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Forest floor CO₂ flux measurements with a dark-light chamber

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Full Screen / Esc

Close

Back

Interactive Discussion



BGD

6, 9301–9329, 2009

Abstract

An automatic closed chamber system for measuring net carbon flux from the forest floor was equipped with both a transparent and an opaque cover. The system was operated in such way that a measurement session with transparent chamber was fol-

- Iowed by a session with dark chamber. This made it possible to estimate besides total daytime respiration and nighttime respiration also the gross assimilation of the vegetation enclosed in the chamber. The chamber was used at two locations, Hyytiäla in Finland and Norunda in Sweden. Results were compared to estimation of gross assimilation by extrapolation of nighttime respiration and the difference between daytime and
- nighttime respiration was analyzed. Estimated gross photosynthesis from the darkening sessions by the chamber resulted in a higher gross photosynthesis then obtained by extrapolation from nighttime respiration for Norunda, but not for Hyytälä. Comparison of obtained gross photosynthesis rates indicated that the forest floor vegetation contributed up to 30% of maximum net ecosystem uptake.

15 **1** Introduction

Together with photosynthesis, the respiration efflux is the most important flux in the net carbon balance of ecosystems. In boreal forests both processes give on annual basis two almost equal sized fluxes of CO₂ to and from the atmosphere, resulting in a relative small net ecosystem exchange (Lindroth et al., 1998). The respiration flux is mainly originating from the soil. Understanding the processes determining those fluxes is crucial for assessment of impacts of climate change. In contrast to the photosynthesis, the mechanistic understanding of the processes behind the soil efflux is still limited, although recent results are showing much progress (e.g. Davidsson and Janssens, 2006).

²⁵ Due to the heterogeneity of the soil it is difficult to obtain a good estimate of the carbon exchange. Different measurements techniques are used, of which several are

BGD

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





based on chambers (Norman et al., 1997; Lankreijer et al., 2003). The so-called closed-dynamic chamber can be considered as one of the most common ways to measure the soil carbon efflux (Strömgren, 2001; Pumpanen et al., 2001). Except for the eddy-covariance technique for measuring the forest floor CO₂ exchange, all other tech niques will need repetition of measurements in space to cover the high heterogeneity of the soil.

- Measurement of the soil carbon flux is mainly difficult due to its heterogeneity, and presence of ground vegetation only increases this heterogeneity. Including the vegetation in the chambers results in a total respiration of both soil and plants under dark
- ¹⁰ conditions, and measurements using transparent chambers will also include the photosynthesis of the ground vegetation. As with above canopy flux measurements, gross photosynthesis of the chamber vegetation can be estimated by, e.g., extrapolating the nighttime respiration to daytime values and take the difference with the measured net flux (Moren and Lindroth, 2000; Valentini et al., 2000; Reichstein et al., 2005). This
- approximation of the gross photosynthesis is based on the assumption that the temperature response of daytime respiration is the same as for the nighttime respiration. This will lead however to an error in the estimate of the gross photosynthetic uptake as respiration in light is suppressed compared to respiration in the dark (Brooks and Farquhar, 1985; Wohlfahrt et al., 2005). It can however be assumed that this error is
 relative small regarding forest floor vegetation and it is not expected be detectable in the chamber measurements. The study by Wohlfahrt et al. (2005) estimated an error

of 11–17% in estimated canopy gross photosynthesis, when using the extrapolation of night-time respiration rates to day-time conditions.

The role of the forest floor vegetation is often neglected when analyzing the ecosystem net carbon exchange from flux towers (Kolari et al., 2006). It is however clear that the photosynthetic capacity of the forest floor vegetation can be significant and is adapted to low light levels. The uptake can be substantial under already low levels of photosynthetic active radiation (Q_{PAR}) (Kolari et al., 2006; Morén and Lindroth, 2000; Widén, 2001), and when the forest canopy is open with a low leaf area index,

BGD

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





the assimilation of the vegetation can be significant part of the total forest assimilation (Morén, 1999; Kolari et al., 2006). During the start of the growing season and in the boreal forest types such as black spruce forests of North America, Scots pine forests in Northern Europe, and larch forests in Siberia, the open canopy makes that the role of the ground vegetation significant (Kolari et al., 2005).

The CO₂ efflux from the soil is the result of CO₂ production in the soil and transport, mainly by diffusion to the soil surface (Fang and Moncrieff, 1999). CO₂ is produced in the soil by autotrophic and heterotrophic respiration, which is strongly temperature dependent as all chemical reactions (Janssens et al., 2003; Davidsson and Janssens, 2006). Autotrophic respiration – or root/mycorrhiza-respiration – is depending also on the assimilate input from the above-ground part of the vegetation and is decreased by water and oxygen limitation, appearing under water-stress and water saturation,

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respectively. Heterotrophic respiration – or decomposition of organic matter – is like autotrophic respiration affected by water and oxygen limitation, and by the "availability"
 or "accessability" of organic matter substrate for the decomposing microbes. Organic substrates can be protected for decomposition by physical and chemical conditions (Davidson and Janssens, 2006).

Root respiration can be a considerable part of the total respiration. Values of 30 to 90% of total respiration are reported in the literature (Bond-Lamberty et al., 2004; Widén and Majdi, 2001; Högberg et al., 2001). It is clear from e.g. girdling experiments

that root/mycorhiza respiration is strongly determined by the assimilation activity of the above vegetation (Högberg et al., 2001). The root respiration/photosynthesis ratios are considered rather stable when averaged over periods of weeks or longer, although variable between different stands of the same species and different between species

²⁵ (Canell and Thornley, 2000). Further it can be considered that the transport of assimilates from tree canopy to the roots is at least delayed by several hours, if not days. Depending on the root density and distribution of roots between the low ground vegetation and trees, a higher daytime root respiration can be found if the roots of the vegetation are responding instantly to photosynthesis input. Another motivation for dif-

BGD

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





ferences in daytime or nighttime CO_2 efflux could be that nighttime concentrations of CO_2 above the forest floor are often higher than during daytime: partly due to stability in the air layers and partly due to daytime photosynthesis of the forest vegetation. Increased concentrations lower the transport of CO_2 along the profile gradient from soil to atmosphere and results in lower net flux during the night.

In this study the well-known type of closed transparent chamber for measuring the carbon exchange from the soil including ground vegetation was equipped with a dark cover. The fully automatic chamber – abbreviated as the Dark-Light (DL) chamber – was used for measuring the net CO_2 exchange of the forest floor. Considering the for-

- ¹⁰ est floor here as the ecosystem, the net flux can be abbreviated as the net ecosystem exchange (F_{NEE}). Kolari et al. (2006) and Kim and Tanaka (2003) performed comparable measurements with dark and light readings, but this developed chamber makes it possible to perform automatic Dark-Light measurements. Assuming that the main environmental conditions, except for light were constant during the 10 minutes period
- of the two readings, the gross assimilation is estimated as the net difference in the flux from the two measurement series. The objectives of this study were i) to test the performance of the new DL-chamber, ii) to estimate the gross primary productivity and respiration of the ground vegetation in two northern European forests and iii) to test if the system can detect differences between daytime and nighttime respiration.

20 **2 Method**

2.1 The measurement principles

The NEE of the forest floor (F_{NEE}) can be expressed as (in μ mol m⁻² s⁻¹):

 $F_{\text{NEE}} = R - A_g$

where $R = R_S + R_R + R_A$.

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber

H. J. M. Lankreijer et al.



(1)

R is the total respiration. R_S is the CO₂ flux from the decomposition of soil organic matter (SOM) or heterotrophic respiration. R_R is the autotrophic respiration from the root/mycorrhiza complex from both the ground vegetation and the trees. R_A is the autotrophic respiration of the above part of the vegetation inside the chamber, including mosses and lichen A is the gross assimilation by mosses lichen and vascular

⁵ ing mosses and lichen. A_g is the gross assimilation by mosses, lichen and vascular plants within the chamber. Photorespiration (R_p) is taken here as part of the gross assimilation. Under dark conditions A_g is zero and the net flux (F_{NEE}) consists only of autotrophic and heterotrophic respiration.

2.2 The chamber system

¹⁰ The net CO₂ flux from the soil and ground vegetation was measured with an automatic closed soil chamber system. The lower end of the chamber consisted of a sharp aluminium frame, which was pressed 1–2 cm into the humus layer and surrounded with a layer of very fine sand. Assuming that leakage from and into the chamber is negligible, the initial rate of change in CO₂ concentration direct after closing the chamber gives the ¹⁵ net flux (F_{NEE}) from the forest floor. The transparent chamber was alternately covered by a dark cover, resulting in measurements of the net flux excluding and including the gross assimilation of the ground vegetation.

The transparent chamber was 0.30 m high, and a ground surface of 0.57 times0.57 m (covering a surface area of 0.32 m^2 , chamber volume of 0.09 m^3), with an automatic lock. The CO₂ concentration was recorded every 10 s while the chamber was closed with a LiCor 6262 IR-gas analyzer (Li-Cor, Inc. Lincoln, USA) in absolute mode. The chamber was closed 4 times an hour in two sessions, each session with a "light" and a "dark" reading within 10 min of each other. Photoactive radiation $(Q_{\text{PAR}}, 400-700 \text{ nm})$ was measured inside the chamber by a JYP 1000 PAR sensor (SDEC, France). The small sensor was placed in the center of the chamber, giving

just an indication of the heterogeneous distributed light in sunspots and shadow within the chamber. Shadowing by the sensor of the vegetation is negligible, but the point measurement is not an optimal representation of the light available in the chamber.





Soil moisture content and soil temperature were measured at a depth of ca. 5 cm in the soil, by a ThetaProbe ML2x soil moisture sensor (Delta-T Devices Ltd, UK) and a P107 temperature probe (Campbell Scientific Ltd., UK), respectively. The standard calibration function supplied by the manufacturer for estimation of soil moisture content ⁵ in percentage was used for organic soils.

During each measurement session the chamber was closed 5 minutes by the transparent lock, open for 5 min to ventilate the chamber and again closed for 5 min with the dark cover. A fan mixed the air inside the chamber. The air sampling system is made such that air is sucked through a perforated tubing, with 10 small holes, ca. 200 cm long which run along the sides of the chamber and then goes to the gas analyzer, through the pump and then sent back to the chamber. The flow rate was ca. 21 min⁻¹.

The net flux (F_{NEE}) of CO₂ is calculated from the rate of change in CO₂ concentration ($\Delta C_s / \Delta t$). The ratio $\Delta C_s / \Delta t$ is estimated as the slope of the linear regression through concentration readings from 50 to 200 s. It can be assumed from the work by

- ¹⁵ Farquhar and co-workers (Farquhar et al., 1980; Sharkey, 1985) that photosynthetic reaction is stopped instantly after darkening of the chamber, but the first 5 readings were excluded from the flux estimation to count for some possible continuation of the CO_2 assimilation. It is further assumed that the suppression of respiration in light (R_{dL}) stops also instantly in the dark and that the period of at least 15 min with open chamber
- ²⁰ between the last dark reading and the next light reading was sufficient to suppress the respiration again at closure of the transparent lock.

2.3 Measurements sites

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Measurements were performed at the Hyytiäla forest research site in Finland between 2 July and 16 August 2005. The system was used thereafter at the Norunda forest site in Sweden. In Norunda the chamber was placed in one location in 2005 where the measurements took place between 19 September and 15 November, resulting in 4048 observations. In 2006 the chamber was placed at a new location in the same stand. The measurements took place between 31 May and 9 October, but due to technical 6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





malfunctioning, the number of observation was limited to 2515.

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The Hyytiäla forest research site is a ca. 45 years old pine stand, located in southern Finland (61°51′ N, 24°17′ E, 180 m a.s.l.) at the SMEAR II field station (Station for Measuring Forest Ecosystem-Atmosphere Relations, Vesala et al., 1998). The site is an

- ⁵ almost exclusively Scots pine (*Pinus sylvestris* L.) stand, sawn in 1962. In the winter of 2002, the majority of the stand was thinned to stem density of 800–1100 trees ha⁻¹. The all-sided LAI of the canopy was estimated to about 6 m² m⁻² (Vesala et al., 2005). The dominant species in the field layer were blueberry (*Vaccinium myrtillus* L.) and lingonberry (*Vaccinium vitis-idaea* L.). The soil is a Haplic podzol on glacial till (Kolari et al., 2006) with a mean depth of the organic layer of 5.4 cm and density 0.13 g cm⁻³. A
- ¹⁰ al., 2006) with a mean depth of the organic layer of 5.4 cm and density 0.13 g cm⁻². A more detailed site description is given by Ilvesniemi and Pumpanen (1997) and Vesala et al. (1998).

During the measurement period in Hyytiälä, measurements were made in 3 locations with different distribution of mosses and dwarf shrubs. Measurements on plot 1 resulted in 558 observations (6 days), for plot 2 in 582 observations (9 days), and for plot 3 in 498 flux estimates (8 days).

The Norunda forest site $(60^{\circ}50' \text{ N}, 17^{\circ}29' \text{ E}, \text{ alt. } 45 \text{ m a.s.l.})$ is a mixed coniferous forest, situated ca. 30 km north of Uppsala, Sweden. The forest around the main observation tower consists of several stands with ages between 70 to 120 years old. The forest consists mainly of Norway spruce (*Picea abies* (L.) Karst.; 66% of the stand

- basal area) and Scots pine (*Pinus sylvestris* L.; 33%). The stand at the experimental plot was about 110 year old and was dominated by Scots Pine (88%), while Norway spruce and deciduous trees were only 10% and 2%, respectively. Dominant stand height was ca. 28 m. The canopy projected leaf area index (LAI) was estimated to 4.7.
- The field and bottom layer consisted mainly of dwarf shrubs and mosses, where *Thuid-ium tamariscinum* and *Hylocomium splendens* were the two most frequent mosses. Major part of the forest floor was covered with varying proportions of moss, *Vaccinium myrtillus* (L.), and bracken (Pteridium aquilinum L.). The soil is a deep, boulder-rich sandy glacial till. A general description of the site is found in Lundin et al. (1999).

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





2.4 Analysis of data

A function proposed by Lloyd and Taylor (1994) was fitted to the temperature response of the net efflux under dark conditions (Eq. 2):

 $F_{\sf NEE} = R_{10} \cdot e^{E_0(\frac{1}{56.02} - \frac{1}{T_s + 46.02})}$

- ⁵ with R_{10} as the respiration rate at 10°C, E_0 an empirical parameter (K) and T_s the actual soil temperature (°C). In order to obtain a better fit with the measured data it was chosen to fit the function for the extra parameter E_0 and not to use the constant value of 308.02 K as proposed by the authors.
- Gross assimilation (A_g) was estimated from the difference in F_{NEE} measured by two consequent light and dark observation in one session. The response of the gross photosynthesis to measured Q_{PAR} was analyzed by fitting a Michaelis-Menten type function (Eq. 3) for estimation of maximum assimilation rate (A_{max}) and the light response coefficient α :

$$A_g = \frac{\alpha Q_{\text{PAR}} A_{\text{max}}}{A_{\text{max}} + \alpha Q_{\text{PAR}}}$$

¹⁵ The gross assimilation was also estimated from the difference in measured net flux and the estimated daytime respiration. Daytime respiration was estimated from a temperature response function fitted to average nighttime flux rates. The gross assimilation was then taken as the difference between the actual net flux (F_{NEE}) and the simulated respiration from daytime soil temperature.

20 3 Results

Average net CO₂ flux was estimated over all observations, over observation during nighttime, and over observation during daytime divided into light and dark sessions. Nighttime was defined when Q_{PAR} was less then $3 \,\mu$ mol m⁻² s⁻¹ inside the chamber.

BGD 6, 9301-9329, 2009 Forest floor CO₂ flux measurements with a dark-light chamber H. J. M. Lankreijer et al. Title Page Introduction Abstract Conclusions References **Tables Figures** Back Close Full Screen / Esc **Printer-friendly Version** Interactive Discussion

(2)

(3)



Flux estimates were only used if the regression line through the CO_2 concentration readings had a high linearity, indicated by a R^2 of above 0.98. This high linearity of the readings indicated a sufficient mixing of the air, low leakage and correct air sampling.

3.1 Hyytiäla 2005

- ⁵ The respiration of both soil and vegetation was in the range of 4 to $6 \mu \text{mol} \text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under dark conditions (Fig. 1). During daylight and with the transparent cover, the assimilation of the vegetation lowers the net efflux and during short moments with sufficient high Q_{PAR} the uptake by photosynthesis is even larger than the respiration from the soil and vegetation.
- ¹⁰ The average F_{NEE} measured during daytime with the transparent cover from all three plots was 3.08 μ mol m⁻² s⁻¹ (*n*=532, std=1.57) and clearly lower than daytime respiration under dark conditions, which on average was 5.14 μ mol m⁻² s⁻¹ (*n*=453, std=0.73) No difference in soil temperature difference was measured under those measurements. The average nighttime respiration was 4.86 μ mol m⁻² s⁻¹ (*n*=498, std=0.82). Average
- ¹⁵ soil temperature during daytime was 14.3°C and lower during night with 13.6°C. Plot 1 was dryer, and showed a larger variability in soil temperature (Fig. 2) between day and night. However, regression analysis of the Lloyd and Taylor equation (Eq. 2) showed that only 13 to 33% was explained by the temperature variation (Table 1).

Comparing dark and light observations taken close to each other in time during one session (10 min) results in an estimated gross assimilation rate of the ground vegetation (Fig. 3). The average gross assimilation rate for all three plots was $2.04 \,\mu$ mol m⁻² s⁻¹ (n= 532, std=1.49).

The assimilation of the ground vegetation shows a fast response to increasing light. From these measurements a maximum assimilation rate, A_{max} , of 5.4 μ mol CO₂ m⁻² s⁻¹ under optimum light conditions can be derived. Light efficiency coefficient (α) was estimated to 0.067 (μ mol μ mol⁻¹) (Table 3).

BGD

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





3.2 Norunda 2005

The soil and ground vegetation respiration measured in Norunda was in the range of 1 to $8 \mu \text{mol m}^{-2} \text{s}^{-1}$ under dark conditions with soil temperature between 4 and 15°C. The average flux during nighttime was $2.96 \mu \text{mol m}^{-2} \text{s}^{-1}$ (*n*=3436, std=1.17), with an average temperature of 9.19°C. The net flux during daylight was on average 2.71 μ mol m⁻² s⁻¹, (*n*=788, std=1.06), again lowered by photosynthesis. Average daytime temperature was only slightly higher with 9.4°C. Average daytime respiration under dark cover was 3.38 μ mol m⁻² s⁻¹ (*n*=523, std=1.2).

In contrast to the measurements in Hyytiäla, the regression of Eq. (2) resulted in a much better R^2 and 76% of variation was explained by the soil temperature (Fig. 4a, Table 1).

Estimation of gross assimilation A_g from the difference of light and dark readings resulted in a low average of 0.45 μ mol m⁻² s⁻¹, because of low light levels at the end of the growing season. The maximum assimilation rate (A_{max}) was 2.04 μ mol m⁻² s⁻¹ and

the light efficiency (α) was 0.03 (μ mol μ mol⁻¹). Note that the measured actual photoactive radiation in the chamber was rather low with only values up to 120 μ mol m⁻² s⁻¹.

3.3 Norunda 2006

The measurements during 2006 took place during the summer period and showed much higher Q_{PAR} values then during 2005 and comparable to Hyytiäla 2005. The weather was relative warm and dry in June and July, with soil temperatures between 8 and 27°C. CO₂ flux measured under nighttime was in the range of 2 to just above $8 \mu \text{mol m}^{-2} \text{ s}^{-1}$, and the average was $4.26 \mu \text{mol m}^{-2} \text{ s}^{-1}$ (*n*=513, std=1.35), at a mean temperature of 16.9°C (Fig. 4b). Dark sessions during daytime resulted in an average flux of $4.42 \mu \text{mol m}^{-2} \text{ s}^{-1}$ (*n*=661, std=1.12). Daytime measurements resulted in an average flux of $2.93 \mu \text{mol m}^{-2} \text{ s}^{-1}$ (*n*=798, std=1.54) Soil temperature during daytime had a mean value of 17.7°C. Figure 4b shows however no increase in the flux with tem-

BGD

6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





peratures above 17°C, while in the range of 8 to 17°C the response was comparable to the measurements in 2005. The soil moisture content was very low during the measurements in May to July, with values between just above zero to only 19% by volume. Fitting the temperature response function to the range of 8 to 17°C and analyzing the

⁵ residuals showed that the soil respiration was limited at low water contents. Respiration was strongly limited when soil moisture content was below 6% (Fig. 5). Regression analysis of the temperature response between 8 and 17°C resulted in a similar relationship with soil temperature compared to 2005, and again 76% of the variation was explained by the soil temperature (Table 1). Except for the estimation of assimilation A_a , the readings with soil temperature above 17°C were excluded from analysis.

Under the summer conditions with high radiation levels the assimilation A_g was higher with an average of $1.52 \,\mu$ mol m⁻² s⁻¹. Regression analysis resulted in an A_{max} of $4.58 \,\mu$ mol m⁻² s⁻¹. Q_{PAR} reaching the forest floor was up to $1200 \,\mu$ mol m⁻² s⁻¹ for sunspots during this warm summer with high air temperatures going up to 29°C.

15 3.4 Estimation of gross photosynthesis through extrapolation of nighttime values

Daytime respiration was estimated by extrapolation of the normalized nighttime respiration using soil temperature. Gross assimilation was then estimated as the difference between the estimated respiration and the actual measured flux. Comparison of the estimated gross assimilation from extrapolation (A_E) with the gross assimilation A_g showed a good agreement for Hyytiäla, but differed for Norunda (Fig. 7). Estimation of gross assimilation from extrapolation of nighttime respiration resulted in an overestimation of 2% for Hyytiäla, but a 21% and 28% underestimation for Norunda 2005 and 2006, respectively.

BGD 6, 9301-9329, 2009 Forest floor CO₂ flux measurements with a dark-light chamber H. J. M. Lankreijer et al. Title Page Introduction Abstract Conclusions References **Tables Figures**

Close



Full Screen / Esc

Printer-friendly Version

Interactive Discussion

14

Back

3.5 Increased daytime respiration

The respiration measured with dark chambers during daytime was on all three locations slightly higher than the average nighttime respiration. In order to analyze if this is a temperature effect or an increased respiration due to other reasons, the nighttime

respiration was normalized with the soil temperature at daytime using the regression function from nighttime respiration. The difference in mean respiration rates of daytimedark and normalized nighttime was tested with a paired-student-t test for significance. The difference was significant for Norunda, but not for Hyytiäla (Table 3).

4 Discussion

- ¹⁰ Compared to previous soil respiration measurements at the site (e.g. Kolari et al., 2006) and assimilation measurements with other systems at the same plot as where the DLchamber was installed, the DL-chamber showed similar CO₂ flux and rates of assimilation (Kulmala et al., 2007).
- The fluxes measured by the chamber in Norunda are in the same range compared to earlier measurements performed by Morén and Lindroth (2000) and Widén (2001). Although using a different exponential regression function, Morén and Lindroth (2000) found a R_{10} of $4.32 \,\mu$ mol m⁻² s⁻¹ from May to October and Widén (2001) a R_{10} of $3.8 \,\mu$ mol m⁻² s⁻¹ in September. The respiration rates at 10°C found in this study are slightly lower then found in the studies by by Morén and Lindroth (2000) and Widén (2001). These differences can be attributed mainly to the fact that the measurements where performed on different locations and thus to the heterogeneity of the soil.

Although soil temperature is a main factor determining the respiration, only 13 to 33% of the variation in the flux at the tree plots in Hyytiälä was explained by the temperature variation. This is low compared degree of explanation for soil temperature of 76% for both years in Norunda. An explanation for the low relationship is that soil

BGD 6, 9301–9329, 2009 Forest floor CO₂ flux measuremerts with a dark-light chamber H. J. M. Lankreijer et al. Title Page Abstract Introduction Conclusions References Tables Figures





moisture variations and rainfall events causes the variation in flux, but it also confirms the importance of root respiration and the its relationship with assimilation in the above ground vegetation.

- Both studies by Morén and Lindroth (2000), and Widén (2002) used the extrapolation of nighttime respiration functions to estimate the gross assimilation. Morén and Lindroth (2000) found that the CO₂ uptake by assimilation of the forest floor vegetation was about 28% of the gross forest floor respiration, while Widén (2001) found 11– 16% for different locations. Uptake of CO₂ by assimilation of the ground vegetation is strongly dependent on light conditions and season and in this study the uptake in Norunda by assimilation was about 13% of respired CO₂ in 2005 and 34% in 2006. In 2005 the measurements were performed in the late part of the growing season, while in 2006 mostly during the warm and sunny June and July months, although dry. The max
- assimilation rates of 2.01 and 4.58 found for 2005 and 2006, respectively are in the same range as the value of $3.3 \,\mu$ mol m⁻² s⁻¹ at 20°C found by Widén (2001) for a blue-¹⁵ berry dominated plot in a 50 year old stand. However, the Q_{PAR} was in the small range of 0–100 μ mol m⁻² s⁻¹ during these measurements, compared to the measurements in 2006.

The measurements in Norunda during 2006 showed a clear increase of respiration with temperature between 8 to 17°C. Above 17°C the data show more a decrease of flux (Fig. 4b). Although limitation of respiration by soil moisture in boreal forests is not reported often, Widén (2001) describes an effect of soil moisture during the dry summer of 1999. Analysis of the data from 1999 showed a limitation of soil respiration when soil moisture content fell below 10%. The results of this study show a decrease in respiration when soil moisture content comes below 3%.

²⁵ A correct measurement of the average Q_{PAR} in the chamber is important to obtain better agreement between estimated assimilation and light levels. The one-point sensor both over- and underestimates the actual light level in the chamber, and this is a clear limitation of the measurement. It is seldom that the Q_{PAR} level measured by the single small sensor in the chamber under the canopy comes above 200 μ mol m⁻² s⁻¹.

BGD

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





However it is clear that in sunspots the light level is sufficient high and the photosynthesis can reach levels up to $6 \,\mu$ mol m⁻² s⁻¹ as for example in Hyytiäla. Under normal light conditions the photosynthesis reaches levels up to $4 \,\mu$ mol m⁻² s⁻¹, which can be equal or higher than the respiration rate, resulting in a net uptake by the ground vegetation.

⁵ In Norunda the maximum level of assimilation was in 2006 up to $4 \mu \text{mol m}^{-2} \text{ s}^{-1}$, but only in a very rare occasions the assimilation was larger then the total respiration.

To obtain an indication of the contribution of the forest floor vegetation to the total CO_2 balance of the forest, a comparison can be made with the maximum NEE described by Lindroth et al. (2007). They estimated F_{csat} for 8 different sites from above canopy NEE measurements, including Norunda and Hyytiäla. F_{csat} can be described as

- ¹⁰ canopy NEE measurements, including Norunda and Hyytiala. F_{csat} can be described as the maximum NEE or uptake by the total forest. Summation of F_{csat} with max respiration results in an estimate of total gross photosynthesis. For Norunda F_{csat} was found to be about 11–15 μ mol m⁻² s⁻¹ in mid summer and dark respiration around 8 μ mol m⁻² s⁻¹. Those values indicate that gross assimilation by the forest floor vegetation constitute
- ¹⁵ up to 30% of the maximum NEE and about 25% of gross assimilation of the total forest. Morén (1999) estimated that the forest floor vegetation contribution was 20% of the total assimilation in Norunda. For Hyytiäla F_{csat} was about $15 \mu mol m^{-2} s^{-1}$ and dark respiration around $5 \mu mol m^{-2} s^{-1}$. Here the contribution of the forest floor vegetation would similar to Norunda with 30–33% of maximum NEE and 25% of gross assimilation. Kolari et al. (2006) report similar values for Hyytiäla for 2003.

Comparison of the gross assimilation rates obtain by direct comparison of light and dark sessions within 10 min and the gross assimilation by extrapolation of nighttime respiration showed clearly for Norunda that both methods can differ strongly with 21 and 28%. For Hyytiäla measurements the difference was very small, only 2%, but the scatter was rather large.

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The method used showed that the difference in daytime and nighttime respiration is small but significant different for the Norunda site. A possible reason for this could be the time lag between the uptake of CO_2 by the canopy and the respiration of the assimilate by the roots. Ekblad et al. (2005) showed that there was a time lag 1–4 days

BGD

6, 9301-9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber





between the assimilation and the respiration by the roots. The time lag depends on several factors including tree size and it is therefore not unreasonable that there are differences between stands of different structure as for instance between Hyytiälä and Norunda. However, a critical assessment of this effect requires other methods, such as direct measurements of root respiration.

Using the combined dark-light measurements shows a clear potential of analyzing the net respiration and assimilation by the ground vegetation. The measurements described here are however limited due to the use of one chamber on a very low number of places. Spatial repetition of measurements is needed to give a better analysis of total respiration and assimilation for the whole stand.

5 Conclusions

10

Use of an opaque cover and measuring both the net CO₂ flux under light and dark conditions improved the analysis of soil respiration and the role of ground vegetation strongly. The method resulted in good estimates of the gross assimilation by the ground vegetation, which can be a substantial part of the total assimilation by the forest. Comparison of the assimilation rates obtained from direct estimation from light and dark readings with the chamber with rates obtained from extrapolated nighttime respiration showed that the last method resulted in an underestimation of gross photosynthesis up to 25%. The measurement results showed also a small but significant difference in 20 daytime and nighttime respiration.

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BGD 6, 9301-9329, 2009 Forest floor CO₂ flux measurements with a dark-light chamber H. J. M. Lankreijer et al. **Title Page** Introduction Abstract Conclusions References **Tables Figures** Back Close Full Screen / Esc **Printer-friendly Version**

Interactive Discussion



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5

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BGD

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15

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BGD

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Title Page		
Abstract	Introduction	
Conclusions	References	
Tables	Figures	
14	N	
	•	
Back	Close	
Full Screen / Esc		
Printer-friendly Version		
Interactive Discussion		



6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber

H. J. M. Lankreijer et al.

Title Page		
Abstract	Introduction	
Conclusions	References	
Tables	Figures	
	►I	
•	•	
Back	Close	
Full Screen / Esc		
Printer-friendly Version		
Interactive Discussion		



Table 1. Values of R_{10} (μ mol m⁻² s⁻¹) and E_0 (K) parameters from fitted Eq. (2) on soil temperature vs. dark chamber CO₂ flux.

Site	R ₁₀	E ₀	R^2
Hyytiäla, plot 1	4.34	130.6	0.24
Hyytiäla, plot 2	3.35	332.6	0.33
Hyytiäla, plot 3	4.12	228.2	0.13
Hyytiäla, all data	4.09	184.3	0.25
Norunda 2005	3.29	555.8	0.76
Norunda 2006	2.30	505.3	0.76

6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber

H. J. M. Lankreijer et al.

Title Page		
Abstract	Introduction	
Conclusions	References	
Tables	Figures	
14	N	
•	•	
Back	Close	
Full Screen / Esc		
Printer-friendly Version		
Interactive Discussion		



Table 2. Values of A_{max} (μ mol m⁻² s⁻¹) and α from the fitted light response functions given in Eq. (3).

Site	A _{max}	α	R^2
Hyytiäla, plot 1	5.18	0.06	0.77
Hyytiäla, plot 2	6.85	0.07	0.87
Hyytiäla, plot 3	2.90	0.11	0.41
Hyytiäla all data	5.38	0.07	0.73
Norunda 2005	2.01	0.03	0.41
Norunda 2006	4.58	0.06	0.73

6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber

H. J. M. Lankreijer et al.

Title Page		
Abstract	Introduction	
Conclusions	References	
Tables	Figures	
•	•	
Back	Close	
Full Screen / Esc		
Printer-friendly Version		
Interactive Discussion		



Table 3. Comparison of mean respiration in μ mol m⁻² s⁻¹ during daytime with dark chamber and nighttime. Nighttime values were normalized to daytime soil temperature. N.S.=not significant.

Site	Daytime	Nighttime	
Hyytiäla, 2005	5.14	5.12	N.S.
Norunda, 2005	3.39	3.21	<i>p</i> <0.001
Norunda, 2006	3.82	3.34	<i>p</i> <0.001





6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber













6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber









6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber







Fig. 5. Residuals of temperature response function versus soil moisture content.

BGD 6, 9301-9329, 2009 **Forest floor CO₂ flux** measurements with a dark-light chamber H. J. M. Lankreijer et al. **Title Page** Introduction Abstract Conclusions References Tables Figures 14 Back Close Full Screen / Esc **Printer-friendly Version** Interactive Discussion





6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber













Fig. 7. Comparison of estimated photosynthesis from daylight measurements with transparent and dark chamber and by extrapolation of night-time respiration to daytime dark-respiration.

BGD

6, 9301–9329, 2009

Forest floor CO₂ flux measurements with a dark-light chamber



