

# Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale

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**Summary** Net CO<sub>2</sub> exchange in a 35-year-old boreal Norway spruce (*Picea abies* (L.) Karst.) forest in northern Sweden was measured at the shoot (NSE), tree (NTE) and ecosystem levels (NEE) by means of shoot cuvettes, whole-tree chambers and the eddy covariance technique, respectively. We compared the dynamics of gross primary production (GPP) at the three levels during the course of a single week. The diurnal dynamics of GPP at each level were estimated by subtracting half-hourly or hourly model-estimated values of total respiration (excluding light-dependent respiration) from net CO<sub>2</sub> exchange. The relationship between temperature and total respiration at each level was derived from nighttime measurements of NSE, NTE and NEE over the course of 1 month. There was a strong linear relationship ( $r^2 = 0.93$ ) between the hourly estimates of GPP at the shoot and tree levels, but the correlation between shoot- and ecosystem-level GPP was weaker ( $r^2 = 0.69$ ). However, the correlation between shoot- and ecosystem-level GPP was improved ( $r^2 = 0.88$ ) if eddy covariance measurements were restricted to periods when friction velocity was  $\geq 0.5 \text{ m s}^{-1}$ . Daily means were less dependent on friction velocity, giving an  $r^2$  value of 0.94 between shoot- and ecosystem-level GPP. The correlation between shoot and tree levels also increased when daily means were compared ( $r^2 = 0.98$ ). Most of the measured variation in carbon exchange rate among the shoot, tree and ecosystem levels was the result of periodic low coupling between vegetation and the atmosphere at the ecosystem level. The results validate the use of measurements at the shoot and tree level for analyzing the contribution of different compartments to net ecosystem CO<sub>2</sub> exchange.

**Keywords:** *cuvette, eddy covariance, gross primary production, photosynthesis, respiration, up-scaling, whole tree chamber.*

## Introduction

Most questions about the long-term impacts of anthropogenic pollutants and climate change on the carbon and water balance of forests concern effects at the ecosystem or landscape scale.

However, most information about processes controlling the structure and function of forest ecosystems is based on relatively short-term studies conducted over limited spatial scales. Up-scaling physiological processes in time and space is a major scientific challenge (cf. Ehleringer and Field 1993). Jarvis (1995) attributed the chief scaling problems to the nonlinearity between processes and variables, and heterogeneity in the properties that determine the processes. Scaling from shoot to tree is greatly affected by both factors, whereas scaling from tree to stand is mainly affected by stand heterogeneity.

Process-based forest models are used to translate experimental results into predictions of tree and forest responses to current and future environmental conditions. Many models have been developed to predict carbon fluxes at the global scale from data at the leaf scale, and to extrapolate from a temporal scale of seconds to centuries (cf. McMurtrie et al. 1992, Ryan et al. 1996, Friend et al. 1998). There is, however, a shortage of long-term data necessary to parameterize and validate these models (cf. Cramer et al. 1999).

Techniques have been developed that allow continuous long-term measurements of CO<sub>2</sub> fluxes of shoots, trees and ecosystems. In this paper we present measurements made at the leaf, tree and landscape scales in a boreal Norway spruce (*Picea abies* (L.) Karst.) forest in northern Sweden. Although measurements were conducted continuously for 4 years, we present only the results obtained during a single week during the second year of the study to illustrate the potential use of such measurements in the parameterization and validation of process-based forest growth models.

## Materials and methods

### Site description

The study was performed in a long-term nutrient optimization experiment at Flakaliden (64°07' N, 19°27' E, 310 m a.s.l.) in northern Sweden that was established in 1986 in a Norway spruce stand planted in 1963. The treatments, which began in 1987, included untreated control plots, irrigation, and two nu-

trient optimization treatments. Stand density was about 2500 trees ha<sup>-1</sup>. For further details about treatments and stand properties see Linder (1995) and Bergh et al. (1999).

Soil at the site is a thin podzolic, sandy, post-glacial till with a mean depth of about 120 cm. The thickness of the humus layer varies from 2 to 6 cm. Mean monthly air temperature at the site varies from -8.7 °C in February to 14.4 °C in July, and snow usually covers the frozen ground from mid-October to mid-May. Mean annual precipitation is about 600 mm and soil water content is normally not limiting for tree growth (Bergh et al. 1999).

In 1996, three systems for continuously measuring gas exchange were installed at the site. An open gas exchange system, with 36 temperature-controlled shoot cuvettes (SC), was installed to monitor gas exchange of individual shoots within the tree crowns. Twelve temperature-controlled, whole-tree chambers (WTC) were built to measure the gas exchange of the aboveground portion of trees and an eddy covariance system (EC) was installed in a neighboring stand to monitor ecosystem CO<sub>2</sub> fluxes. The three systems were operated year-round, beginning in 1997. For the purpose of this study, only data from an untreated control plot obtained during a single week in July 1998, when CO<sub>2</sub> fluxes were high and there were pronounced between-day differences in weather conditions, are presented.

#### *Shoot-level CO<sub>2</sub> exchange (cuvettes)*

Net shoot CO<sub>2</sub> exchange (NSE) was measured on a single 1-year-old shoot on the fifth or sixth whorl from the top of each of three trees enclosed within WTCs. A 55-mm portion of each shoot was enclosed in a temperature-controlled, 0.15-l cuvette fitted with a transparent Perspex (Plexiglas) top. Temperature in the cuvette tracked ambient temperature by means of a Peltier heat exchanger. To prevent water condensation in the cuvette, incoming air was passed through a cooled water trap at a temperature 3 °C below ambient. Air from the shoot cuvette and a parallel reference cuvette was passed through an infrared gas analyzer (CIRAS-1, PP systems, Hitchin Herts, U.K.) running in open mode with 36 parallel channels. Air-flow rates were regulated with mass flow controllers (F-201C, Bronkhorst High Tech, The Netherlands). The CO<sub>2</sub> exchange of each shoot was measured for 30 s at 30-min intervals and expressed on a projected needle area basis. Projected needle area was measured with an LI-3100 leaf area meter (Li-Cor, Inc., Lincoln, NE).

#### *Tree-level CO<sub>2</sub> exchange (whole-tree chambers)*

Net tree CO<sub>2</sub> exchange (NTE) was measured with a WTC (one of 12 installed at the experimental site) enclosing a single tree on a control plot (i.e., without irrigation or fertilization). The chamber was constructed of cylindrical aluminum frames (2.5 m high, 3.25 m diameter) covered with transparent, 0.4-mm PVC film and topped with a 3-m-high conical section. The chamber was adjusted to the height of the enclosed tree that was 4.9 m high in 1998. Fresh air was drawn into the chamber with a fan at about one chamber volume per hour. Air within the chamber was conditioned by circulating it at

12,000 m<sup>3</sup> h<sup>-1</sup> through a heat exchanger. A floor inside the chamber was sealed around the stem of the tree to prevent gas exchange between chamber and soil.

The chamber was ventilated with air containing near ambient CO<sub>2</sub> concentration (360 mmol CO<sub>2</sub> mol<sup>-1</sup>). An infrared CO<sub>2</sub> analyzer (SBA-1, PP Systems) monitored chamber CO<sub>2</sub> concentration, and pure CO<sub>2</sub> was injected into the air circulating within the WTC to maintain the chamber CO<sub>2</sub> concentration within 5% of the ambient concentration.

Chamber and ambient air samples were analyzed (in sequence with samples from other chambers) for CO<sub>2</sub> concentration (WMA-3, PP Systems) and dew point temperature (MP 400, Rotronic, Switzerland). Net CO<sub>2</sub> flux of the tree (NTE) was estimated from the volume and CO<sub>2</sub> concentration of the ambient air supplied to the chamber and the amount of pure CO<sub>2</sub> added to maintain the target CO<sub>2</sub> concentration within the chamber. Each measurement sequence took 45 min to complete.

Chamber temperature was made to track ambient temperature by controlling the volume of air passing through the heat exchanger. The heat exchanger was cooled with glycol at the ambient dew point by passage through a 150-kW refrigeration unit. In case of system breakdown resulting in overheating of the chambers, a powerful fan increased ambient airflow through the chamber. In the event of a power failure, emergency ventilation fans were powered by a back-up gasoline generator.

Estimated total projected needle area of the tree enclosed in the WTC was 9.5 m<sup>2</sup>, based on allometric relationships derived from previous biomass harvests in the stand (Flower-Ellis 1996).

#### *Ecosystem-level CO<sub>2</sub> exchange (eddy covariance)*

Net ecosystem exchange (NEE) was measured with an eddy covariance system placed in a tower located close to the WTC, in a stand established at the same time and with the same nursery stock as the stand where the shoot and whole-tree measurements were made. A detailed description of the design and performance of the system is given in Grelle and Lindroth (1996) and Lindroth et al. (1998).

Briefly, the eddy covariance system consisted of a sonic anemometer (Solent 1012R2, Gill Instruments, Lymington, U.K.), an infrared gas analyzer (LI-6262, Li-Cor, Inc.), a pump, and a control system and software (Grelle 1997a). The gas analyzer and pumps were placed in a weatherproof box mounted in a tower about 6 m away from the sonic anemometer. The sonic anemometer was mounted at the end of a 2-m boom 15 m above ground. Air was drawn through 4-mm inner diameter, high-density polyethylene tubing at a rate of about 10 l min<sup>-1</sup> from an intake located adjacent to the sonic measurement paths. The system displayed long-term stability with a long-term energy balance closure of 98% (Grelle 1997b). Fluxes of CO<sub>2</sub> and friction velocity ( $u_*$ ) were calculated for 30-min periods and expressed per unit of ground area. For the purpose of comparing fluxes in the different systems, a flux into the ecosystem was expressed as a positive value, contrary to the micrometeorological convention.

The stand surrounding the tower had a maximum height of about 12 m and a leaf area index of 2.2, determined with a Li-Cor LAI-2000 plant canopy analyzer calibrated against biomass samples. The distance from the tower to the borders of the homogeneous stand varied from 150 to 250 m. Beyond this area were younger and shorter stands. Based on 9 m as the zero plane displacement height and adopting the 1:30 rule of thumb for forests (Gash 1986), the estimated minimum fetch requirement was 180 m. The fetch conditions were therefore not ideal, but the good energy balance closure indicated that the measurements were representative of the area surrounding the tower.

#### Light and temperature measurements

Photosynthetic photon flux density (PPFD) above the canopy was measured with a cosine-corrected quantum sensor (Li-Cor LI-190SA) on a tower close to the WTCs. The PPFD was measured at each shoot cuvette with a leveled and cosine-corrected quantum sensor (PAR-1(M), PP Systems). Ambient air temperatures were measured adjacent to the shoot cuvettes, and for the WTC, within the surrounding stand. Air temperature above the canopy was measured at the flux tower. Soil temperatures presented are the means of two sensors at 10-cm depth on a nearby plot.

#### Estimation of gross photosynthetic production

Relative respiratory mass and the components contributing to respiration at the shoot, tree, and ecosystem levels differed. Therefore, net exchange of CO<sub>2</sub> at the different scales of measurement were transformed to gross primary production (GPP) for the purpose of comparison, although shoot and tree GPP did not include ground vegetation, which contributed to ecosystem GPP. The GPP was calculated by adding estimated total respiration (excluding light-dependent respiration) to the net exchange (NSE, NTE and NEE) at each level. Total respiration rate ( $R_t$ ) was calculated from the relationship between respiration and temperature:

$$R_t = R_0 \exp^{k_r T}, \quad (1)$$

where  $R_0$  is respiration at 0 °C,  $k_r$  is the temperature coefficient and  $T$  is temperature (°C). The values of  $R_0$  and  $k_r$  were determined by fitting net CO<sub>2</sub> exchange data to Equation 1, measured over a range of temperatures at a PPFD  $\leq 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ . At the ecosystem level, only data measured at  $u_w \geq 0.3 \text{ m s}^{-1}$  were used, and the curve fitting included all data from July that met this criterion. Fluxes were calculated as half-hourly or hourly means. At the shoot and tree levels, fluxes were expressed per unit of projected leaf area, whereas ecosystem fluxes were expressed per unit of ground area.

## Results

Good control of cuvette and WTC temperatures was maintained (Figure 1), except for a few hours one morning when the cooling unit for the WTC failed (cf. Figure 1b). Daily max-

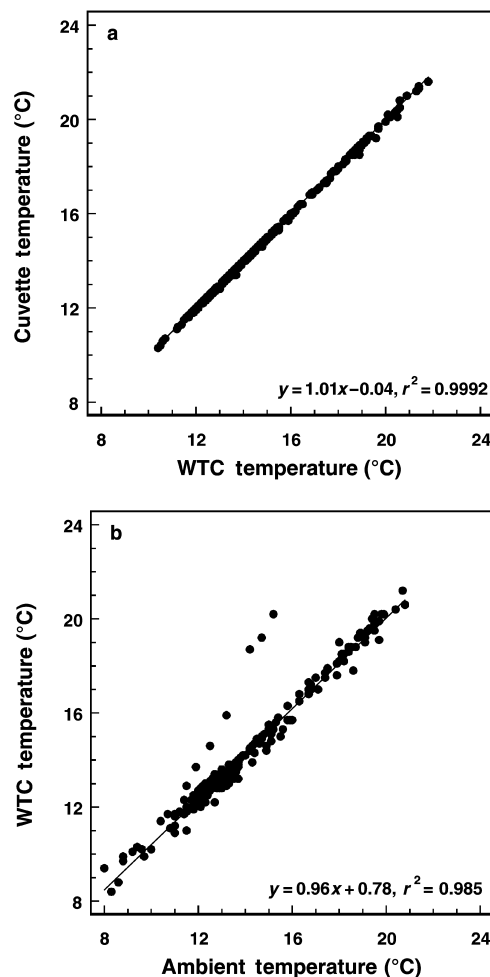


Figure 1. Relationship between inside and outside temperatures during July 24–30, 1998, in (a) a shoot cuvette versus the whole-tree chamber (WTC) temperature, and (b) WTC temperature versus ambient air temperature. The WTC temperature in (a) and (b) was measured with different sensors at different heights. The seven outliers in (b) are the result of a failure of the cooling system for a few hours one morning. The outliers are not included in the regression line.

imum air temperature ranged from 14 to 19 °C (Figure 2). Mean air and soil temperatures during the week were 13.7 and 12.0 °C, respectively. Diurnal fluctuations in air temperature (Figure 2) were strongly related to PPFD (Figure 3a).

Patterns of diurnal variation in net CO<sub>2</sub> exchange of the shoots (NSE), the tree (NTE) and the ecosystem (NEE) were similar and strongly related to incident PPFD above the canopy (Figure 3).

#### Respiration

Cumulative negative fluxes (respiration) at the shoot, tree and ecosystem levels during the measurement period were 3.3, 6.7 and 86% of the positive fluxes (net photosynthesis), respectively. The large differences reflect differences in the ratio of respiratory to photosynthetic mass between levels. Soil fluxes explained most of the ecosystem respiration. The temperature coefficients ( $k_r$ ) for nighttime respiration were estimated to be

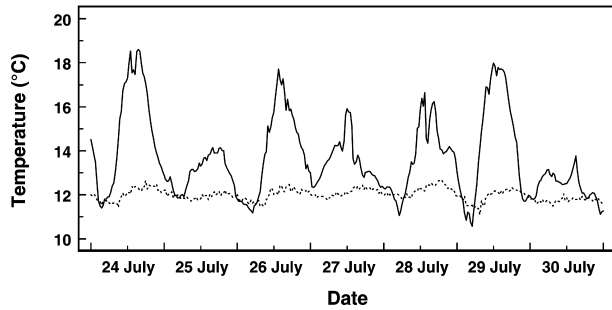


Figure 2. Mean hourly air (—) and soil temperatures (---) during the study period. Air temperature was measured above the canopy, at 15 m, and soil temperature at a depth of 0.1 m.

0.77, 0.75 and 0.16 and estimated respiration at 0 °C ( $R_0$ ), calculated with a model (Equation 1), was 0.13, 0.22 and 1.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , for the shoot, tree and ecosystem, respectively, giving an estimated  $Q_{10}$  of 2.2, 2.1 and 4.9, respectively. These coefficients were used to estimate the diurnal dynamics of total respiration rate ( $R_t$ ) at each level. Measured mean nighttime NSE and NTE (PPFD  $\leq 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were  $-0.32$  and  $-0.56 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ , respectively. Compared with measured values, the model underestimated nighttime  $R_t$  by less than 5% for the shoots and less than 1% for the tree. Measured mean nighttime NEE, at PPFD  $\leq 2 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $u^* \geq 0.3 \text{ m s}^{-1}$ , was  $-7.0 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ , which was about 2% higher than the model-estimated ecosystem respiration during the study period (Figure 4).

#### Gross primary production (GPP)

Mean daily GPP, which was estimated for each level by adding model-estimated  $R_t$  to measured net exchange rate at each level (Figure 3), was 3.0, 3.0 and 7.9  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$  at the shoot, tree and ecosystem levels, respectively. The diurnal variation in estimated ecosystem GPP is shown in Figure 4. To compare the GPP between the different scales of measurement, shoot GPP was plotted against tree GPP based on hourly and daily means, and against ecosystem GPP based on half-hourly and daily means (Figures 5a–d). There was a strong linear correlation between shoot GPP and tree GPP based on hourly ( $r^2 = 0.93$ ) and daily ( $r^2 = 0.98$ ) means, whereas the correlation between estimated shoot and ecosystem GPP was weaker. When all half-hourly mean values were used,  $r^2$  was slightly below 0.7, and excluding night values did not improve the correlation; however, using only data measured at  $u^* \geq 0.5 \text{ m s}^{-1}$  increased  $r^2$  to 0.85–0.90 (Figure 6). The correlation between daily means of shoot GPP and ecosystem GPP was strong ( $r^2 = 0.94$ ), even when data measured at all  $u^*$  were included (Figure 5d). The scaling factor estimated from the slopes of the regression lines in Figure 5 was 0.99 for shoots versus the tree, and 2.5 ( $= 0.99/0.40$ ) for the tree versus the ecosystem.

#### Light response

The response curves of GPP against incident PPFD showed a normal asymptotic form at all levels (Figure 7). Shoot GPP

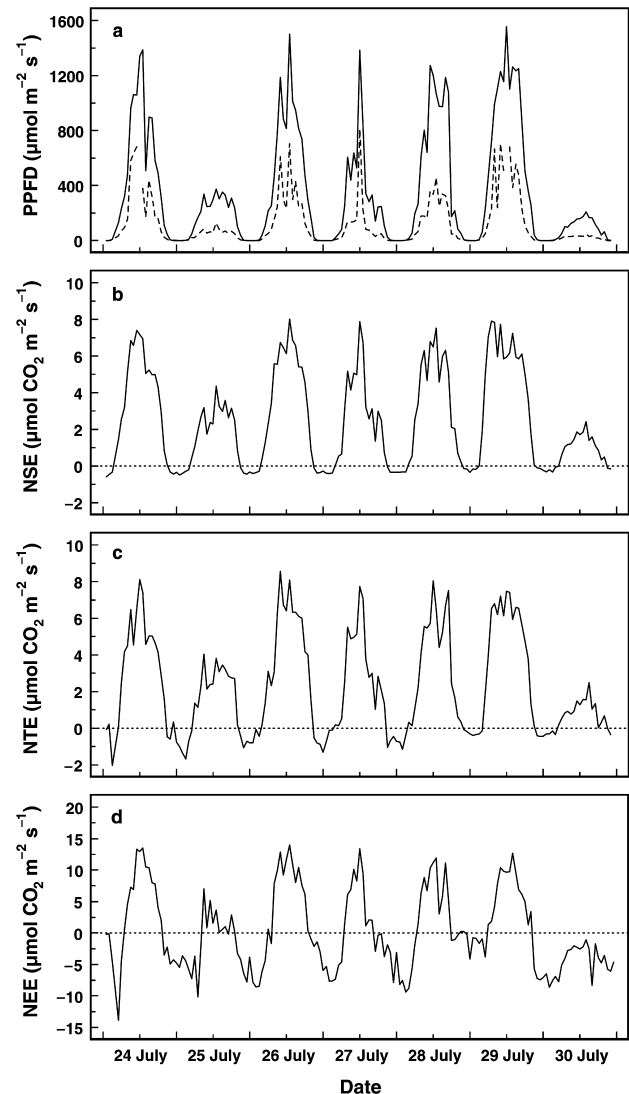


Figure 3. (a) Photosynthetic photon flux density (PPFD) above (—) and within (---) the WTCs (fifth to sixth whorl from the top of the trees); (b) net shoot exchange (NSE); (c) net tree (aboveground) exchange (NTE); and (d) net ecosystem exchange (NEE) for one week in July 1998. The values of NSE and NTE are expressed on a projected needle area basis and NEE on a ground area basis. Shoot exchange (NSE) is the mean of measurements on three 1-year-old shoots on the fifth to sixth whorl on three trees within different WTCs. All values are hourly means.

reached saturation at an incident PPFD (measured next to the shoots) of about  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 7a). Based on an incident PPFD at the shoot between 2 and  $100 \mu\text{mol mol}^{-1}$ , the apparent yield of the shoot was  $0.034 \mu\text{mol mol}^{-1}$ . Plotting the same shoot data against incident PPFD above the canopy, the saturation value was less distinct, but only a small increase in the rate of photosynthesis occurred at PPFDs above  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 7b). Tree and ecosystem GPP did not reach light saturation within the range of observed PPFDs (Figures 7c and 7d). Based on an incident PPFD above the canopy between 2 and  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ , the apparent quan-

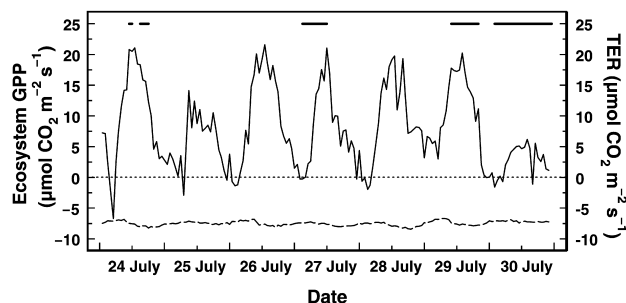


Figure 4. Ecosystem gross primary production (GPP; —) estimated from NEE (cf. Figure 3d) and total ecosystem respiration (TER; - - -). The TER was calculated as:  $TER = 1.1 \exp^{0.167T}$ , where  $T$  is soil temperature at 0.10-m depth (cf. Figure 2). The bold line at the top indicates periods when  $u^*$  was  $\geq 0.5 \text{ m s}^{-1}$ .

tum yield of the shoots (inside WTCs) and the whole tree was  $0.013 \mu\text{mol mol}^{-1}$ . The corresponding value for the ecosystem, after dividing the values by the scaling factor (2.5), was  $0.012 \mu\text{mol mol}^{-1}$ .

## Discussion

The diurnal course of net CO<sub>2</sub> exchange was similar at the shoot (NSE), tree (NTE) and ecosystem (NEE) levels, and the within- and between-day variations were closely related to

variation in incident PPFD (Figure 3). When expressed per unit leaf area, light-saturated photosynthetic rates were similar for the 1-year-old shoots and the whole tree, and are consistent with earlier studies of gas exchange at the same site (Roberntz and Stockfors 1998, Bergh and Linder 1999). The apparent quantum yield of photosynthesis was relatively low, but within the range reported for 1-year-old shoots of Norway spruce (Wallin et al. 1992).

Estimated  $Q_{10}$  of dark respiration for the shoots (2.2) and the tree (2.1) were close to published values for needle (Stockfors and Linder 1998a) and stem respiration (Stockfors and Linder 1998b) in the same stands. Estimated  $Q_{10}$  of ecosystem respiration (4.9) was high compared with that of the plant compartments and other reports on soil CO<sub>2</sub> fluxes (e.g., Rayment and Jarvis 1997, Law et al. 1999a, 1999b), but similar to values reported for a temperate hardwood forest (Davidson et al. 1998) and a northern temperate coniferous forest (Morén and Lindroth 2000). Reasons for the large variation in soil CO<sub>2</sub> fluxes and their sensitivity to temperature include differences in the distribution of respiring biomass in the soil profile in relation to the soil temperature profile and the depth at which soil temperature is monitored (cf. Rayment and Jarvis 2000), the ratio between heterotrophic and autotrophic respiration (Boone et al. 1998), and variation in soil water content (Davidson et al. 1998).

When GPP at the different levels was estimated by adding estimated dark respiration to measured net CO<sub>2</sub> flux, there was

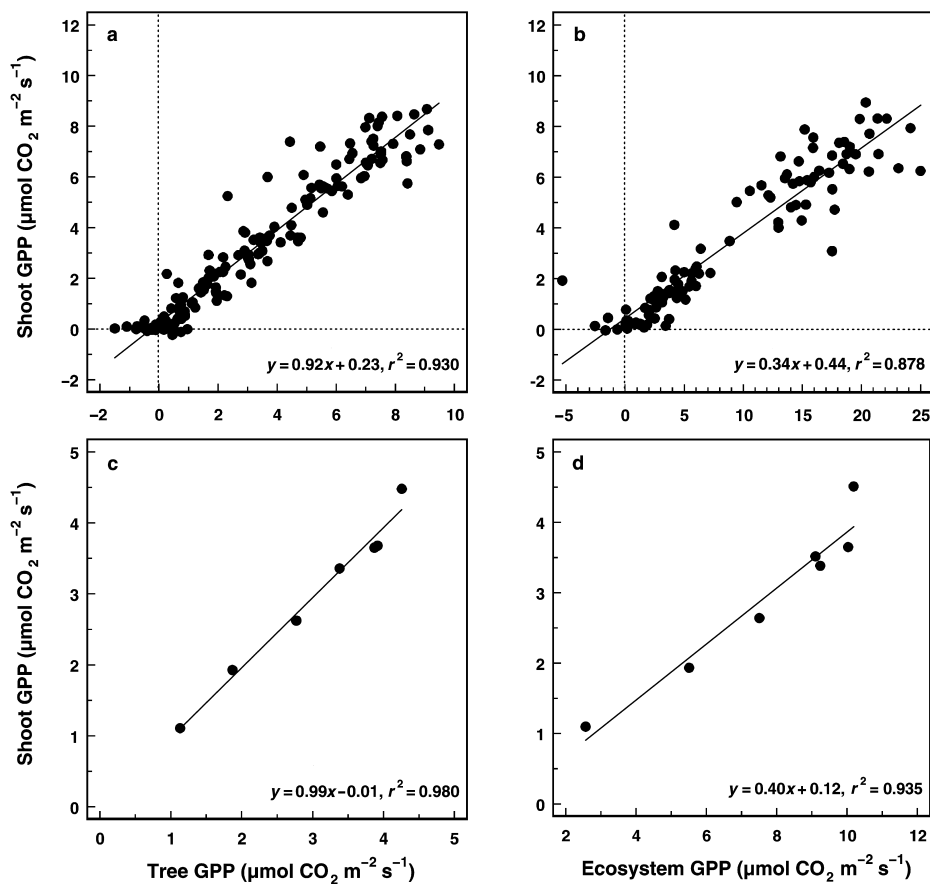


Figure 5. Relationships between gross primary production (GPP) at shoot, tree and ecosystem levels. (a) Hourly means of shoot versus tree; (b) half-hourly means of shoot versus ecosystem ( $u^* \geq 0.5 \text{ m s}^{-1}$ ); (c) daily means of shoot versus tree; and (d) daily means of shoot versus ecosystem (all data).

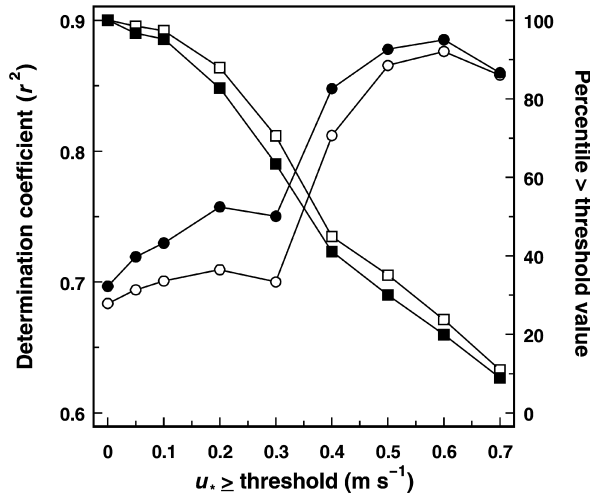


Figure 6. Coefficient of determination ( $\circ$ ,  $\bullet$ ) for the correlation of shoot GPP versus ecosystem GPP at friction velocities ( $u_*$ ) above a certain threshold and the percentile above each threshold ( $\square$ ,  $\blacksquare$ ). Filled symbols include all values and open symbols represent daytime values only ( $\text{PPFD} \geq 2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

a strong linear relationship between hourly ( $r^2 = 0.93$ ) or daily ( $r^2 = 0.98$ ) shoot and tree fluxes (Figures 5a and c). The relationship between shoot and ecosystem GPP was weaker ( $r^2 = 0.69$ ) when all data were considered, but there was a closer relationship ( $r^2 = 0.88$ ) when the comparison was restricted to periods when  $u_*$  was  $> 0.5 \text{ m s}^{-1}$  (Figure 6). Similarly, Lindroth et al. (1998) reported that net ecosystem flux measurements above a boreal coniferous forest were consistent when  $u_*$  was  $> 0.4\text{--}0.5 \text{ m s}^{-1}$ . Thus, the relatively low correlation between shoot and ecosystem GPP when all data were considered indicates low coupling between the atmosphere and the vegetation. The source of the remaining variation may be a slight lack of synchronization as well as differences in response time of the different measuring systems during periods of rapidly changing environmental conditions. At least half of the variation could be attributed to these factors, because the  $r^2$  value increased from 0.88 to 0.94 when the analysis was based on daily instead of half-hourly means (Figures 5b and 5d). Thus, when comparing data measured at different scales, it is important to correct or compensate for periods with low coupling at the stand or ecosystem level as well as for differences in the temporal or spatial resolution of the measurements. To determine the scaling factor between the different levels it appears best to use data integrated over a day or obtained when  $u_* > 0.4\text{--}0.5 \text{ m s}^{-1}$ . However, perfect correlation between the fluxes at the tree and ecosystem levels cannot be expected, because the contribution of the understory to ecosystem flux was not included in the tree measurements.

Differences in the light responses of shoots, trees and canopies may contribute to a lack of consistency between shoots versus tree and shoots versus ecosystem. When mutual shading increases as a result of increasing LAI, the typically asymptotic shape of the photosynthetic light response curve becomes more linear when integrated over the range of inci-

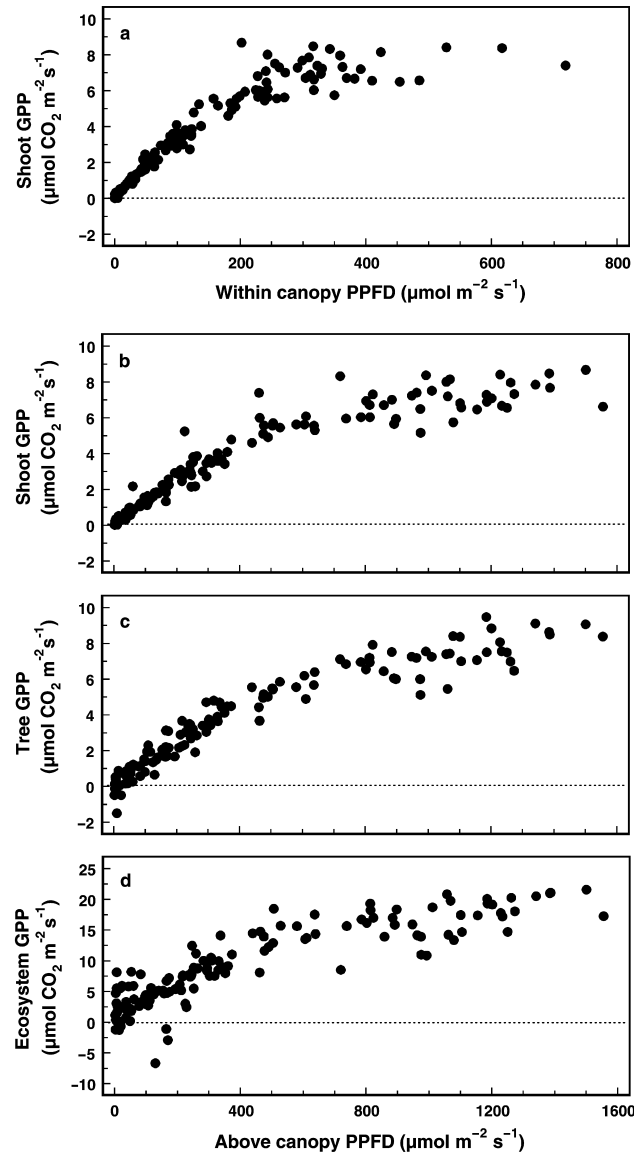


Figure 7. Responses of gross photosynthetic production (GPP) versus incident photosynthetic photon flux density (PPFD) measured at different levels: (a) shoot GPP versus PPFD measured at the shoot; (b) shoot GPP versus PPFD measured above the canopy; (c) tree GPP versus PPFD measured above the canopy; and (d) ecosystem GPP versus PPFD above the canopy.

dent PPFDs (Jarvis and Leverenz 1983). In the present study, LAI was low (2.2), and the light response curves at all levels were asymptotic, although GPP at the tree and ecosystem levels never reached light saturation (Figure 7). This result is supported by a modeling exercise by Pury and Farquhar (1997), where a big-leaf model was compared to a multi-layered and a sun/shade leaf model. The result showed that the simulated assimilation rates were similar at LAIs below 2, but deviated increasingly among models as LAI increased above 2. This implies that the linear relationship between GPP measured at different scales is to be expected only in forests with a low LAI. The low apparent quantum yield of GPP (0.012–

0.013  $\mu\text{mol mol}^{-1}$ ) at all levels, based on incident quantum flux above the canopy, is similar to, but slightly higher than, that observed by Hollinger et al. (1999) who measured canopy flux of CO<sub>2</sub> in a *Larix gmelini* (Rupr.) forest (LAI = 1.4) in eastern Siberia.

The scaling factor of GPP between the shoot and tree levels was close to 1, indicating that the mean value for the three 1-year-old shoots from the fifth whorl used in this study was representative of the average shoot on the tree. Although the shoots were selected to be representative of the crown, good quantitative agreement has to be considered a coincidence. Up-scaling of GPP from shoots to a whole tree, at given ambient conditions, must take into account the variation in light interception and photosynthetic responses within the crown. Because this variation cannot be covered by measurements only, detailed process models such as MAESTRO (Wang and Jarvis 1990) or FOREST (Cescatti 1997a and 1997b) must be used for the up-scaling.

Scaling of GPP from a tree within a stand to the stand is less complex than scaling from a shoot to a tree, because the vertical and horizontal variation in properties controlling light interception and photosynthesis should be similar at the tree and stand levels. Therefore, the main question is how well the selected tree represents all the trees in the stand. In the present example, the similarity in the values of the apparent quantum yield of photosynthesis estimated for the tree and the ecosystem indicates that the selected tree was representative of all trees in the stand. Because tree GPP was expressed on a per unit leaf area basis, the scaling factor from tree to stand is LAI. The LAI of the stand was 2.2 and the estimated factor for the scaling-up of GPP from the tree to the ecosystem was 2.5. The difference of 0.3 between these values may result from ignoring the LAI of the understory. Further measurements are required to determine the contribution of ground vegetation to net CO<sub>2</sub> fluxes in this ecosystem.

In conclusion, measurements at three spatial scales—shoot, tree and ecosystem—gave consistent information on the diurnal course of net CO<sub>2</sub> exchange. The strong qualitative and quantitative relationships between the results obtained with the different methods validate use of such results for parameterization of process-based simulation models operating at different temporal and spatial scales and for separating the compartmental fluxes contributing to the total net ecosystem exchange of CO<sub>2</sub>.

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