Utilizing a Multipoint Measuring System of Photosynthetically Active Radiation in Photosynthetic Studies within Canopies

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Palva, L., Garam, E., Palmroth, S., Sepponen, R. & Hari, P. 1998. Utilizing a multipoint measuring system of photosynthetically active radiation in photosynthetic studies within canopies. Silva Fennica 32(4): 311–319.

A novel multipoint measuring system of photosynthetically active radiation (PAR) has been constructed and operated within a Scots pine canopy. A regular grid of 800 measuring points has been incorporated into a cuvette to observe the spatial and temporal distribution of PAR incident on the needles of a twig along with simultaneous measurements of the CO_2 exchange in order to determine the dependence of photosynthesis on PAR. It was shown that large errors can result if the photosynthetic rate is estimated using the mean value of PAR instead of the instantaneous values of PAR detected at given points in the region of the needles. The results demonstrate that the obtained regression between the CO_2 exchange rate estimated using the multipoint PAR measuring system and the measured CO_2 exchange rate is as good within a canopy as in unshaded conditions.

Keywords carbon dioxide, instrumentation, measurement, photosynthetically active radiation
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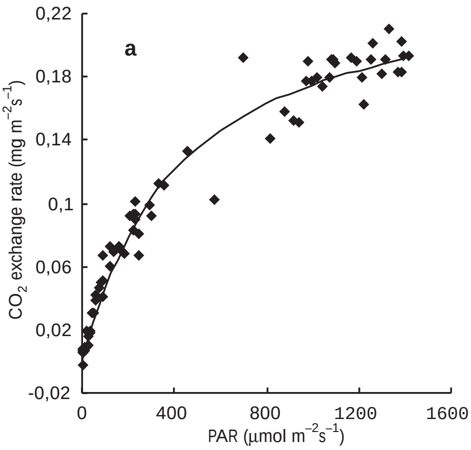
Received 5 March 1998 **Accepted** 5 August 1998

1 Introduction

The dependence of photosynthesis on photosynthetically active radiation (PAR) is needed in the analysis of the canopy photosynthetic production. PAR, which is expressed as the number of photons in the waveband 400–700 nm per unit area unit time (µmol m^{-2} s^{-1}) (McCree 1972, Shibles 1976, Salisbury 1991), is the dominating environmental factor affecting the photosynthesis of Scots pine (Hari et al. 1981, Korpilahti 1988).



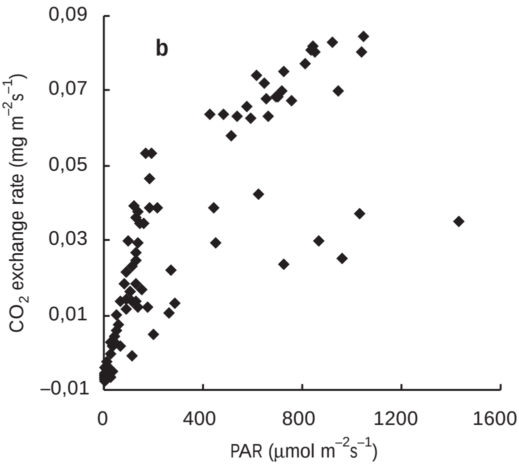


Fig 1. Regression between measured CO_2 exchange rate and PAR in unshaded conditions (a) and within canopy (b). Measurements 5–11 August 1996, Hyytiälä measurement station.

The measurement of the CO_2 concentration in a closed cuvette is used in estimating the efficiency of photosynthesis (Shibles 1976, Field et al. 1989). Since the CO_2 exchange rate is a result of the photosynthesis and respiration, modeling of the two processes is required (Hari et al. 1991). The Michaelis-Menten function f is generally used to describe the nonlinear dependence of the photosynthetic rate on PAR:

$$f(I, a, p_{\max}) = \frac{p_{\max} I}{I + a} \quad (1)$$

where I denotes PAR, Parameter a (µmol m^{-2} s^{-1}) determines the shape of the curvature and $p_{\max}$ (mg m^{-2} s^{-1}) describes the level of maximal photosynthesis. The shape of the dependence can be seen in Fig. 1a. Respiration depends mainly on the temperature. Thus simultaneous measurements of the PAR, temperature and CO_2 exchange are needed in order to analyse the dependence of photosynthesis on PAR.

The spatial variation of direct PAR at a given moment within canopies depends on the amount of shading foliage and occurrence of gaps in the direction of the sun. In plant canopies, PAR availability decreases from the top of the canopy towards the lower layers. Acclimation to different environmental variables has been reported with several plant species. In Scots pine the radiative regime within crowns is reported to influence needle morphology (Kellomäki and Oker-Blom 1981). In general, the maximum photosynthetic rate is suggested to be higher in the sun-acclimated leaves, whereas in the shade-acclimated leaves the response curve saturates earlier, resulting in a higher efficiency at low levels of PAR (e.g. Björkman 1981, Schulze and Hall 1982, Walters et al. 1993). Hence, measurements in the different layers of the canopy are needed in studies of the dependence of photosynthesis on PAR within canopies.

Problems in analyzing the dependence of the CO_2 exchange on PAR within Scots pine canopies are demonstrated with field measurements. PAR is measured using a single sensor (quantum sensor, LI-190SA, LI-COR Ltd, England). The effect of the respiration rate on the variations in the CO_2 exchange rate is reduced by analysing the results in a narrow temperature range. As a non-uniform distribution of PAR is avoided by the placement of the cuvette at the top of a tree and by bending the needles on a plane, a regression between the CO_2 exchange rate and PAR as tight as presented in Fig. 1a is obtained. As the cuvette is placed within the canopy, the regression between the CO_2 exchange rate and PAR is poor, as demonstrated in Fig. 1b. The inaccuracy in PAR measurements is obviously one of the major reasons for the weaker relation.

Due to the nonlinear dependence of photosynthesis on PAR, the spatial and temporal distribution of PAR on the needle area should be observed for studies on the dependence of photosynthesis on PAR (Norman et al. 1971, Sheehy and Chapas 1976, Gutschik et al. 1985, Baldocchi et al. 1986, Myneni et al. 1989, Pearcy 1989). The evaluation of the photosynthetic rate as a function of the mean PAR can result in errors which depend on the shape of the response curve and on the variability of PAR (Hari et al. 1984, Stenberg 1995).

The accuracy in measuring the spatial and temporal distribution of PAR should be so good that the regression between the measurements of CO_2 and PAR is as tight within the canopies as above the canopies. In order to obtain this goal, a multipoint PAR sensor was incorporated into a cuvette for accurate measurement of PAR incident on the needles of a Scots pine twig. The purpose of this study is to 1) demonstrate the benefit of the multipoint PAR measurement over the single point measurement 2) compare the approaches of a) using instantaneous PAR values at given points in the needle region and b) using the mean value of PAR, when determining the dependence of the photosynthetic rate on PAR within a Scots pine canopy.

2 Materials and Methods

2.1 Measurement Object

The object of the measurements was a Scots pine tree in the vicinity of SMEAR II (Station for Measuring Forest Ecosystem Atmospheric Relations) at Hyytiälä Forestry Field Station in southern Finland (61°51'N, 24°17'E, 175 m a.s.l.) (Hari et al. 1990, Vesala et al. 1996). This tree is in a 30-year-old stand with an average tree height of 13 m and leaf area index of 3.9. Three twigs were selected for the measurements: one at the top of the tree, one at the height of 9 m and one at the height of 8.5 m.

2.2 Determination of Dependence of Photosynthetic Rate on PAR

The mean photosynthetic rate of the twig during the measuring periods is estimated using the following expression

$$P_E(a, p_{\max}) = \frac{\sum_{i=1}^{N}\sum_{j=1}^{M} f\left(I\left(x_i, t_j\right), a, p_{\max}\right)}{NM} \quad (2)$$

where f denotes the Michaelis-Menten function (Eq. (1)), $I(x_i,t_j)$ denotes the measured PAR value at point x_i at moment t_j, N the number of selected measuring points, M the number of measurement times (Hari et al. 1983).

The respiration rate of the twig depends on temperature exponentially (Korpilahti 1988). Within canopies, needle temperature is close to the ambient air temperature most of the time due to the small heat capacity of the needles and due to the effects of conveyance by the wind (Gates 1980). In an open cuvette the velocity of the air is approximately 0.5 m s^{-1} which corresponds to the average wind speed within canopies during calm days (Hari et al. 1990). Thus needle temperature is assumed to follow the air temperature closely. Let R_E denote the estimated mean respiration rate of the twig

$$R_E = r_0 e^{cT} \quad (3)$$

where r_0 (mg m^{-2} s^{-1}) and c (°C^{-1}) denote the parameters and T the air temperature inside the cuvette.

The values of Parameters a, $p_{\max}$ and r_0 were estimated from the measurements of the PAR, temperature and CO_2 exchange. The values of Parameters a and $p_{\max}$ were estimated to give the highest R^2 in the regression between the measured and estimated (Eqs (1), (2) and (3)) rates of CO_2 exchange. The value of 0.077 °C^{-1} was applied to Parameter c (Luoma 1997).

2.3 Measurement of CO_2 Exchange

The measurement of the CO_2 exchange is done by monitoring the changes in the CO_2 concentration inside an acrylic cuvette (Hari et al. 1990). The volume of the cuvette is 3.6 litres. The meas-

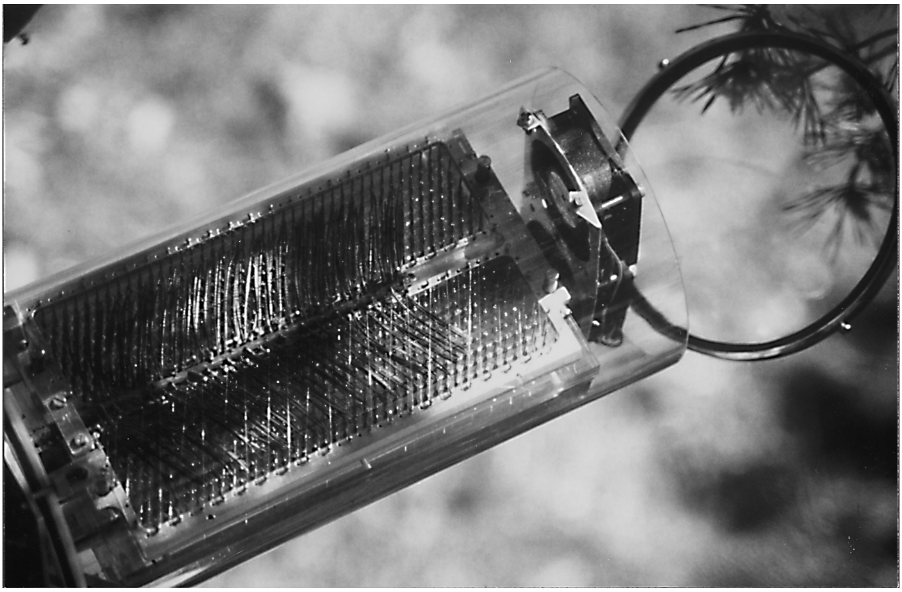


Fig 2. Measuring point grid attached to cuvette.

uring cuvette is trap-type: the cover is mostly open but closed during measurements. A fan is used to improve the ventilation when the cuvette is open and to improve air circulation inside the closed cuvette in order to generate an even CO_2 concentration distribution.

2.4 Multipoint Measuring System of PAR

The measuring system of PAR includes a multichannel sensor head based on fiberoptics, an Intel486-based microcomputer and interface electronics. Two sensor heads have been used: one with 800 and the other with 400 fiber channels. The optical fibers of these channels are joined together to make one bundle for transmitting all the radiation to a charge coupled device (CCD) sensor. Each fiber channel can be monitored with an average number of 10 pixels in the 160 × 160 pixel CCD-matrix (VVL 1070, VLSI Vision Ltd, Scotland) of the 800-channel sensor and 4 pixels in the 2048-pixel CCD-line sensor (ILX511, Sony Corp, Japan) of the 400-channel sensor. The measuring points of both sensor heads are arranged in a regular grid of 11 × 20 cm on a plane (Fig. 2). The diameter of the entrance component of a PAR measuring point, a plastic diffuser, is circa 0.25 mm. The measuring system of 800 points is described in Palva et al. (1998).

The relative spectral responses of the fiberoptic sensors are shown in Fig. 3. The spectral response of the fiberoptic sensor of 800 measuring points was measured using a reference spectrometer (Palva et al. 1998). The relative spectral response of the fiberoptic sensor of 400 measuring points was determined as follows. The relative spectral transmittance of the combination of the diffuser-fiber bundle was measured using a reference spectrometer. The typical relative spectral response of the CCD-sensor and the spectral transmittance of the bandpass filter (10SWF-750, Newport Corp., USA) were given by the manufacturers. The relative spectral response of the fiberoptic sensor was calculated by multiplying the spectral response and the transmittances. The fiberoptic sensors were calibrated in direct, unshaded sunlight using quantum sensor LI-190SA with an LI-190SB millivolt adapter (LI-COR Ltd, England) as a reference.

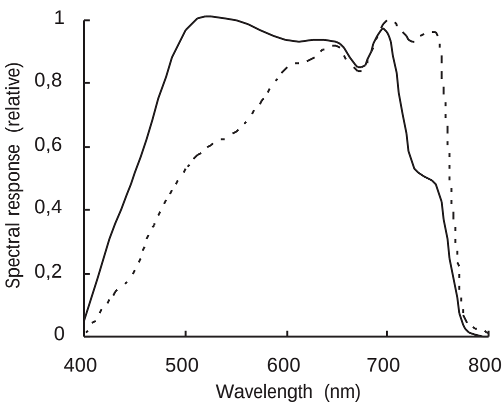


Fig 3. Relative spectral responses of fiberoptic sensors of 400 (solid line) and 800 measuring points (dotted line).

2.5 Measurements and Experimental Arrangements

The PAR incident on the twig at the heights of 8.5 m and 9 m were monitored with the fiber-optic sensors of 800 and 400 measuring points, respectively. At the height of 8.5 m a single sensor (quantum sensor, LI-190SA) was placed beside the twig for comparison. Another sensor of the same type was also used at the top of the tree. The measurements at the top of the tree and at the height of 8.5 m were performed during a sunny week 5–11 August 1996. At the height of 9 m the measurements were performed during a partly sunny and partly cloudy day on 3 September.

The CO_2 exchange measurements of the two cuvettes were performed in turns. During one measurement cycle the selected cuvette was closed for 69 seconds and the CO_2 concentration measurements were made every five seconds. The measurements of the same cuvette were automatically repeated every 25 minutes.

The needles of the twigs were bent in a plane to avoid mutual shading of the needles. The measuring points covering the needle region were used in the analysis, while the remaining points were disregarded. In the 8.5-m measurement, 588 of the 800 points and in the 9-m measurement, 192 of the 400 measuring points were selected for the analysis. Measurements were recorded twice a second during each CO_2 measuring period. The integration time was 3 ms (800 measuring points) and 2 ms (400 measuring points). The mean photosynthetic rate was estimated using Eq. (2) and the mean value of the 2nd, 3rd and 4th ten-second period after the closure of the cuvette was used in the analysis.

Air temperature was measured at one point inside the cuvette to estimate the respiration rate, using Eq. (3). The effect of the temperature on the analysis in the sunny week of August was reduced by selecting a narrow temperature range, 16–22 °C, while the PAR above the canopy ranged between 0 and 1500 µmol m^{-2} s^{-1}. As the measurements were performed at 9 m height on 3 September, the temperature varied between 6 and 18 °C.

The total needle area of the twigs at the heights of 8.5 m and 9 m were determined by measuring the length, thickness and width of each needle after finishing the measuring season. In the top twig the total needle area was estimated by multiplying the mean needle area of the 40 sample needles from the same whorl by the number of needles in the twig.

3 Results

The regression between the measured CO_2 exchange rate and the estimated CO_2 exchange rate at the height of 8.5 m (multipoint sensor, $R^2 = 0.98$; single quantum sensor, $R^2 = 0.86$) and at the top of the tree ($R^2 = 0.98$) are presented in Figs 4a, 4b and 5 respectively. The estimated values of Parameters a and p_{max} in Eq. (2) in the case of the top twig were 430 µmol m^{-2} s^{-1} and 0.25 mg m^{-2} s^{-1} respectively, and in the case of the lower twig 120 µmol m^{-2} s^{-1} and 0.12 mg m^{-2} s^{-1}. The Michaelis-Menten dependence of Eq. (1) according to these parameters is presented in Fig. 6.

In the case of the twig at a height of 9 m the approach of using Eq. (2) was compared to the approach of using Eq. (1) and to the mean value of the 192-point measurements. The regression between the measured and estimated CO_2 exchange rate is shown in Fig. 7 for the case of the first approach. For both cases of estimation R^2 was 0.99. The estimated values of Parameters a

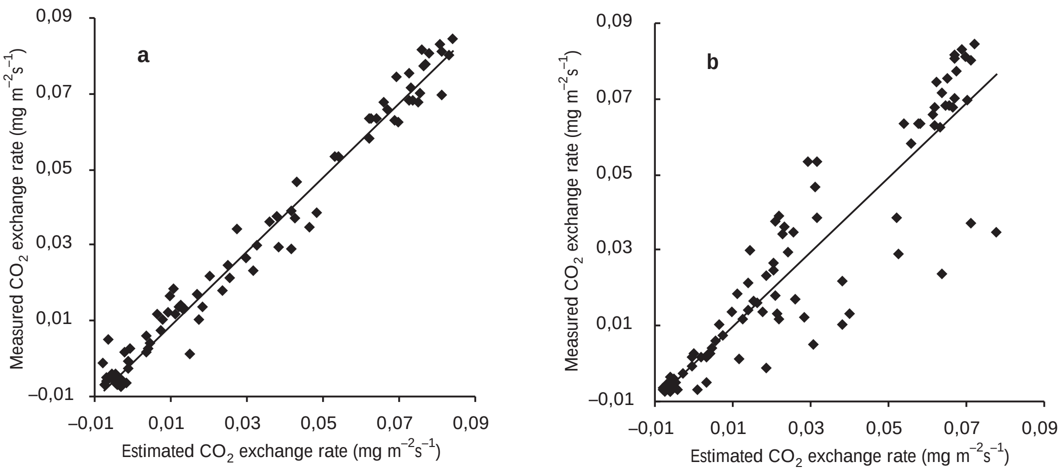


Fig 4. Regression between estimated and measured CO_2 exchange rate in case of (a) multipoint PAR measuring system and Eqs 2 and 3 are used (b) and single quantum sensor (LI-190SA) and Eqs (1) and (3) are used. Measurements at 8.5 m within Scots pine canopy 5–11 August 1996.

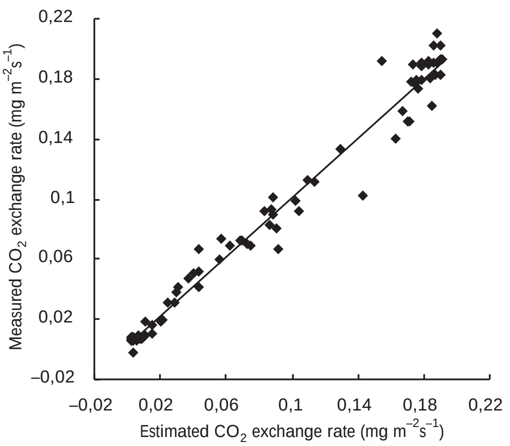


Fig 5. Regression between estimated (Eqs (1) and (3)) and measured CO_2 exchange rate. PAR is measured using single sensor (LI-190SA) at top of a tree. Measurements 5–11 August 1996.

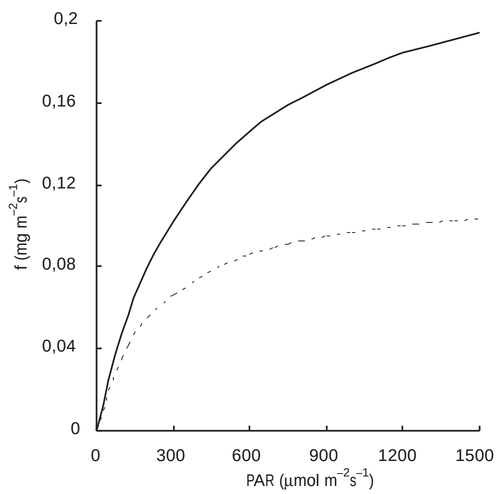


Fig 6. Michaelis-Menten dependence on PAR in case of top twig (solid line) and in case of twig at 8.5 m (dotted line). Measurements 5–11 August 1996.

and p_{max} obtained using the first approach were 340 µmol m^{-2} s^{-1} and 0.17 mg m^{-2} s^{-1} respectively, and for the second approach they were 240 µmol m^{-2} s^{-1} and 0.14 mg m^{-2} s^{-1}. The Michaelis-Menten dependence for the two approaches is presented in Fig. 8.

In order to investigate the reason for the differences between the results of the two approaches, the effect of the PAR variability on the estimation is analysed. The mean value and standard deviation of the 192-point measurements during the 30-second CO_2 measurement periods are presented in Fig. 9. The difference between the estimated photosynthetic rates using a) Eq. (2) and b) using the mean value of the 192-point measurements with the parameter values obtained

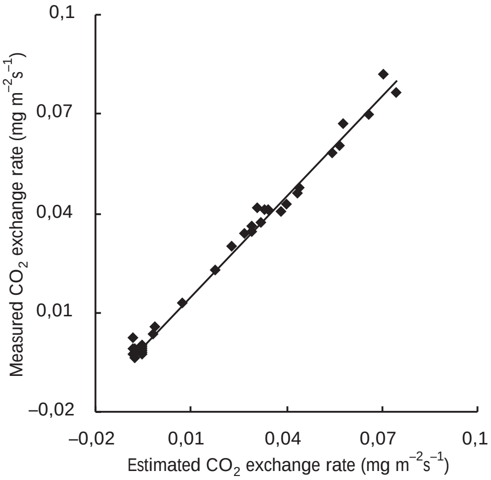


Fig 7. Regression between estimated (Eqs (2) and (3)) and measured CO_2 exchange rate. Measurements at 9 m 3 September 1997.

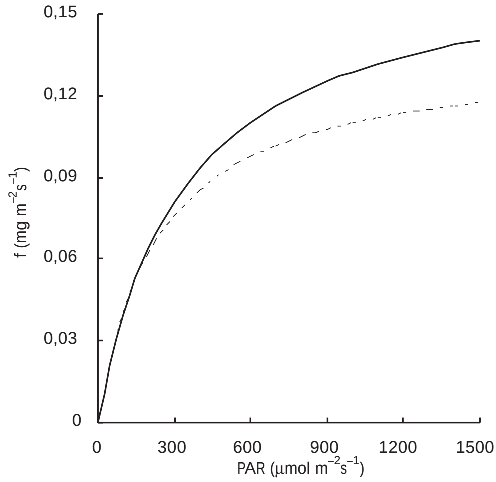


Fig 8. Michaelis-Menten dependence on PAR obtained by using Eq. 2 (solid line) and by using Eq. (1) with mean value of PAR (dotted line). Measurements at 9 m 3 September 1997.

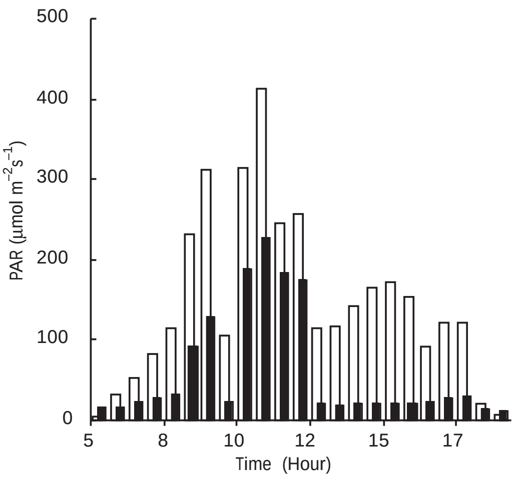


Fig 9. PAR measured during 30-second CO_2 measurement periods (□) mean value (■) standard deviation. Measurements at 9 m 3 September 1997.

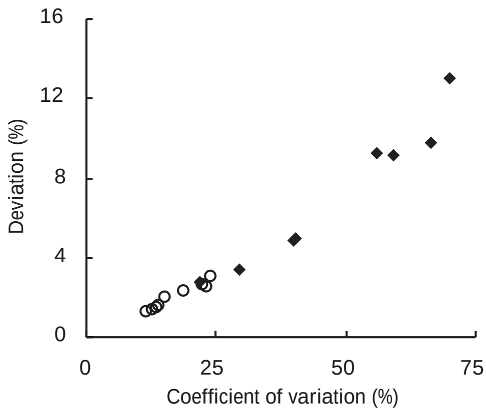


Fig 10. Deviation between estimated photosynthetic rates obtained by using Eq. (2) and by using Eq. (1) with mean value of PAR as a function of CV. Measurements before noon (♦) afternoon (o) at 9 m 3 September 1997.

by Eq. (2), are presented in Fig. 10 as a function of the coefficient of variation (CV; the ratio between the standard deviation and the mean of the 192-point measurements).

4 Discussion

The multipoint measuring system of PAR has been successfully integrated into the field measurement system of photosynthesis. The results in Figs 4a and 5 demonstrate that the regression between the CO_2 exchange rate estimated using the multipoint PAR measuring system and the measured CO_2 exchange rate is as tight within a canopy as in unshaded conditions. In the case of a single sensor used in the 8.5-m measurement, the regression is considerably weaker (Fig. 4b), which hampers parameter estimation.

The estimated value of Parameter *a* (Eq. (2)) of the twig at the height of 8.5 m was approximately three times smaller than that of the top twig. Thus, the detected radiation response curve saturates earlier in the case of the shade acclimated twig as shown in Fig. 6. The detected level of saturation was also lower in the case of the 8.5-m twig: the estimated value of p_{max} (Eq. (2)) was circa one half of that of the top twig. These results are in agreement with the results obtained with other species (eg. Björkman 1981, Walters et al. 1993).

As the photosynthetic rate was estimated as a function of the mean PAR instead of averaging the photosynthetic rate according to Eq. (2), a significant difference in the shape of the Michaelis-Menten type response curve resulted (Fig. 8). The deviations in the estimated values of p_{max} and *a* were as high as 21% and 30 %, respectively. This is due to the PAR variability during the measurements (Fig. 9). The deviations in the estimated photosynthetic rates between the two approaches are clearly higher before noon (Fig. 10) than in the afternoon (more uniform light distribution). Notably, as the PAR variability is higher before noon, the values of the mean PAR and photosynthetic rate are then also higher than is the case of the more diffuse PAR caused by clouds in the afternoon. Thus the influence of the estimation approach on the value of R^2 has been negligible in this case.

The novel system for measuring PAR has clear benefits. The parameter values in the models of the photosynthetic rate can be estimated more reliably within canopies than in the case of the traditional single point sensor. However, this applies to the case where the needles of the shoot are bent on a plane (Fig. 2). The shoot structure would be more complicated for PAR measurements, since the distribution of PAR in a shoot is affected by the mutual shading of the needles and the needle angle in addition to the shading by the canopy.

Since instantaneous values of PAR are detected at given points in the region of the needles, the undesired averaging of PAR can be avoided. As the novel measuring system permits the detection of the size, duration and frequency of temporarily varying sun/shade regions in the region of the needles over longterm periods, the radiation response curve can be related to the PAR environment of the twig. Consequently, other environmental factors affecting the photosynthetic response can then be estimated more accurately.

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