found for the lowest level under clear-sky conditions.

4.3. Net ecosystem exchange

The calculated carbon dioxide exchange estimates Eq. (7) are compared with that measured by the EC technique Eq. (1). It should be noted that a significant random error is inherently present in all measured 1/2 h flux values because of the statistical nature of turbulence. For the measurements considered here, the most frequent error is about 10% (Rannik and Vesala, 1999). Fig. 5 presents the comparison, which shows that the procedure adopted in this study to convert PAR readings to photosynthesis rates is without any significant systematic error. Only measurements done during the unstable stratification (the Monin–Obukhov length L being $-10^5 \text{ m} \leq L \leq 0$; see e.g., Seinfeld and Pandis, 1998) or with the large friction velocity ($u_* > 0.25$) are included in the comparison. A more detailed analysis

Fig. 5. Comparison of the 1/2 h net ecosystem exchange values measured on 16 and 17 July 1997, by the eddy covariance technique and calculated using the high-resolution PAR measurements and the photosynthesis response curve parameterised by the shoot-scale gas exchange measurements. Only values measured under unstable atmospheric conditions or high friction velocity have been used.

revealed that the calculated fluxes were consistently larger than the measured between 7:00 and 11:00 hours partly due to heterogeneity of the canopy and the northwest-southeast orientation of the booms so that single trees or gaps create similar shading conditions on the whole measurement system at the same time.

5. Conclusions

A set-up with 161 photosynthetically active radiation (PAR) sensors was used to investigate spatio-temporal variations of PAR on five horizontal arrays within a Scots pine canopy. Four 1/2 h periods for the combinations of clear-sky or partly cloudy and the low or significant foliage shading conditions were analysed as regards the spatial and temporal averaging in the canopy CO₂ exchange calculations. Overall the horizontal spatial averaging over 2–5 m gave larger errors than 1/2 h averaging in the case of cloudless skies whereas under partly cloudy conditions the inaccuracy caused by 1/2 h averaging exceeded that of the spatial one. The maximum relative error corresponding to these cases is 20–30% whereas 2 min averaging generates an inaccuracy of a couple of percent. The

calculated net ecosystem exchange values agreed with those measured by the eddy covariance method.

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