

Dissertationes Forestales 132

Photosynthesis of ground vegetation in boreal Scots pine
forests

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Academic dissertation

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public examination in Auditorium 1041, Biocenter 2, Viikki (Viikinkaari 5, Helsinki), On November 11th 2011, at 12 o'clock noon.

Title of dissertation: Photosynthesis of ground vegetation in boreal Scots pine forests

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Dissertationes Forestales 132

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ISSN 1795-7389

ISBN 978-951-651-354-9 (PDF)

(2011)

Publishers:

Finnish Society of Forest Science

Finnish Forest Research Institute

Faculty of Agriculture and Forestry of the University of Helsinki

School of Forest Sciences of the University of Eastern Finland

Editorial Office:

The Finnish Society of Forest Science

P.O. Box 18, FI-01301 Vantaa, Finland

<http://www.metla.fi/dissertationes>

Kulmala, L. 2011. Photosynthesis of ground vegetation in boreal Scots pine forests. *Dissertationes Forestales* 132. 45 p. Available at <http://metla.fi/dissertationes/df132.htm>

ABSTRACT

Research on carbon uptake in boreal forests has mainly focused on mature trees, even though ground vegetation species are effective assimilators and can substantially contribute to the CO₂ uptake of forests. Here, I examine the photosynthesis of the most common species of ground vegetation in a series of differently aged Scots pine stands, and at two clear-cut sites with substantial differences in fertility. In general, the biomass of evergreen species was highest at poor sites and below canopies, whereas grasses and herbs predominated at fertile open sites. Unlike mosses, the measured vascular species showed clear annual cycles in their photosynthetic activity, which increased earlier and decreased later in evergreen vascular species than in deciduous species. However, intraspecific variation and self-shading create differences in the overall level of photosynthesis. Light, temperature history, soil moisture and recent possible frosts could explain the changes in photosynthesis of low shrubs and partially also some changes in deciduous species. Light and the occurrence of rain events explained most of the variation in the photosynthesis of mosses. The photosynthetic production of ground vegetation was first upscaled, using species-specific and mass-based photosynthetic activities and average biomass of the site, and then integrated over the growing season, using changes in environmental factors. Leaf mass-based photosynthesis was highest in deciduous species, resulting in notably higher photosynthetic production at fertile sites than at poor clear-cut sites. The photosynthetic production decreased with stand age, because flora changed towards evergreen species, and light levels diminished below the canopy. In addition, the leaf mass-based photosynthetic activity of some low shrubs declined with the age of the surrounding trees. Different measuring methods led to different momentary rate of photosynthesis. Therefore, the choice of measuring method needs special attention.

Keywords: CO₂ exchange, chamber method, forest floor, mosses, low shrubs, annual cycle

ACKNOWLEDGEMENTS

I wish to express thanks to many people who have helped me during my research work. First and foremost I express my deepest gratitude to Prof. Emeritus Pepe Hari for the time you invested in me. I owe my scientific thinking, reasoning and enthusiasm to you. I thank you for kicking off the present study, for the guidance throughout these years, for your trust and for the open door. You are a very exceptional teacher and person indeed.

I greatly appreciate the practical guidance and help from Jukka Pumpanen. Thank you for sharing your professional experience during the field measurements and especially during the manuscript preparation. I could not have done those without you.

I thank Prof. Timo Vesala for his supportive and positive attitude and for the numerous conversations that have gotten me back on track time and time again. Prof. Eero Nikinmaa is acknowledged for scientific advising and background support.

I am very appreciative of the teamwork with the other co-authors. Pasi Kolari deserves my most sincere thanks for sharing his knowledge and experience in Mathematica, chamber measurements and modelling photosynthesis. The collaboration with Samuli Launiainen was very edifying and productive. Thank you Lauri Laakso and Tiia Grönholm for the exceptional view and pleasant company during the hot air balloon campaigns.

I want to thank my thesis pre-examiners, Dr. Jukka Alm and Dr. Michael Bahn, for their helpful and encouraging comments on the thesis manuscript.

There are a number of other people who deserve recognition for their help. I thank the staff at the Hyttiälä forest field station and SMEARII for providing me with their excellent facilities and the convenient working environment. This work would not have proceeded without the technical assistance by Eki Siivola, Topi Pohja, Heikki Laakso, Janne Levula and Veijo Hiltunen. Besides your high expertise, you are cool and unique people. I am grateful for meeting you. Special thanks also to Varpu Kuutti for the field assistance in 2006. The summers in Hyttiälä left plenty of ineradicable memories. I am especially happy for the friends I made there: Terhi, Pannu, Leena, Natalia, Hanna and others.

I thank the co-workers in the department of Forest Sciences for the conversations, encouragement and company. The working environment in the Ecophysiology group has been relaxed and pleasant. Thank you everyone! The Division of Atmospheric Sciences, headed by Prof. Markku Kulmala, is also gratefully acknowledged. I am thankful for being able to join the multidisciplinary APFE-group.

This work was supported by the Graduate school in *Physics, Chemistry, Biology and Meteorology of Atmospheric composition and climate change*. The financial support from the EU projects ICOS and GHG-Europe are also acknowledged.

Finally, I would like to thank my family and friends who encouraged me during these years. Especially I want to thank my parents for their support.

LIST OF ORIGINAL ARTICLES

The thesis is based on the following research articles, which are referred to in the text by their Roman numerals. Articles are reproduced with the kind permission from the publishers.

- I Kulmala, L., Grönholm, T., Laakso, L., Keronen, P., Pumpanen, J., Vesala, T., Hari, P., 2009. Pressure responses of portable CO₂ concentration sensors. *Boreal Env. Res.* 14: 754–760
<http://www.borenv.net/BER/pdfs/ber14/ber14-754.pdf>
- II Kulmala, L., Launiainen, S., Pumpanen, J., Lankreijer, H., Lindroth, A., Hari, P., Vesala, T. 2008. H₂O and CO₂ fluxes at the floor of a boreal pine forest. *Tellus* 60B: 167–178
doi: 10.1111/j.1600-0889.2007.00327.x
- III Kulmala, L., Pumpanen, J., Hari, P., Vesala, T. 2009. Photosynthesis of boreal ground vegetation after a forest clear-cut. *Biogeosciences* 6: 2495–2507
<http://www.biogeosciences.net/6/2495/2009/bg-6-2495-2009.html>
- IV Kulmala, L., Pumpanen, J., Hari, P., Vesala, T. 2011. Photosynthesis of ground vegetation in different aged pine forests: Effect of environmental factors predicted with a process-based model. *Journal of Vegetation Science* 22: 96–110
doi: 10.1111/j.1654-1103.2010.01228.x
- V Kulmala, L., Pumpanen, J., Kolari, P., Muukkonen, P., Hari, P., Vesala, T. 2011. Photosynthetic production of ground vegetation in different aged Scots pine forests. *Canadian Journal of Forest Research*. In press.
doi: 10.1139/x11-121.

Author's contribution

- I L. Kulmala was the main author, participated in planning of the research and was responsible for the measurements and data analysis.
- II L. Kulmala was the main author, participated in planning of the research and was responsible for the measurements and data analyses, except for the automatic light-dark chamber and Eddy covariance measurements and their data analyses. The article was included in the doctoral thesis of Samuli Launiainen.
- III-IV L. Kulmala was the main author, participated in planning of the research and was responsible for the measurements and data analyses.
- V L. Kulmala was the main author, participated in planning of the research and was responsible for the measurements and data analysis, except for the estimation of light attenuation.

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INTRODUCTION

Background

Sources and sinks for atmospheric carbon dioxide (CO₂) are widely monitored and quantified, due to its role in atmospheric radiative transfer. A variety of interactions with the biosphere affects the concentration of CO₂; in photosynthesis, CO₂ is absorbed, whereas metabolic plant processes or the decomposition of organic matter release CO₂ back to the atmosphere. Study of the CO₂ exchange of the biosphere seeks knowledge both of the dynamics of biological communities and the effects of the biosphere on atmospheric CO₂ concentration.

In the carbon balance of Earth, forests are particularly significant, containing nearly a quarter of all terrestrial vegetation and soil carbon (Watson et al. 2000). The boreal forest is the second largest forest biome in the world, covering Russia, Fennoscandia, and North America (Landsberg and Gower 1997). The carbon dynamics of boreal forests are largely driven by periodic disturbances, such as fire, insects and harvesting (Kurz and Apps 1999, Chen et al. 2000, Kurz et al. 2008). Overall, boreal forests act as carbon sinks but their status is poorly understood, due to high spatial and interannual variability (Amiro et al. 2006). The carbon balance of even a single forest varies radically during stand development and the annual cycle.

Boreal forests have a vegetation structure consisting of a tree layer and a diverse layer of ground vegetation with ericaceous shrubs, herbs, grasses, mosses and lichens. The group includes vascular and nonvascular, perennial and deciduous, fast- and slow-growing, shade-tolerant and -intolerant species – each species adapted to compete in a specific growing environment with varying capability for acclimating to changes in the environment. Research on carbon uptake in boreal forests has mainly focused on mature trees, even though ground vegetation species are effective assimilators and can substantially contribute to the CO₂ uptake of forests, especially in the early phases of succession when the tree seedlings are small and do not shade the ground layer. Thus, a study of the CO₂ exchange of ground vegetation increases our awareness of forest carbon cycling and our ability to estimate the responses of boreal forests to future climate change.

Succession and other factors determining species composition

Ground vegetation communities are dynamic and change considerably with tree architecture and composition along with the soil substrate status (Hart and Chen 2006). Species composition is mainly driven by climate, which determines air temperatures, and by latitude, which determines light intensities (Fig. 1). However, natural plant communities influence the present environment as well. Succession describes these natural changes in an ecosystem. Plant species, especially trees, change the air humidity, soil moisture, light, nutrient and soil conditions. Therefore, dominant species at the ground level vary over the course of time. It is generally believed that environmental variability, such as fluctuation in temperature, energy exchange and soil moisture, is the highest in early succession, because in later phases, fluctuations are buffered by the vegetation itself (Bazzaz 1979). Succession usually describes the changes in plant species while fauna adjusts to these changes.

Primary succession begins when plant species colonize an environment without previous vegetation, such as lava flows or postglacial rebound. Secondary succession is a process started by disturbance that reduces or removes an already established ecosystem, e.g. a forest. Disturbances can be anthropogenic, such as logging. Typically small natural disturbances are caused by snow, disease and pest infestation, while fires, windstorms and severe flooding usually result in large-scale changes. The character of natural disturbances is irregular, creating a mosaic of differently aged structures varying in species composition (Hart and Chen 2006). In addition to the effects of mosaic and differently aged canopy structure, the ground layer is characterized by decaying litter and wood, rocks and spatial differences in soil properties, such as the water-holding capacity etc, resulting in a spatially heterogeneous species composition at the ground level.

In the early phases of succession, pioneer species colonize unvegetated land and initiate the chain of succession. The dominant species are herbaceous, fast-growing and short-lived herbs and grasses (Lindholm and Vasander 1987) specially adapted to the extremes that they may experience. Typical pioneer species that colonize open areas in boreal pine forests include the perennial wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.), which forms loose tussocks of deciduous thin leaves, the herb fireweed (*Epilobium angustifolium* L., also known as *Chamerion angustifolium* (L.) Holub), whose leaves are annual but the rhizome-like, widespread roots are perennial, the herb raspberry (*Rubus idaeus* L.) with annual leaves, biennial stems and perennial root system, and deciduous grasses in the genus *Calamagrostis* Adans.

Later in succession, trees begin to dominate and the species at ground level change to shade-tolerant, slow-growing and evergreen species, such as dwarf shrubs and feather mosses (Palviainen et al. 2005, Tonteri et al. 2005) with low photosynthetic rates (Bazzaz 1979). Dwarf shrubs have overwintering perennial woody growth. Evergreen, slow-growing lingonberry (*Vaccinium vitis-idaea* L.), heather (*Calluna vulgaris* (L.) Hull), and fast-growing bilberry (*V. myrtillus* L.) with short-lived and poorly defended leaves are common dwarf shrubs. These ericaceous plants grow over large areas of the Northern Hemisphere (Demontigny and Weetman 1990) often predominating in nitrogen-poor soils with high levels of organic matter (Ingestad 1973). They are adapted to grow in shade and suffer from intense sunlight, high temperatures, decreased air humidity and episodic drought. They are able to suppress competitors, both directly and indirectly. These species form mycorrhizae, in which fungi grow in and around the roots and provide the plant with nutrients.

Feather mosses are the dominant ground vegetation species in upland boreal forests, typically growing in carpets on moist, humic soils below a closed canopy (Benscoter and Vitt 2007) and occupying a significant proportion of land (Chapin and Shaver 1989). Mosses live in dense communities that are believed to have both a positive effect by increasing water retention and a negative effect by reducing light availability (Pedersen et al. 2001). Schreber's big red stem moss (*Pleurozium schreberi* (Brid.) Mitt.), the Dicranum moss (*Dicranum polysetum* Sw.) and the splendid feather moss (*Hylocomium splendens* (Hedw.) Schimp.) are the most common and abundant mosses in forests in Finland. In addition, *P. schreberi* occurs throughout the Boreal Zone and subarctic regions. The moss cover increases during successional age, accounting for from 60% to over 80% of the ground cover in boreal forests (DeLuca et al. 2002). Although photosynthesis is driven by light, the fraction of feather moss ground cover is negatively related to canopy transmittance of photosynthetically active radiation (PAR) (Bisbee et al. 2001). However, the highest productivity in mosses is often near the border of the tree crown projection,

probably due to limiting effect of water supply (Bonan and Shugart 1989). Soil depth also affects the occurrence of species i.e. only lichen and mosses stand the small water and nutrition supply on shallow soils such as bare rocks.

The idea that succession ends in a climax community, where species composition changes no longer occur in time, has a long history, but currently it is commonly believed that a steady state is never reached since matured forests also face disturbances that act on varying spatial and temporal scales, frequently removing part of the previous plant community (Cook 1996).

Succession is driven by the community, which affects the light and temperature environments that further show feedback to species composition. Nevertheless, the species composition at the ground level also show two-way interactions by many other factors (Fig. 1), such as fertility and soil moisture properties that affect tree species as well as the ground vegetation composition. Mainly trees but also mosses and lichens affect soil temperature that further affects the mineralization of nutrients i.e. soil fertility. Even if the biomass of species in the ground vegetation in mature forest ecosystems is relatively low, their high turnover rate implies that they produce a great deal of litterfall and contribute substantially to total annual nutrient uptake. Accordingly, these species play a critical role by affecting belowground processes such as decomposition, nutrient flow and build-up of soil nutrients (Nilsson and Wardle 2005).

Fast-growing *Vaccinium myrtillus* and slow-growing *V. vitis-idaea* have positive effects on litter decomposition and soil microbial activity (Nilsson and Wardle 2005, Wardle and Zackrisson 2005). It has even been shown that the relationship between successional stage and decomposer activity is driven by the ericaceous shrubs present (Nilsson and Wardle 2005). Feather mosses produce litter that decomposes slowly and releases nitrogen more slowly than the litter of trees and dwarf shrubs (Wardle et al. 2003). The piled layer of moss litter, with living mosses on top, is important in retaining moisture and it accelerates the decomposition rates associated with litters from vascular plant species (Wardle et al. 2003). The layer also buffers soil against temperature changes that affect nutrient uptake and litter decomposition. Mosses are very effective in absorbing available nutrients (cited in Nilsson and Wardle 2005) and the mycorrhizal hyphae of ericaceous shrubs take up nutrients directly from recently dead moss tissue (Zackrisson et al. 1997). Therefore, the nutrients released from mosses are not easily available for trees. In general, nutrient-use efficiency is lowest in deciduous species, intermediate in evergreen shrubs and highest in mosses (Chapin and Shaver 1989).

At least *Vaccinium myrtillus* and *Deschampsia flexuosa* bypass nitrogen mineralization and take up organic nitrogen (Näsholm et al. 1998). In addition, nitrogen-fixing symbiosis between a cyanobacterium and *P. schreberi* fixes between 1.5 and 2 kg nitrogen ha⁻¹ y⁻¹ in mid- to late-successional forests in Scandinavia and Finland (DeLuca et al. 2002). This is an important contributor to both nitrogen accumulation and nitrogen cycling. However, nitrogen fixation may start in late succession when nitrogen recycling is limited and fixation may be of greater benefit to ground vegetation than to trees (Zackrisson et al. 2004). Moreover, nitrogen additions to *P. schreberi* at late-successional sites basically eliminated the nitrogen fixation rates, and therefore, increasing nitrogen deposition will affect the fixation. Salemaa et al. (2008) observed that the effect of nitrogen on biomass production and density of *P. schreberi*, *H. splendens* and *D. polysetum* was nonlinear and was favoured by low or moderate nitrogen addition, but declined with high nitrogen exposure.

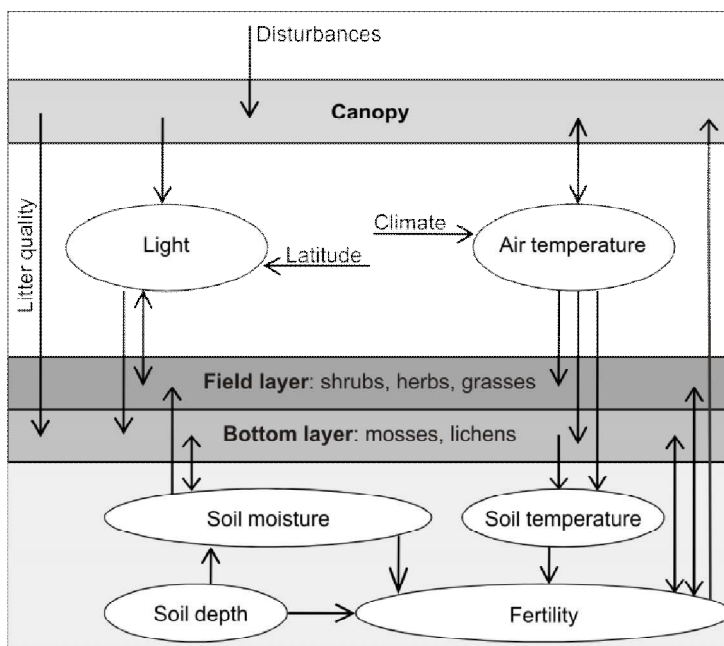


Figure 1. Interactions between vegetation and environment in a forest at the field layer of shrubs, herbs and grasses and at the bottom layer of mosses and lichens. Species composition is mainly driven by light and temperature, which change according to latitude and climate, but also along the canopy by its size and flora that are occasionally affected by disturbances. Light is intercepted by the canopy and further by the field layer, which creates a smaller-scale canopy for the bottom layer. Mosses affect soil temperature and moisture which further affect fertility by increasing or decreasing mineralization of nutrients or nitrogen fixation. The tree canopy have an effect on species composition on the forest floor by litter quality: deciduous litter decreases, whereas conifers increase the occurrence of mosses. Soil depth affects both soil moisture and fertility. Only lichens and mosses tolerate the low water and nutrient supply in shallow soils, such as on bare rocks.

Photosynthesis and respiration

Plants are photoautotrophs, because they can produce the needed organic compounds from atmospheric CO_2 and water, using the energy of solar radiation. The process is called photosynthesis. Temperature, temperature history, light frequency and atmospheric CO_2 concentration affect the efficiency of converting radiation into chemical energy. Plants use this captured energy for growth or for maintaining vital functions, which releases CO_2 back into the atmosphere.

The theoretical understanding of photosynthesis is well-established. In summer, photosynthesis is mainly driven by light (Medlyn et al. 2003, Strengbom et al. 2004, Hart and Chen 2006), which is controlled by latitude and shading by competitors or by the plant architecture itself. The light environment also affects photosynthesis by leaf morphology: exposed plants have higher stomatal densities than plants in a dense community of individuals (Woodward et al. 2002). The higher the stomatal density, the higher is the rate

of photosynthesis. The morphology of leaves affects photosynthesis; e.g. annual, thin leaves have higher mass-based photosynthesis than evergreen leaves with a waxed surface.

In photosynthesis, carbohydrates are synthesized from the atmospheric CO_2 that is taken up by the stomata. Meanwhile, the plant loses water and therefore, the uptake of CO_2 must be controlled because plants undergo water stress if water availability in the soil decreases. Under water stress, the rate of photosynthesis declines as the leaf water potential decreases and the stomata tend to close. Ground vegetation is especially sensitive to drought, because its roots are located in the topmost layers of soil that dry out first. The water supply is dependent not only on the precipitation, transport structure, root architecture and morphology of a plant, but also on soil properties that further affect fertility. Site fertility affects the nitrogen concentration of leaves. It is well known that photosynthesis is highly correlated with leaf organic nitrogen content as a result of differences among species, leaf age, nitrogen availability or light levels during growth (Chapin et al. 1987).

In summer, photosynthesis is driven by light, but the relationship between light and photosynthetic rate is saturated because the availability of CO_2 begins to limit photosynthesis at high light intensities (Thornley 1976, Taiz and Zeiger 2006). Respiration accompanies the observable CO_2 exchange. The saturating relationships of the light-response curve are illustrated in Fig. 2.

One very commonly used equation describing the saturating relationship between light and photosynthesis is the so called Michaelis-Menten-type equation (Michaelis and Menten 1913). Photosynthetic studies also use other models for describing the relationship between photosynthesis and light, such as a nonrectangular hyperbola that has parameters for the initial slope and for the convexity of the curve. This type of model is actually often preferred, because the dual-parameter functions are assumed to be too inflexible to fit properly to changes in the photosynthetic light-response curve (Kull 2002). Biochemical models (Farquhar et al. 1980, Hari et al. 1986) also exist, in which the limiting factors, such as ambient CO_2 concentration and water pressure deficit, are modelled in detail. In addition, numerous other functions are found in the literature.

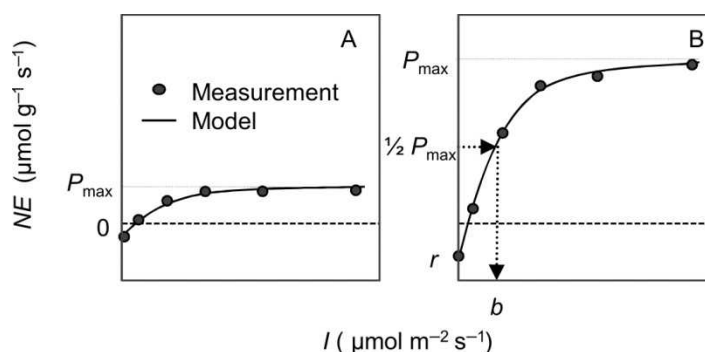


Figure 2. The net exchange (NE) of CO_2 is a sum of photosynthesis and respiration. Photosynthesis predominates in high light intensities (I) and only respiration (r) occurs in zero light. P_{max} describes the saturation level of the light-response curve i.e. the photosynthetic activity and b the light intensity when photosynthesis is half of the P_{max} . The light-response curve (solid line) is fitted to the measurements (spheres). Photosynthesis is low in spring and late autumn (A) and highest in summer (B).

Temperature affects the enzymatic reactions in photosynthesis and, as a result, there is a clear seasonal cycle in photosynthesis in boreal regions. Photosynthesis usually increases with temperature, being highest in summer and lowest in winter. For example, Skre (1975) found that photosynthesis increases with temperature, the optimum for mixed populations of *Vaccinium vitis-idaea* and *Deschampsia flexuosa* being 15–25 °C. *Vaccinium myrtillus* had very high optimum temperatures (27 °C). However, the optimum temperature increases during the growing season and in increased solar radiation (Williams and Flanagan 1998).

In boreal regions, temperature as well as photosynthesis has clear annual cycle. Several studies have successively used state of development (S) to predict the temperature-related seasonal changes in the light-saturated photosynthesis of Scots pine (*Pinus sylvestris* L., Pelkonen and Hari 1980, Mäkelä et al. 2004). Kolari et al. (2006) used the same model in describing the annual cycle of ground vegetation. The level of S follows air temperature with a time constant (τ). The smaller the value of τ , the closer S follows the temperatures measured. The commonly used time constant for *Pinus sylvestris* is 200–330 hours (Mäkelä et al. 2004, Kolari et al. 2007, Magnani et al. 2007). Fig. 3 illustrates the relationship between S and different values of τ . The values of the light-saturated rate of photosynthesis (P_{max}) are assumed to be linearly related to S .

Many mosses are ectohydric plants lacking roots, water-transport systems, and a mechanism to store water or to reduce water loss and therefore, mosses are dependent on a continuous water source (Busby et al. 1978). Mosses absorb water well through their entire surface, and they are easily desiccated on warm sunny days (Bonan and Shugart 1989). Photosynthesis of mosses decreases with increasing water stress (Kellomäki and Hari 1976, Bonan and Shugart 1989). Nonvascular plants are often more limited by throughfall precipitation than by light (Busby et al. 1978) and water relations and drought resistance fundamentally control the growth and distribution of mosses (Busby et al. 1978, Skre and Oechel 1981, Bonan and Shugart 1989). After prolonged dry periods, mosses go into a consequential dormancy that continues as long as the reduced water levels persist (Peterson and Mayo 1975). Skre and Oechel (1981) found that after 4 d of desiccation, the photosynthesis of *P. schreberi* had decreased by 25%, and after 8 d, there was only 25% activity left. The photosynthesis rate of *H. splendens* decreased even more rapidly with desiccation. This phenomenon was also found by Williams and Flanagan (1998), who reported decreasing photosynthesis rates with decreasing water content in the mosses. Gas exchange is also reduced in shoots with very high water content. This is known to inhibit photosynthesis (Busby and Whitfield 1978).

Moss photosynthesis saturates at low light levels, while high light levels actually cause evaporation stress (Bisbee et al. 2001), as well as high temperatures that increase evaporation of water from moss tissues (Busby et al. 1978, Skre and Oechel 1981). Optimal temperatures for moss photosynthesis are lower than with vascular plants. Kallio and Heinonen (1971) observed that *Dicranum* Hedw. has an optimal temperature of 5 °C, but they found no significant changes in the photosynthetic activity between 5 and 10 °C. Goulden and Crill (1997) observed that the maximum photosynthesis of sphagnum occurred at 8 °C, whereas the optimal temperature for feather moss and sphagnum was at 5–8 °C by Bergeron et al. (2008).

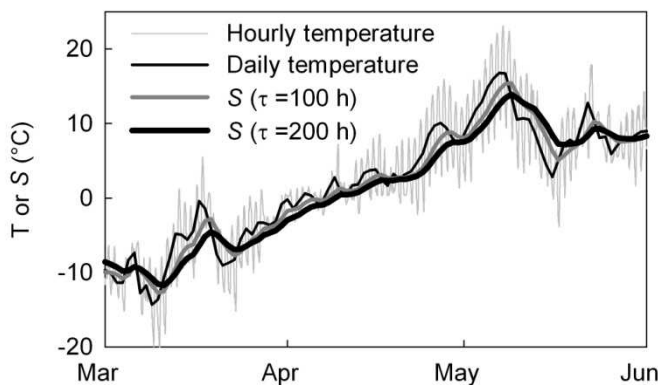


Figure 3. Hourly and daily average temperatures ($^{\circ}\text{C}$) and S ($^{\circ}\text{C}$) with two different time constants. The smaller the time constant, the closer it follows the daily average temperature. Temperature was measured at 4.2 m at SMEARII in spring 2006.

Determining photosynthetic production

The CO_2 exchange of a plant is a sum of photosynthesis and respiration i.e. absorbed and released CO_2 . On an ecosystem scale, the microbial respiration of decaying organic matter (heterotrophic respiration) also takes part in the CO_2 exchange by releasing CO_2 . The eddy covariance (EC) technique is a direct micrometeorological method for determining the average whole-ecosystem energy and gas exchange. Briefly, EC measures CO_2 concentrations and the three wind components in a high-response manner. CO_2 exchange is derived from the concentration differences in the upwards- and downwards-directed wind. The result is net ecosystem exchange (NEE) over a ground area, the size of which is dependent on wind speed, atmospheric stability and measuring height. It is widely and routinely used in flux measurements in forests (Baldocchi 2003), for example, and it has been used below the forest canopy to measure the net CO_2 exchange between the forest floor and the atmosphere (Baldocchi and Vogel 1996, Wilson and Meyers 2001, Launiainen et al. 2005, Misson et al. 2007).

The net ecosystem exchange (NEE) achieved is widely divided into gross primary production (GPP) and total ecosystem respiration (TER), but most often smaller-scale measurement techniques, e.g. different chamber-based systems, are used for the detailed analysis of CO_2 fluxes between different releasing and absorbing components. There is a huge variety in available chamber size and principles, including open and closed, static and dynamic chambers measuring soil, a whole plant, or a specific plant part. Usually in CO_2 exchange measurements, CO_2 concentration as well as air temperature, light intensity and air humidity are measured. A fan is placed inside the chamber to mix the air during measurements. The flux is determined within a few minutes' period in a closed chamber by the changes in the CO_2 concentration (C). The net flux ($\Delta C/\Delta t$) is calculated from the time derivative of respective concentration. Usually, the $\Delta C/\Delta t$ is estimated from the slope of the linear regression through concentration readings, but nonlinear regressions are also used (Kutzbach et al. 2007).

Ground vegetation is often ignored in the ecosystem carbon modelling due to complex light-climate conditions and heterogeneous species diversity and physiological response.

However, predicting the future photosynthetic production of forest ecosystems associated with possible changes in species composition or climate requires species-specific knowledge of photosynthesis of ground vegetation. The aim of the present study is to determine the associations between photosynthesis and environmental factors, such as light, temperature, soil moisture, fertility and age of the surrounding trees to determine the annual photosynthetic production of the ground vegetation.

In the present study, we examined methods, i.e. different chambers and the EC, to measure the CO₂ exchange of the ground vegetation (II) and the reliability of CO₂ analysers by determining how the readings should be corrected for pressure (I). The amount of photosynthetic production varies from site to site, depending on the phase of succession and the environmental factors, such as fertility. We studied the species distribution and species-specific annual patterns of photosynthesis at two clear-cut sites (III) with very different levels of fertility and in a series of five differently aged but otherwise well-matched sites (IV). We attempted to find a method for predicting species-specific photosynthesis (P_{max}) by the affecting environmental factors, such as light, temperature history, soil moisture and rain events (III, IV). Finally, we interpolated and upscaled the photosynthetic production over the entire growing season, using the photosynthesis responses, and the measured and modelled environmental factors and species distributions (III, V).

MATERIALS AND METHODS

Study sites

The measurements were located at and nearby the SMEARII (Station for Measuring Ecosystem-Atmosphere Relations; Hari and Kulmala 2005) in Hyytiälä, southern Finland (61.52°N, 24.17°E). During the period from 1960 to 2000, the annual mean temperature was +3.3 °C and precipitation 713 mm. February was the coldest month (mean -7.8 °C) and July the warmest (mean +15.5 °C, Drebs et al. 2002). The measurements for studying the different measuring techniques of CO₂ fluxes of the ground vegetation (II) were performed at the SMEARII station, which is located in a 45-year-old *Pinus sylvestris* stand. The soil at the site was exposed to prescribed burning and ploughing before sowing in 1962. In summer 2005, the predominant height of the stand was 16 m and the tree density 1100–1200 ha⁻¹. *Vaccinium vitis-idaea*, *V. myrtillus* and mosses, mainly *Pleurozium schreberi* and *Dicranum polysetum* predominated on the forest floor. According to the Finnish forest site-type classification (Cajander 1926), the forest belongs to the *Vaccinium* site-type (VT), which is of medium fertility.

A study of the effect of site fertility on the photosynthesis of ground vegetation (**III**) was performed at two clear-cut sites separated by app. 1 km and app. 7 km from the SMEARII station. Both sites were app. 1 hectare in size, but differed substantially in soil fertility. The fertile site belonged mainly to the Myrtillus type (MT) and partly to the Oxalis Myrtillus type (OMT) according to the Finnish forest site-type classification. The infertile type belonged to the Calluna type (CT). The fertile site was planted with Norway spruce (*Picea abies* (L.) H. Karst.) and the infertile site was sown with Scots pine seeds. Fast-growing and opportunistic dominant species, such as *Deschampsia flexuosa*, *Epilobium angustifolium* and *Rubus idaeus* predominated at the fertile site. The dominant species at the infertile site were evergreen and slow-growing, such as *Calluna vulgaris* and *Empetrum nigrum* L. The details of the trees and ground vegetation at the clear-cut sites are introduced in Table 1.

To study the successional changes in CO₂ exchange of the ground vegetation (**IV, V**), we measured the CO₂ exchange of the most common forest floor species at five differently aged but otherwise well-matched VT sites located near the SMEARII station. Typically, the field layer in VT-type forests is predominated by *Vaccinium vitis-idaea*, *V. myrtillus* and *Calluna vulgaris*. *Pleurozium schreberi* is predominant in the bottom layer, but cup lichen (*Cladonia* P. Browne) species are also common, especially in the early phases of succession. *Pinus sylvestris* is the most common tree species, but *Picea abies*, silver birch (*Betula pendula* Roth.) and downy birch (*B. pubescens* Ehrh.) are also present. The 45-year-old site was located at the SMEARII station and the 20-year-old site app. 500 m north from there. The 6-, 12-, and 120-year-old sites were located next to each other app. 2 km southwest of the SMEARII station. The details of the trees and ground vegetation at the differently aged VT sites are introduced in Table 1.

Table 1. Tree age, forest type, average aboveground biomass of low shrubs, mosses, grasses and herbs, regeneration type (p = plantation, n = natural, s = sowing), soil type (GD = glaciofluvial deposit), height (h) and number of trees at the measuring sites (**II–V**).

Article	III	III	IV, V	IV, V	IV, V	II, IV, V	IV, V
Tree age	5	5	6	12	20	45	120
Forest type	CT	MT-OMT	VT	VT	VT	VT	VT
Low shrubs (g m ⁻²)	277	44	111	269	200	204	118
Mosses (g m ⁻²)	64	34	208	101	69	58	83
Grasses and herbs (g m ⁻²)	20	163	53	9	9	5	0
Regeneration	s	p	n	p	p	s	n
Soil type	GD	till	GD	GD	till	till	GD
h of <i>Pinus sylvestris</i> (m)	0.9	0.4	–	3	13.7	14.3	22.1
# of <i>Pinus sylvestris</i> (ha ⁻¹)	1200	1800	–	3560	1500	1544	267
h of <i>Picea abies</i> (m)	0.15	0.4	–	–	–	4	11
# of <i>Picea abies</i> (ha ⁻¹)	200	5000	–	270	0	20	666
h of <i>Betula</i> sp. (m)	1.2	1.5	–	5	–	10	26
# of <i>Betula</i> sp. (ha ⁻¹)	710	16000	–	1170	0	20	33

CO₂ exchange measurements

Pressure correction for CO₂ analysers

The challenges in measuring the CO₂ exchange begin with the demands of measuring the CO₂ concentration. Variable conditions, especially fluctuations in temperature and pressure, make the use of the analysers difficult. The measurement results of the CO₂ analysers are proportional to the absolute number of CO₂ molecules in a specific air volume. The raw measurements must be corrected for changes in gas density with pressure and temperature and also for the pressure-broadening effects (Burch et al. 1962) on the infrared (IR) absorption properties. The IR absorption by CO₂ is affected also by Background gases, such as water vapour and oxygen

Previous studies have illustrated that the pressure corrections provided by the manufacturer are insufficient (Pimenoff 2005, Laakso et al. 2007). Therefore, we tested various portable, IR-based CO₂ analysers: the Vaisala CARBOCAP® Carbon Dioxide Probe GMP343 (Vaisala Oyj, Vantaa, Finland), ADC LCA-2 (ADC Bioscientific Ltd., Hoddesdon, Hertfordshire, UK), and three different EGMs (PP Systems, Mauchline, Ayrshire, UK). To determine the effect of ambient pressure on the CO₂ concentration readings, we decreased the pressure by removing air out of a tank that contained a homogeneous CO₂ concentration inside. Based on the results, we determined new and device-specific second-order polynomial pressure-correction functions (I) that were able to reproduce the pressure response reasonably well (Fig. 4).

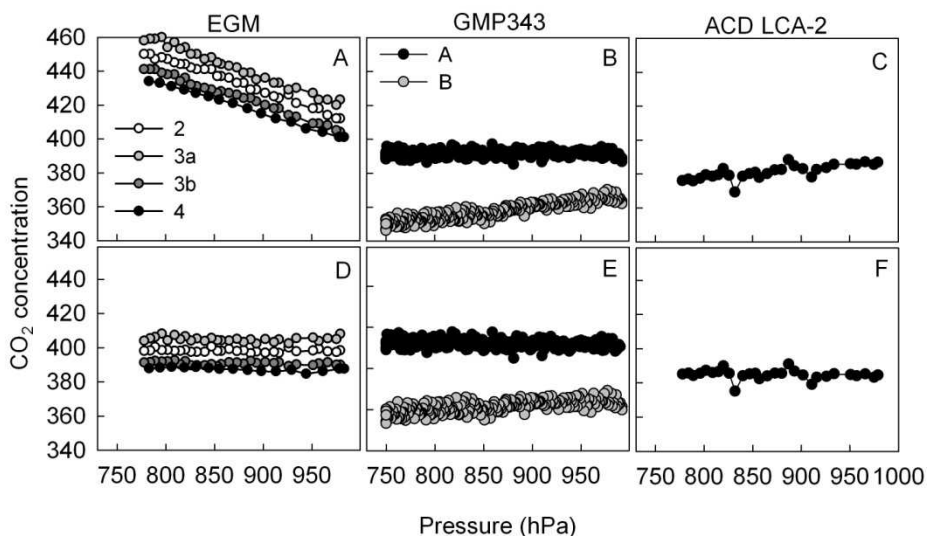


Figure 4. CO₂ concentration measured as a function of pressure by the EGM-2, two EGM-3s and the EGM-4 (panels A and D), by two similar GMP343 sensors (panels B and E) and the ADC LCA-2 (panels C and F). In the upper panels (A-C), the concentration is corrected with the pressure corrections of the manufacturers. In the lower panels (D-F), the correction is done with the independently determined device-specific parameters (I).

Net CO₂ exchange of the forest floor

We measured the net CO₂ exchange (*NE*) of the forest floor with the EC method at a 3-m height at the SMEARII station (**II**, Launiainen et al. 2005). The wind field was measured by a 3-D sonic anemometer (USA-1; Metek GmbH, Elmshorn, Germany) and the gas concentrations by a closed-path IR gas analyser (Li-Cor LI-7000; Li-Cor Biosciences Inc, Lincoln, NE, USA) at 10-Hz frequency. We calculated the fluxes using standard methods (Aubinet 2008).

In comparison, we measured the net CO₂ exchange from the forest floor with an automatic chamber system, later referred to as the NE chamber, described in detail by Pumpanen et al. (2001). The transparent NE chamber was closed approximately once every hour for 3 min. During the closure time, air was drawn out of the chamber and compensation air of known CO₂ concentration was simultaneously introduced into the chamber at a similar flow rate. The net exchange was determined from the flow rate and from the concentration differences between the inflow and outflow.

We also used an automated chamber that is designed for measuring exchange of CO₂ and H₂O from the soil and ground vegetation under light and dark conditions (**II**, Lankreijer et al. 2009). This chamber is later referred to as the light-dark chamber. The exchange of CO₂ was measured twice per hour by closing a transparent Plexiglas lid for 5 min. After the measurement and short ventilation, the lid was closed again and immediately thereafter the darkening apparatus was automatically positioned such that the entire chamber was covered in complete darkness. The momentary photosynthesis of the ground vegetation was determined from the difference between the CO₂ exchanges in the darkened and in the transparent chamber.

Species-specific photosynthesis and cellular respiration

We measured the light-response curves for the photosynthesis of the most common vascular plant species of the ground vegetation at app. two-week intervals with a manual, cylindrical chamber based on the nonsteady-state nonthroughflow chamber technique (**II–IV**).

The chamber was 0.30 m in diameter, 0.30 m in height and opened downwards. During the measurements, the chamber was placed on a polyvinylchloride (PVC) collar that was perforated to allow air to circulate freely under the chamber (Fig. 5). There was a 1-cm-thick sheet of cellular plastic between the collar and the chamber. The shoots entered the chamber through a cut in the plastic. Hence, we could measure the same shoots several times in their natural growing environment without causing any change or disturbance to the shoots. Some of the experimental shoots grew taller than 30 cm. Then we used an otherwise identical chamber, but 0.40 m in height. Due to its tussock-like growth form, *Deschampsia flexuosa* was measured with the higher chamber, but no cellular plastic was used as a bottom (**III**). A solid plastic collar was placed in the soil and the shoots entered the chamber freely. The measurement signal was then a sum of the soil CO₂ efflux and photosynthesis of *D. flexuosa*. The same procedure was applied to mosses, but then the smaller chamber was used (**IV**).

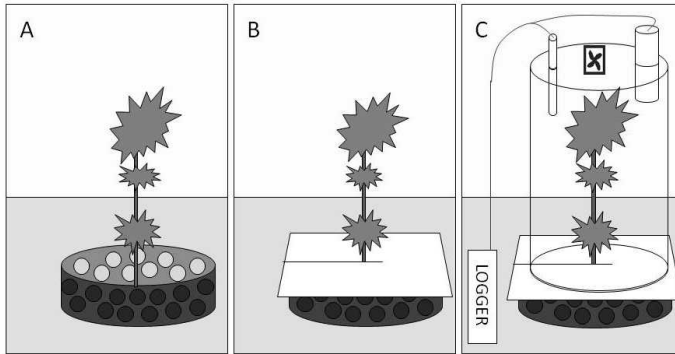


Figure 5. Schematic illustration of the chamber measurements (II–IV). A: First, a perforated collar is placed around the individual measured. B: a sheet of soft cellular plastic with a cut is placed on the collar. The individual measured can pass the plastic through the broadened cut without any harm to the plant. C: A chamber equipped with a fan, CO₂ and temperature/moisture sensors is placed on the cellular plastic. The weight of the chamber seals the cut in the plastic as well as the space between the plastic and the chamber. After measuring for a few minutes, the chamber is held up, ventilated and taken back for three to six repetitions at different light intensities.

The CO₂ concentration inside the chamber was monitored during the measurement with a CO₂ probe (GMP343) attached inside the chamber. The humidity and temperature values used in the CO₂ correction were obtained from a temperature and humidity probe (HMP75; Vaisala) attached inside the chamber and connected to a data recorder (MI70; Vaisala). Pressure was measured at SMEARII. The instantaneous light intensity was measured with a PAR sensor (LI-190; Li-Cor Biosciences) attached outside the chamber after we had tested that the Plexiglas does not significantly capture incoming light. The rate of CO₂ exchange was estimated from a linear regression fitted to CO₂ readings over a 3-min time. The measuring period was shortened to 1 min in high solar radiation during high rates of photosynthesis to avoid heating of the chamber (III, IV).

One set of measurements consisted of four to six measurements with different light intensities and one dark measurement. Between the measurements, the chamber was ventilated by carefully raising it up from the experimental shoot. The highest light intensity was direct sunlight and the other three to five light intensities were created by shadowing the chamber with layers of netted fabric. The chamber was fully darkened with an aluminium cover during the last measurement.

We fitted the Michaelis-Menten-type equation for each set of our measurements to study the changes in photosynthesis (Fig. 2):

$$NE(I) = \frac{P_{max} I}{b + I} - r \quad (1)$$

In the equation, $NE(I)$ is the rate of net CO₂ exchange per ground area ($\mu\text{mol m}^{-2} \text{s}^{-1}$) or per full-grown leaf mass ($\mu\text{mol g}^{-1} \text{s}^{-1}$), I is the light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$), the b -

parameter describes the steepness of the curve by standing for the light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) when the photosynthesis rate is half the rate of light-saturated photosynthesis (P_{max} , $\mu\text{mol m}^{-2} \text{s}^{-1}$ or $\mu\text{mol g}^{-1} \text{s}^{-1}$). In the whole-plant measurements, P_{max} indicates both the changes in photosynthesizing leaf area and the amounts and catalytic activities of photosynthetic enzymes (Pearcy et al. 1987). Later, P_{max} is referred to as the photosynthetic activity. After the campaign the aboveground parts of the plants measured were collected, dried for 24 h at 60 °C and weighed to obtain the leaf and total biomasses (II–IV).

In the middle-aged forest, we measured the respiration and photosynthesis of mosses with an automatic chamber (II, Pumpanen et al. 2001) approximately 60 times per day. We removed patches of *Pleurozium schreberi* and *Dicranum polysetum* from the soil 1 month before the measurements and placed them on quartz sand to separate the photosynthetic signal of the mosses from the soil CO₂ efflux. The patch on the sand was placed on the forest floor in the natural temperature, humidity and light environment. After the measurement campaign, the green parts of the mosses were dried and weighed and a Michaelis-Menten-type light-response curve (Eq. 1) was fitted to the measurements of each day.

Environmental effects on photosynthetic activity

Environmental factors such as temperature and soil-water affect photosynthesis, which can be seen in the value of P_{max} (Eq. 1). Therefore, we constructed a simple model (III) in which P_{max} is simulated by the temperature history. Species-specific (i) temperature history (S_i^j , °C) follows site-specific (j) air temperature, $T^j(t)$ (°C) at moment t , with a time constant τ_i (h):

$$\frac{dS_i^j}{dt} = \frac{T^j(t) - S_i^j}{\tau_i} \quad (2)$$

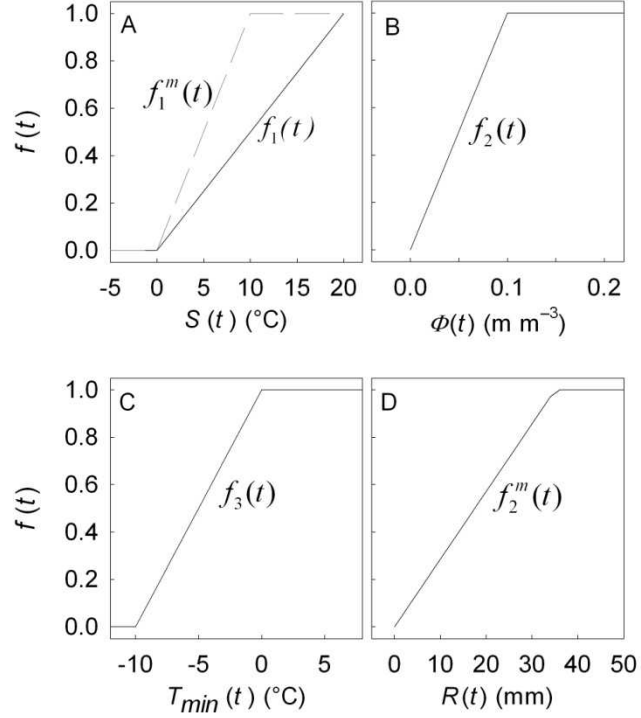
The initial value of S is usually set to be the first temperature of the year. The light-saturated \bar{P}_{max}^i was assumed to be linearly related to S (Mäkelä et al. 2004). We developed the model further (IV) by including the effect of soil-water content (f_2) and recent frosts (f_3). Thus, the simulated daily \bar{P}_{max}^i values were

$$\bar{P}_{max}^i(t) = f_1(t) f_2(t) f_3(t) P_{max}^i(t_{st}^i). \quad (3)$$

If S_i^j was smaller than 0 °C, f_1 was set to zero. Otherwise, f_1 (Fig. 6A) is the site- (j) and species-specific (i) relationship between momentary temperature history, and the temperature history in early summer (t_{st}^i):

$$f_1(S_i^j(t)) = \begin{cases} \frac{S_i^j(t)}{S_j^i(t_{st}^i)} & \text{if } S_i^j(t) > 0^\circ\text{C} \\ 0, & \text{if } S_i^j(t) < 0^\circ\text{C} \end{cases} \quad (4)$$

Figure 6: Schematic illustrations of the functional forms of
 A) the temperature history S (f_1 and f_1^m), where $S(t) < 20$ °C (Eqs. 4 and 8),
 B) soil-water content Φ (f_2), where $\alpha = 0.1 \text{ m m}^{-3}$ (Eq. 5),
 C) the minimum temperature (T_{min}) during last 24 h (f_3 , Eq. 6) and
 D) cumulative rain (R) during the previous 5 or 7 days (f_2^m), where $\beta = 35 \text{ mm}$ (Eq. 9).



In low volumetric soil moisture (Φ_j , m m^{-3}), we set the f_2 value to decrease as follows (Fig. 6B):

$$f_2(\phi_j(t), \alpha_j) = \begin{cases} 1, & \text{if } \phi_j(t) \geq \alpha_j \\ \frac{\phi_j}{\alpha_j}, & \text{if } \phi_j(t) < \alpha_j \end{cases}, \quad (5)$$

where α_j is a critical value of volumetric soil moisture. If soil moisture decreases below α_j , soil moisture hinders \bar{P}_{max}^i .

The expression f_3 takes into account the carry-over effect from the night-time frost; it is assigned the value 1 if the minimum air temperature in the previous 24 h (T_{min}) was above zero. The value of f_3 decreases with temperature below 0 °C, reaching zero at -10 °C (Fig. 6C):

$$f_3(T_{min}(t)) = \begin{cases} 1, & \text{if } T_{min} > 0 \text{ °C} \\ \frac{T_{min}}{10} + 1, & \text{if } -10 \text{ °C} < T_{min} < 0 \text{ °C} \\ 0, & \text{if } T_{min} < -10 \text{ °C} \end{cases} \quad (6)$$

The simulated species-specific photosynthetic activity (\bar{P}_{max}^i) was assumed to equal one of the measured values, $P_{max}^i(t_{st}^i)$, in early summer (t_{st}^i) when the values were assumed not to have been influenced by environmental factors other than air temperature history, i.e. f_2 and f_3 (Eq. 3) were equal to 1.

For mosses, we modified the model (Eq. 3) because the optimal temperatures are reached much earlier than with vascular plants. The simulated \bar{P}_{max}^m of mosses was assigned the maximum of all the measured values (P_0^m), and the \bar{P}_{max}^m was assumed to be constant when S (Eq. 2) was higher than 10 °C. Otherwise, \bar{P}_{max}^m was scaled by daily $S(t)$ when $S(t)$ was between 0 and 10 °C (Fig. 6A), i.e.:

$$\bar{P}_{max}^m(t) = f_1^m(t) f_2^m(t) P_0^m, \quad (7)$$

where

$$f_1^m = \begin{cases} 0, & \text{if } S(t) < 0 \text{ °C} \\ \frac{S(t)}{10 \text{ °C}}, & \text{if } 0 < S(t) < 10 \text{ °C} \\ 1, & \text{if } S(t) > 10 \text{ °C} \end{cases} \quad (8)$$

Feather mosses are ectohydric plants without root systems. Isolated shoots dry out without external moisture supply. They absorb water through their entire surface, but conducting systems are not well developed and they have no special structures designed to prevent evaporation of water, e.g. stomata. Therefore, we assumed that the daily \bar{P}_{max}^m values were affected by recent precipitation (Fig. 6D):

$$f_2^m = \text{Min} \left\{ 1, \frac{R}{\beta} \right\}, \quad (9)$$

where R is the cumulative precipitation during the present day and previous days (mm), the number of days depending on time of the year. β is a site-specific parameter that increases with stand age, due to increased interception of rain by tree crowns in a mature forest. The used model and its application are introduced in detail in the article **IV**.

Momentary photosynthesis and annual photosynthetic production

We estimated the average forest floor biomass at the study sites by systematically collecting aboveground samples of ground vegetation. We separated each sample into different species, and each species into leaves and stem. From mosses, we separated the green parts. Then we weighed the different segments after drying at 60 °C for 24 h. The details of each sampling appear in **II**, **III** and **V**.

We upscaled the mass-based and species-specific measured P_{max} (Eq. 1 in **II**) or simulated \bar{P}_{max}^i (Eqs. 3 and 8) over all the sites for the momentary photosynthesis (P , $\mu\text{mol m}^{-2} \text{ s}^{-1}$), using full-grown leaf masses acquired from the sampling (**II–IV**):

$$P(t) = \sum_i m_i \frac{\bar{P}_{max}^i(t) I(t)}{b_i + I(t)}. \quad (10)$$

In the equation, m_i (g m^{-2}) is the areal average of the full-grown leaf mass of species i , \overline{P}_{max}^i and b_i the species-specific parameters (Eq. 1) and $I(t)$ a 30-min average PAR intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$) measured at the SMEARII station. To estimate the photosynthetic production over the entire season i.e. annual carbon uptake (GPP), we integrated the momentary photosynthetic rates by the continuous PAR intensities that were measured (**II**, **III**) or simulated (**V**):

$$GPP = \int_{t_1}^{t_2} P(t) dt \quad (11)$$

The upscaling periods (t_1 and t_2) are introduced in detail in **III** and **V**. Later, this procedure is referred to as the species-specific method.

RESULTS

Seasonality of species-specific photosynthetic activity

The deciduous species have higher summertime maxima in the photosynthetic activity (P_{max}) than mosses or species with evergreen leaves (Fig. 7). Unlike mosses, the measured vascular species showed clear annual cycles in their P_{max} levels. In general, the P_{max} of evergreen vascular species increased earlier and decreased later than that of the deciduous species. However, the measured values of *Calamagrostis* sp., *Deschampsia flexuosa*, and *Vaccinium myrtillus* were still striking as late as in late September and even in October (**III**, **IV**), although the active period of *Epilobium angustifolium* was very short, ending already in early autumn (**III**).

Rubus idaeus at the fertile clear-cut site resulted in the highest summertime maximum in the leaf mass-based P_{max} of the species measured but the values of another shade-intolerant pioneer species, *Epilobium angustifolium*, were similar to those of *Calamagrostis* sp. and even *Calluna vulgaris* in early spring (Fig. 7A, **II–IV**). The shade-tolerant *Calluna vulgaris* and *Vaccinium vitis-idaea* with thick and wax-surfaced leaves had relatively low P_{max} (summertime max. $\sim 0.07 \mu\text{mol g}^{-1} \text{s}^{-1}$) in the middle-aged forest (Fig. 7B), compared with *Vaccinium myrtillus* and *Calamagrostis* sp., which have very high leaf mass-based P_{max} values (maxima ~ 0.19 and $0.16 \mu\text{mol g}^{-1} \text{s}^{-1}$). The leaf mass-based P_{max} of mosses in the middle-aged forest was low (max. $0.02 \mu\text{mol g}^{-1} \text{s}^{-1}$, **II**, Fig. 7B) and even lower mass-based values were measured at the clear-cut site in 2006 (Fig. 7A, **IV**).

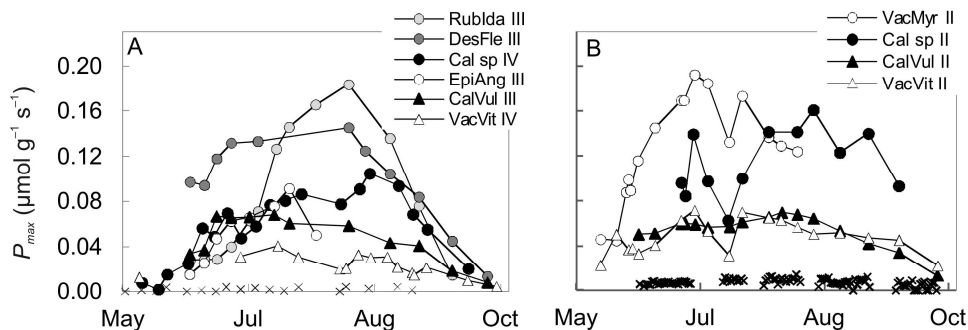


Figure 7. Measured species-specific P_{max} values for *Rubus idaeus*, *Deschampsia flexuosa*, *Calamagrostis* sp, *Epilobium angustifolium*, *Calluna vulgaris*, *Vaccinium vitis-idaea*, *V. myrtillus* and mosses at a clear-cut site (A) and in a middle-aged Scots pine forest (B). Deciduous species are marked with spheres and evergreen species with triangles. The Roman numeral refers to the article number. Measurements in II and III were performed in 2005 and those in IV in 2006.

Environmental effects on photosynthetic activity

In addition to the annual cycle, the photosynthetic activity (P_{max}) of vascular ground vegetation was influenced by soil moisture, recent frosts, soil fertility and age of the surrounding trees, whereas recent precipitation mostly affected the changes in photosynthesis of mosses.

Soil moisture decreased in summer 2005 and even more in summer 2006. In 2005, half of the *E. angustifolium*, *R. idaeus* and *C. vulgaris* individuals measured reacted to the decrease in soil moisture by depressed P_{max} whereas the low soil moisture seemed not to affect the other shoots (III). At the same time, the short but intensive drought caused sharp declines in the measured P_{max} of *Vaccinium myrtillus* and *V. vitis-idaea* in the middle-aged forest (II, Figs. 7B and 8AB). The P_{max} value for *V. vitis-idaea* nearly doubled when the soil was rewetted. The P_{max} of *Calluna vulgaris* seemed not to react as intensively to such decreases in soil moisture (II, Figs. 7B and 8C).

The more severe drought in 2006 affected especially the dwarf shrubs, causing a depression in the P_{max} measured during July and August (Fig. 8, IV), whereas the drought effects on grasses and herbs were not consistent (IV). The P_{max} levels of *Vaccinium vitis-idaea* in the middle-aged forest (Fig. 8B) were lower than those during previous years during most of the growing season and did not attain the previous level until late autumn.

The responses to drought were inconsistent in differently aged forests. The effect was most clear in *Vaccinium vitis-idaea* at the oldest sites, while at the youngest sites, the effect was most prominent in *Calluna vulgaris* (IV).

Tree age also influenced the levels of leaf mass-based P_{max} of the low shrubs *Calluna vulgaris* and *Vaccinium vitis-idaea*. The P_{max} of *C. vulgaris* was highest at the open site and decreased thereafter (Fig. 9A, IV). The P_{max} of *Vaccinium vitis-idaea* decreased radically in the oldest phase of succession (Fig. 9B, IV). The P_{max} levels of *Calamagrostis* sp. at different sites were quite similar, but P_{max} increased at the slowest rate below the canopies (Fig. 4A in IV).

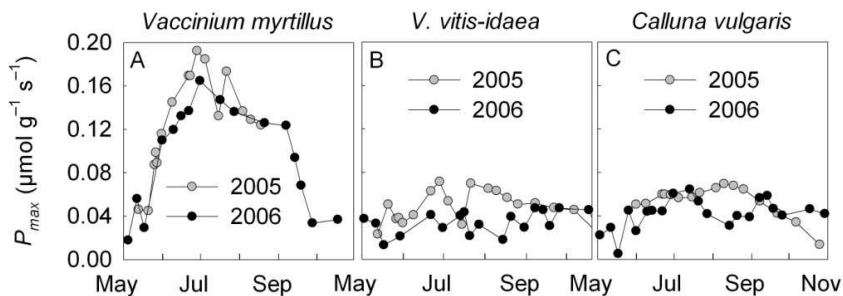


Figure 8. Annual cycle of P_{max} of *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Calluna vulgaris* at the middle-aged stand in 2005–2006. Soil moisture decreased in midsummer 2005, also decreasing the P_{max} of *Vaccinium* sp. and slightly that of *Calluna vulgaris*. The drought was more severe in July–August 2006, causing a depression in the P_{max} of all of the species measured.

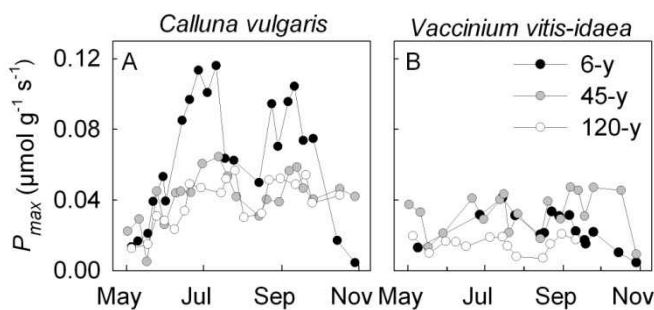


Figure 9. P_{max} measured of *Calluna vulgaris* (A) and *Vaccinium vitis-idaea* (B) at the 6-, 45- and 120-year-old sites (IV).

The whole-plant measurements of deciduous *Epilobium angustifolium* and *Calamagrostis* sp. indicated weak short-term responses in P_{max} to changes in environmental factors, such as soil moisture, compared with the evergreen species. However, the measured P_{max} values of *D. flexuosa* increased by more than 50% attaining the level of the previous year at the 12-year-old site after the drought ended in late August 2006 (see later Fig. 12B).

Epilobium angustifolium was the only species that was measured in significantly different soil types (III) in the present study. The shoots at the infertile site had higher leaf mass-based P_{max} levels than those at the fertile site. Nevertheless, the shoot-based P_{max} was higher on fertile site.

We derived a model based on temperature history to simulate the changes in the P_{max} measured at the clear-cut sites (III). The simulation of \bar{P}_{max} in *Deschampsia flexuosa* was able to predict the changes in P_{max} measurements (Fig. 5 in III). The P_{max} measured in *Calluna vulgaris* was also comparable to the simulation, with a minor underestimation in spring and overestimation in autumn (Fig. 4 in III). However, intraspecific variation occurred between sparse and dense shoots. The dense shoots showed drought-related

decreases in P_{max} that the model was unable to predict, but the sparse shoots did not show such decreases (Fig. 4 in **III**).

Later, we modified the model to include additional terms concerning frost and soil moisture (Eq. 3). The modified model succeeded relatively well in simulating the changes in P_{max} for the evergreen species *Calluna vulgaris* (Fig. 10) and *Vaccinium vitis-idaea* (Fig. 3 in **IV**). Although the timings of the changes were mostly correct, the model simulation underestimated the P_{max} of both species in 45- and 120-year-old sites in September and October, and furthermore *V. vitis-idaea* in early summer, which suggests that below the tree canopies, the growing season was prolonged compared with open areas, even when the differences in the site-specific temperatures (T^j) were taken into consideration (**IV**).

The model based on temperature history and recent precipitation (Eq. 7) appeared able to simulate the rapid changes in the P_{max} of mosses, even though some outliers were present (Figs. 6–7 and Table 2 in **IV**). The values measured did not show a clear seasonal cycle, but the low values occurred after the rain-free period and high values after precipitation. The automatic measurements showed, on the other hand, that there was a strong relationship between the CO₂ efflux from the quartz sand and P_{max} ; increase in water content increased both the photosynthesis and CO₂ efflux (Fig. 11).

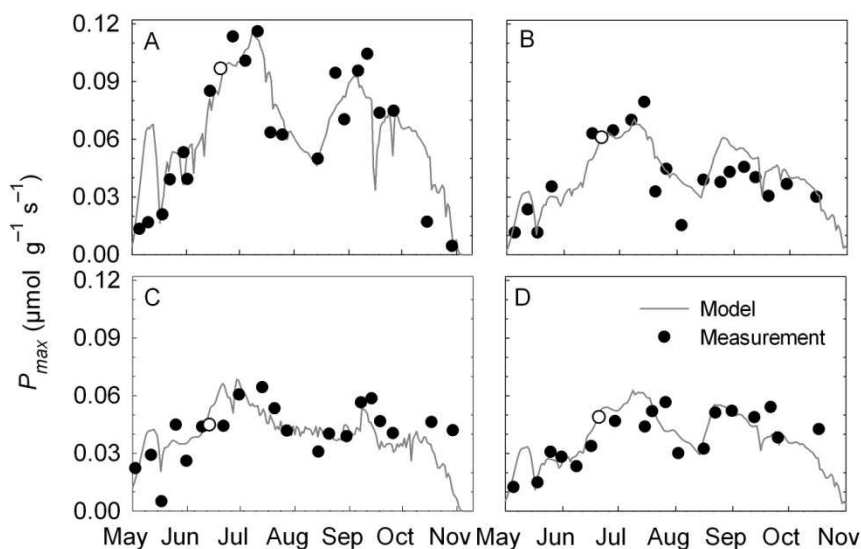


Figure 10. Measured (dots) and simulated (line) photosynthetic activity (P_{max}) of *Calluna vulgaris* for the 6- (A), 12- (B), 45- (C) and 120-year-old (D) stands (**IV**). The model simulation is fitted on one of the measurements that are marked with empty circles (Eq. 3).

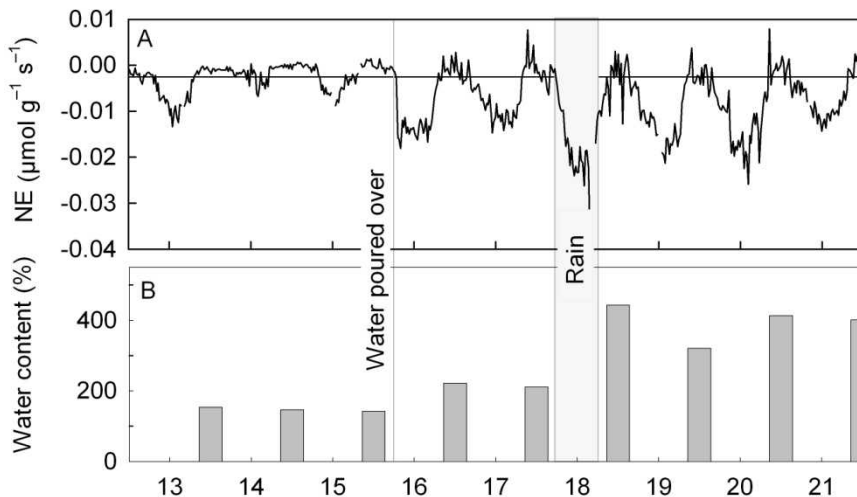


Figure 11. Measurements of CO_2 exchange over a moss population in the middle-aged stand (II) during July 13–19, 2005 (A) and the water content of the measured moss population and the underlying humus layer (B). On July 15th, 0.5 l of water was poured on the population. Rain event of 11 mm occurred 2 days later.

Level of photosynthetic activity of differently sized shoots

The levels of photosynthesis and respiration of a whole-plant were more similar between the differently sized plant individuals at the clear-cut sites than the results based on full-grown leaf mass (III). The levels of leaf mass-based photosynthetic activity (P_{max}) of the four *E. angustifolium* shoots differed substantially throughout the measuring period. However, the shoot-based values were more similar (Fig. 3 in III). A dense *Calluna vulgaris* shoot also had substantially lower leaf mass-based P_{max} values than the sparser shoot (III). Comparison between the mass-based measurements of *Deschampsia flexuosa* led to the same conclusion: the sparser population occasionally showed leaf mass-based P_{max} values twice as high as those of the denser population. These results indicate that the levels of photosynthesis of differently sized individuals are more equal when ground-based than when leaf mass-based, implying that the species-specific rates of photosynthesis are rather similar, regardless of the size, leaf area or leaf mass of that individual.

Comparison of the leaf mass-based P_{max} values of *Epilobium angustifolium*, *Deschampsia flexuosa* and *Calluna vulgaris* at the clear-cut sites (III, IV) are presented in Figure 12. The results are not unambiguous, especially because the growing seasons differ, 2006 being drier than 2005. The forest site-type also differs (Table 1). However, the comparison partially supports the observed role of plant size. The leaf mass-based P_{max} of *Calluna vulgaris* (Fig. 12C) at the clear-cut sites are more similar in plants with similar leaf masses than in the differently sized individuals and the level of P_{max} decreases with plant leaf mass. Usually, the level of P_{max} is lowest with measured individuals showing the highest leaf masses. *Deschampsia flexuosa* (Fig. 12B) is an exception, because the values in 2006 were much lower during early and midsummer than in the previous year.

Momentary photosynthesis and CO₂ exchange per ground area

It is possible to calculate the ground area-based momentary rate of photosynthesis of all species using the momentary species-specific P_{max} , light intensity and inventoried leaf mass of the site. The higher the light intensity, the occurrence of grasses and herbs and the P_{max} of present species, the higher is the momentary rate of photosynthesis. Therefore, the momentary maximum rates of photosynthesis decreased with the canopy tree age, being lowest at the 120-year-old site (V), and the rates differed substantially according to site fertility; The summertime maximum rates of photosynthesis were 3.3 and 9.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the 5-year-old poor (CT) and fertile (MT-OMT) sites, respectively (III), whereas the rates at the 6- and 12-year-old sites with intermediate fertility (VT) fell midway: 4.1 and 4.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (V).

At the middle-aged site, the ground area-based momentary rate of photosynthesis obtained was dependent on the measuring method. The highest rates in the light-dark chamber were 4.5–6.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (II) whereas the simulations by the species-specific method were in most cases lower: 2–3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in 2005 (II) and 1.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in 2006 (V). However, the simulation by the species-specific method using the leaf masses in the light-dark chamber instead of inventory data on the area resulted in higher total photosynthesis than the measurements in the light-dark chamber itself (Fig. 6 in II).

The nocturnal net CO₂ exchanges measured by the NE chamber and the light-dark chamber were first comparable ($\sim 5\text{--}6 \mu\text{mol m}^{-2} \text{s}^{-1}$), but the result differed after relocations of the light-dark chamber (II). The diurnal amplitude differed greatly, but the diurnal pattern was similar in the different chambers. The daytime net forest floor exchange measured with the EC method ($0\text{--}1 \mu\text{mol m}^{-2} \text{s}^{-1}$) was similar to that measured with the chambers. Some night-time values had to be neglected, due to weak turbulent mixing, but otherwise, the nocturnal data by EC were both similar and dissimilar with the different chamber measurements, depending on the chamber and its location. In general, the CO₂ efflux measured with EC was lower than that measured with the chambers (Fig. 4 in II).

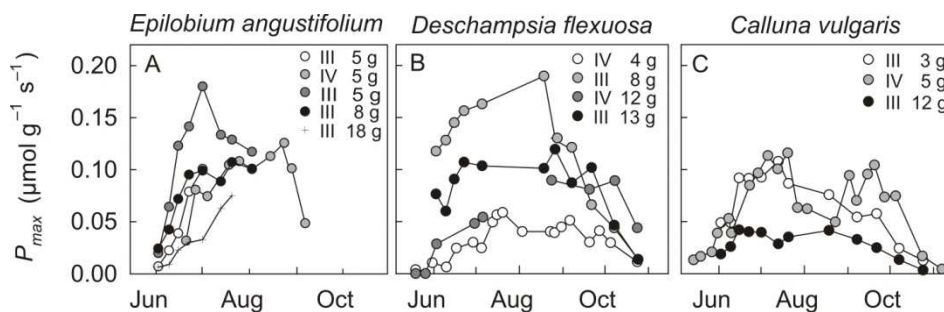


Figure 12. Leaf mass-based P_{max} (III,IV) of some individuals measured at clear-cut sites. A) *Epilobium angustifolium*, B) *Deschampsia flexuosa*, C) *Calluna vulgaris*. The original article and the leaf masses are introduced in the legend. Measurements were performed in 2005 (III) and 2006 (IV).

Annual photosynthetic production of ground vegetation

The ground vegetation differed at the measuring sites (Table 1), being mostly deciduous with highest P_{max} at the open sites where the light intensity was also highest. As a result, the photosynthetic production decreased with stand age (Fig. 13, **V**). The annually photosynthesized carbon by ground vegetation was approximately 350 g C m^{-2} at the 6- and 12-year-old VT sites when all species were considered (**V**, Fig. 13). Due to the high photosynthesizing biomass, as well as the occurrence of species with high photosynthetic rates, the production was higher ($760 \text{ g C m}^{-2} \text{ y}^{-1}$, **III**) at the fertile (MT-OMT) site whereas at the infertile (CT) site, the annual production was the smallest ($300 \text{ g C m}^{-2} \text{ y}^{-1}$, **III**). After canopy closure, the photosynthetic production was app. 168, 142 and 42 g C m^{-2} at the 20-, 45- and 120-year-old sites, respectively (**V**, Fig. 13). If we consider only the site-specifically measured species without assumptions for the other species present at the site, the GPP values were 328, 324, 157, 139 and 41 g C m^{-2} at the 6-, 12-, 20-, 45- and 120-year-old sites, respectively (**V**). The small difference between the integrated values can be explained by the minor biomass of species, whose photosynthesis was not measured.

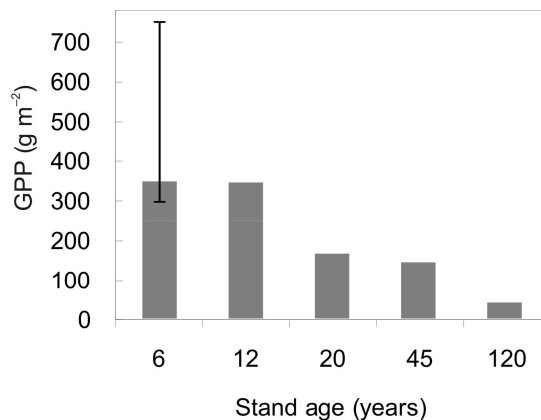


Figure 13. Annually photosynthesized carbon by ground vegetation in differently aged Scots pine forests in southern Finland (**V**) in 2006. The error bars represent the photosynthetic production at the poor (CT) and fertile (MT-OMT) clear-cut sites (**III**) in 2005.

DISCUSSION

Applicability of the different approaches

In the present study, we applied four different methods for studying the photosynthesis of ground vegetation:

1. Species-specific measurements of the photosynthetic activity (P_{max}) of the most common ground vegetation species (II–IV)
2. A soil chamber measuring the net CO₂ exchange of the forest floor (II) i.e. the NE chamber
3. A soil chamber measuring the net CO₂ exchange of the forest floor, including a darkening apparatus that made it possible to partition the soil CO₂ efflux from the photosynthetic signal of the ground vegetation, i.e. the light-dark chamber (II)
4. Eddy covariance (EC) which measures the net CO₂ exchange of the forest floor (II)

All of the methods include uncertainties, benefits and drawbacks concerning partitioning of the net exchange, temporal and spatial coverage etc. (Table 2). The various methods resulted in different momentary rates (II) and therefore, the choice of method and the generalization of the results obtained should be considered carefully. However, the methods introduced should not be considered as exclusionary or competing approaches; rather they complement each other. With limited resources, the aim of the study should determine the method to be used (Fig. 14). For instance, simulations of photosynthesis or photosynthetic production of ground vegetation under different environmental conditions or outside the study site require model parameter development and detailed knowledge of the underlying processes and of the separate responses of different species. Such requirements are met in the species-specific method (1) as well as in a chamber that includes a darkening apparatus (3). However, an automatic light-dark chamber needs notable technical supervision and financial investments.

EC measurements (4) is a good tool for obtaining the average photosynthesis over a large area but the partitioning of the signal to photosynthesis and respiration is needed. It is performed by first determining a relationship between the soil temperature and CO₂ efflux, the latter being the only flux during night-time when photosynthesis is hindered due to lack of light. The daytime respiration can be calculated from the temperature relationship if continuous measurements of soil temperature are available. The estimated respiration is then derived from the net exchange measured during the day light hours. Using the same procedure, it is possible to determine the photosynthesis of ground vegetation by also using NE chambers (2) that measure the sum of the soil CO₂ efflux and the photosynthesis of the ground vegetation.

Nevertheless, the soil CO₂ efflux is not controlled only by soil temperature but also by soil moisture (II, Simunek and Suarez 1993, Pumpanen et al. 2003) and recent photosynthesis (Tang et al. 2005, Stoy et al. 2007, Vargas et al. 2010). Therefore, the partitioning of soil efflux and photosynthesis during daytime can be inaccurate. In addition, the EC method requires turbulent mixing, which is often weak and insufficient during night-time below closed canopies. The estimation of diurnal patterns or the partitioning of different flux components is impossible, if most of the night-time values must be ignored

due to weak mixing (II). In addition, the photosynthetic signal of ground vegetation is smaller than the soil CO₂ efflux, especially late in the season. Therefore, inaccuracy in determining the soil CO₂ efflux can lead to striking inaccuracy in photosynthetic signal. As a result, such methods that require the partitioning of the net flux are not optimal for process studies.

Table 2: Summary of the characteristics of the various measurement methods used in the present study for determining the photosynthesis of ground vegetation. The eddy covariance (II) and the chambers (II) measure the sum of the soil CO₂ efflux and CO₂ exchange of the ground vegetation, whereas the species-specific method (II–IV) is based on species-specific measurements that are upscaled, using biomass inventory. The number of plus signs (+) corresponds to the benefits of the method and the minus sign (–) to missing features or drawbacks.

	Eddy covariance	NE chamber	Light-dark chamber	Species-specific method
Spatial coverage	+++	+	+	–
Temporal coverage	+	++	+++	+
Species-specific changes	–	+	++	+++
Photosynthetic signal	+	++	+++	+++
Automatic	+++	+++	+++	–
Portable	–	+	+	+++
Price	+	++	+	+++

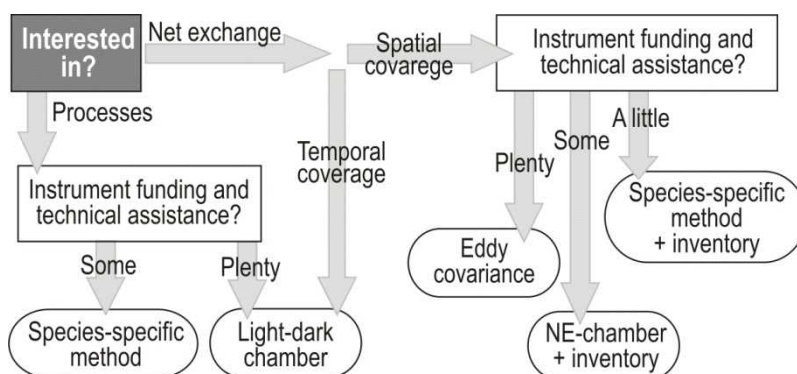


Figure 14. A decision tree for choosing a method for studying the photosynthesis of ground vegetation

EC (4) and the soil chambers (2, 3) are automatic, so they provide diurnal pattern on the net exchange unlike the species-specific method (1), which is operated manually. However, the species-specific method provides light-response curves that can with relative safety be also used outside the measuring moment if continuous light measurements exist. On the other hand, other environmental factors affecting photosynthetic activity, such as soil moisture and temperature, also vary. Therefore the result of species-specific method cannot be averaged over a long period of time. Nevertheless, the EC method often lacks temporal coverage below the canopy, because the results are reasonable only if the turbulent mixing is sufficient. As a result, the best method for measuring temporal changes in photosynthesis of ground vegetation is the light-dark chamber (3) but again, it requires technical supervision and financial investments (Fig. 14).

Since soil characteristics and vegetation are usually heterogeneous, a large-scale method such as EC would be the choice if the aim is to achieve reliable spatial average values for CO₂ exchange (Fig. 14). The net exchange chamber-based results cannot be averaged over a larger area without detailed information on the vegetation that usually is very variable spatially and also includes species that do not occur in the measurement chamber. The inventory data needed for justifying or upscaling the chamber measurements are usually not available or include wide confidence intervals. Upscaling of the species-specific method (1) is also used in addition to the inventory data, because the photosynthesis measurements are based on leaf mass.

Species-specific light-response parameters, together with measurements of light and the dry mass of the species within the light-dark chamber, allowed comparison between the photosynthesis measured over the entire plant community by the light-dark chamber (3) and the sum of the simulated photosynthesis of the respective species, i.e. the species-specific method (1) (II). The simulated photosynthesis for a plant community was generally higher than the measured photosynthesis. The comparison between these two methods demonstrates the difficulties in upscaling. The results differed, even though the area over which the upscaling and measurement occurred was relatively small and homogeneous. At the same time, the sum of the simulated photosynthesis by the inventoried species composition was generally smaller than the photosynthesis determined from the light-dark chamber, because the chamber contained more vegetation than was present in the area on average. The momentary rates of photosynthesis reported below the closed canopies were 0–3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for mosses and 0.5–6.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for all ground vegetation, the chamber based measurements being the highest (Table 3). The chambers are usually placed on undisturbed soil surfaces with well-developed ground vegetation, although forest floors normally also have unvegetated surfaces, such as bare rocks, stones or logging waste, which influence the average net exchange. Davidson et al. (2002) discussed why chamber measurements result in larger fluxes than EC-based estimates and concluded that the disagreement cannot be readily attributed to any of the known and well-characterized sources of error in chamber measurements. The chambers also resulted in higher fluxes than EC in the present study (II). If we assume that the EC measurements are correct, the clearest reason must therefore be the spatial variation. On the other hand, EC also has possible drawbacks (Aubinet 2008), such as advection of CO₂.

Table 3. Reported momentary photosynthesis (P , $\mu\text{mol m}^{-2} \text{s}^{-1}$) of feather mosses and all ground vegetation species below closed coniferous tree canopies. Age=tree age, Loc=Location. Species-sp.=Species-specific.

Species	P	Age	Loc.	Method	Reference
Mosses	0.6	69	Be	Chamber/ EC	Janssens et al. (2001)
Mosses	0.4	120	Fi	Species-sp.	V
Mosses	1	120	Ca-Sk	Chamber	Swanson and Flanagan (2001)
Mosses	2.2–3.0	–	Ca-Qc	Chamber	Bergeron et al. (2009)
Mosses	1.9 ^b	–	Ca-Sk	Portable ^a	Whitehead and Gower (2001)
Mosses	1.1 ^c	>200	Ca-Bc	Chamber	Botting and Fredeen (2006)
Mosses	0.5–1.0	–	Ca-Mb	Chamber	Goulden and Crill (1997)
All	2	20	Fi	Species-sp.	V
All	4–6.5	45	Fi	Chamber ^d	II
All	~2	45	Fi	Chamber	Kolari et al. (2006)
All	~2	45	Fi	Species-sp.	Kolari et al. (2006)
All	2–3	45	Fi	Species-sp.	II
All	1.7	45	Fi	Species-sp.	V
All	1.2–4.3	70	S	Chamber	Moren and Lindroth (2000)
All	2.7/5.7	70	S	Chamber	Widen (2002)
All	0.5	120	Fi	Species-sp.	V

^a portable system for photosynthesis

^b per leaf area

^c in CO₂ concentration of 430 ppm

^d A chamber with darkening apparatus (i.e. the light-dark chamber)

Additionally, research involving the vertical concentration profiles, comparisons between different instruments over a period in which the ambient air pressure can significantly change, or chamber measurements at different altitudes involves the risk of inaccuracy caused by incorrect pressure correction. At least in the case of relatively inexpensive and portable analysers, each device needs to be tested individually for changing conditions, because we observed even sensor-specific reaction to pressure changes (**I**).

Photosynthesis of vascular ground vegetation

The model for photosynthetic activity (Eq. 3) succeeded relatively well in simulating P_{max} for evergreen species *Calluna vulgaris* and *Vaccinium vitis-idaea*, indicating that the momentary level of photosynthetic activity in the species measured is mainly influenced by temperature history and soil moisture. However, intraspecific differences also exist, such as individual reactions to drought. These may be due to genetic differences or different shoot-root ratios, which affect the ability to withstand drought stress. However, local environmental variations in resource availability, due either to competition or microsite

quality, affect the associations, e.g. between reproductive output and net primary production (NPP) or plant size and survival, probably more strongly than do genetic differences between individuals (Pearcy et al. 1987). Therefore, intraspecific variation may be caused by microsite variation in the soil properties, i.e. water and nutrient availability that has affected photosynthetic activity.

There are not many studies on the annual pattern of photosynthesis of the ground vegetation in boreal regions but Gerdol et al. (2000) observed that the net CO₂ exchange of *V. myrtillus* declined from June to September. In the present study, apart from the shoots that suffered from the drought, the photosynthetic activity remained high until early September at the 45-year-old site and as late as until late October at the 120-year-old site.

Several studies have reported that early-successional species have high rates of photosynthesis (Bazzaz 1979). The rate of photosynthesis has also been positively associated with growth rate (Atkin et al. 1997). In general, the species in the present study that are fast-growing and can be associated with early succession have higher leaf mass-based momentary rates of photosynthesis compared to low shrubs and mosses.

A number of studies have found that the rates of photosynthesis per leaf weight, specific leaf area and leaf mass ratio are higher in plants grown in high-nitrogen soils (Field et al. 1983, Field and Mooney 1983, Poorter et al. 1995, Masarovicova et al. 2000). Reduction in nitrogen supply adversely affects photosynthesis, since nitrogen forms the basic constituent of chlorophyll. Chapin (1980) showed that wild plants from fertile habitats respond to moderate nutrient stress by decreased photosynthetic rate. *Epilobium angustifolium* was the only species that was measured in significantly different soil types in the present study, but the shoots at the infertile site actually had higher leaf mass-based photosynthetic activity (P_{max}) than those at the fertile site (III). Erley et al. (2001) found that under a low-nitrogen supply, the leaves of some grasses had higher amounts of vascular bundles and fibrous cells and lower amounts of intercellular space and therefore higher densities of the leaves. The differing composition and density of leaves may also explain the unexpected differences in the mass-specific expression of our results with *E. angustifolium*. Nevertheless, the shoot-based photosynthesis was higher at the fertile site.

Erley et al. (2002) found that the nitrogen supply extends the life span of the leaf. In contrast to the shoots at the infertile site, the photosynthetic activity of the experimental shoots at the fertile site did not decrease significantly at the end of the campaign (Fig. 3B in III). However, confirming the results of Erley et al. (2002) would need prolonged measurements, because the campaign ended early for *E. angustifolium*.

Below a closed canopy, *Vaccinium myrtillus* has high and mosses low mass-based rates of photosynthesis, whereas the rates of *V. vitis-idaea* and *Calluna vulgaris* are intermediate (Fig. 7, Table 4). The other values reported are more or less similar. The decrease in overall leaf mass-based level of photosynthesis of *Vaccinium vitis-idaea* and *Calluna vulgaris* as related to increased tree age (Fig. 9, Table 4) can be associated with lower levels of nitrogen in leaves of shade-adapted plants, a prediction generally supported by numerous studies (Chapin et al. 1987), because the availability of nitrogen for ground vegetation possibly also decreases with increasing tree age. The number of stomata may also decrease in shade (Woodward et al. 2002).

Photosynthesis of mosses

The rates of photosynthesis of mosses are low compared with that of vascular plants (Tables 3, 4) and the photosynthetic activity seemed not to have a clear seasonal cycle. Low photosynthetic activity (P_{max}) occurred after the rain-free period and high values after precipitation. The model (Eq. 7) based on temperature history and recent precipitation seemed able to predict the rapid changes in the photosynthetic activity of mosses (Figs. 6,7 and Table 2 in IV). The rain events are reported to act as the main cause of growth (Busby et al. 1978, Skre and Oechel 1981, Bonan and Shugart 1989). Our results indicate that the photosynthetic rate of mosses in natural growing environments is mainly explained by recent rain events. The maximum mass-based P_{max} of mosses observed at the 120-year-old site was higher than the maximum at the clear-cut, but most values were within the same range (IV). The mass-based values were highest at the 12-year-old site, probably due to the lowest population density compared with the other sites and thus the least amount of self-shading.

Table 4. Leaf mass-based maximum P_{max} values ($\text{nmol g}^{-1} \text{s}^{-1}$) reported for feather mosses and low shrubs and the prevailing tree age (y), location and reference in Scots pine forests.

Species	P_{max}	Age	Loc.	Reference
feather moss	20	–	–	Mccall and Martin (1991) ^a
feather moss	20	45	Fi	Kolari et al. (2006)
feather moss	15	45	Fi	II
feather moss	11	120	Fi	V
feather moss	17	120 ^b	US-Ak	Skre and Oechel (1981)
<i>Vaccinium myrtillus</i>	55	–	–	Widen (2002)
<i>Vaccinium myrtillus</i>	69	–	–	Wielgolaski (1975) ^a
<i>Vaccinium myrtillus</i>	139	45	Fi	Kolari et al. (2006)
<i>Vaccinium myrtillus</i>	184	45	Fi	II
<i>Vaccinium myrtillus</i>	171	45	Fi	V
<i>V. vitis-idaea</i>	55	–	–	Widen (2002)
<i>V. vitis-idaea</i>	41	6	Fi	V
<i>V. vitis-idaea</i>	37	12	Fi	V
<i>V. vitis-idaea</i>	33	45	Fi	Kolari et al. (2006)
<i>V. vitis-idaea</i>	57	45	Fi	II
<i>V. vitis-idaea</i>	47	45	Fi	V
<i>V. vitis-idaea</i>	21	120	Fi	V
<i>Calluna vulgaris</i>	107	5	Fi	III
<i>Calluna vulgaris</i>	116	6	Fi	V
<i>Calluna vulgaris</i>	79	12	Fi	V
<i>Calluna vulgaris</i>	62	45	Fi	Kolari et al. (2006)
<i>Calluna vulgaris</i>	64	45	Fi	V
<i>Calluna vulgaris</i>	69	45	Fi	II
<i>Calluna vulgaris</i>	57	120	Fi	V

^a Cited in Widen (2002)

^b Black spruce (*Picea mariana* (P. Mill.) B.S.P.) forest

The photosynthetic measurements of mosses in their natural growing environments appeared to be very challenging, due to their low photosynthetic signal and the growth form that prevents any possibility of enclosing only the shoots in the chamber (II, IV). Therefore, the measurement was a sum of the photosynthesis of mosses and soil CO₂ efflux, in which the latter signal predominated. In manual measurements, the weak photosynthetic signal of mosses together with the measuring setup that also included soil CO₂ efflux led to very scattered light-response curves (IV, Fig. 15), and therefore, also unreliability in the parameters obtained. The automatic measurement setup (II) measured daily app. 60 times, allowing more detailed analysis of the results and the parameters of the Michaelis-Menten-type light-response curve used (Eq. 1). Parameter b was small during rainy days and generally lower in midsummer than in spring or autumn, meaning deeper penetration of light into the population at high solar elevations. The most noteworthy observation is, however, the strong relationship between the CO₂ efflux from the quartz sand and P_{max} (Fig. 11): both the photosynthesis and CO₂ efflux were restricted by low water content. Precipitation or artificial increase in water content increased both fluxes, which indicates the rather poor carbon-holding capacity of mosses.

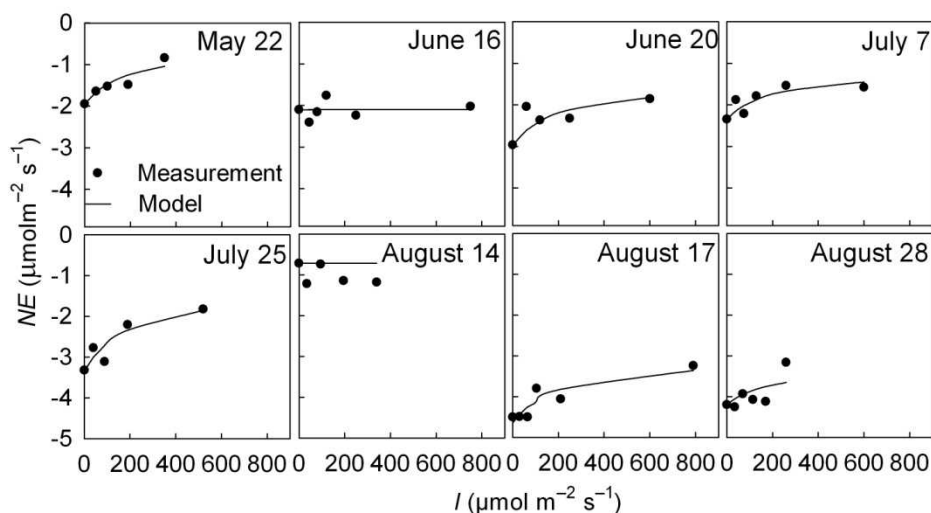


Figure 15. Examples of some measured and modelled (Eq. 1) light (I)-response curves in the net CO₂ exchange of mosses at the 6-year-old site in 2006 (IV). The photosynthesis on June 16 and August 14 is considered to have been restricted by rain-free periods.

Self-shading

Below the canopy, light conditions are often patchy, with short-time sunflecks on the otherwise shaded forest floor. Irradiance also decreases steeply inside the ground vegetation and further in the moss layer. The differences in prevailing light conditions lead to different types of light responses in the upper leaves and lower leaves of a plant. The same difference occurs between early- (shade-intolerant) and late-successional (shade-tolerant) species. Usually the upper leaves have high photosynthetic activity whereas the steepness of the curve is low while the situation is reversed in leaves near the ground.

Due to the low number of measurements per light-response curve, we had to use a light-response with a low number of parameters, a Michaelis-Menten-type equation (Eq. 1). In addition, we also had to keep the b -parameter constant, because it is closely related to P_{max} , which makes the simultaneous parameter estimation unstable. However, parameter b shows some signs of inconstancy. The value for b is small at low solar angles and in low-light environments, such as on cloudy days. The leaf mass increases during the growing season, which affects interception and attenuation of light in the crown, i.e. self-shading. However, to determine the nature of b would need more frequent high-quality data.

The levels of photosynthesis and respiration of a whole-plant were more similar between the plant individuals than the results based on full-grown leaf mass (III). With the exception of size, there were no clearly visible differences in the shoots, such as colour or mortality of the leaves. A dense *Calluna vulgaris* shoot also had substantially lower leaf mass-based P_{max} values than the sparser shoot and comparison between the mass-based measurements of *Deschampsia flexuosa* led to the same conclusion: The sparser population occasionally showed leaf mass-based P_{max} values twice as high as those of the denser population (Fig. 12C).

The effect of self-shading could be one explanation for the various leaf mass-based levels of photosynthesis. Self-shading creates a heterogeneous light environment that influences both the rate of photosynthesis and acclimation to the contrasting light environment. Acclimation of photosynthesis to self-shading occurs even in mature leaves (Ishida et al. 1999). On the other hand, there could be physiological factors that limit photosynthesis in the species measured. The water transport or root systems of these species may not be capable of efficiently supplying shoots with high leaf mass.

Simulated photosynthesis of the respective species within the light-dark chamber was generally higher than the chamber measurement (Table 3, II) probably due to high levels of self-shading caused by the dense vegetation in the light-dark chamber. The photosynthetic parameters were obtained from species-specific measurements during which the shoots never shaded each other, whereas the shoots and leaves overlapped when the whole-plant community was measured in the chamber. In addition, the species-specific photosynthesis of mosses was measured with no shading from other vegetation, while the light intensities below the dense shrub population in the chamber or at the measuring site in general were probably low.

Annual photosynthetic production

Photosynthetic production by ground vegetation decreases with stand age (Fig. 13, Table 5) because 1) light availability decreases with stand development, 2) the dominant species below the canopy have lower rates of photosynthesis than species in open areas and 3) the biomass of the ground vegetation decreases with stand age.

Below the closed canopy, the GPP of the ground vegetation was 146 and 41 g C m⁻² at the 45- and 120-year-old sites, the younger site of which is in the upper end of the published results that are summarized in Table 5. The published results differ, due to differences in climate, biota and abiotic factors, such as light intensity. Therefore, comparison of photosynthetic production over successive or different vegetation compositions based on the published results is impossible, because mosses, shrubs, herbs and grasses vary in their occurrence and the species have specific strategies for projecting the changes in environment to their photosynthetic rates.

Calluna vulgaris and *Vaccinium vitis-idaea* showed increased growing season length below the canopy, compared with open sites even if the site-specific temperatures were included in the analysis. The spring and fall periods may be important to the annual carbon gain of evergreen plants and Landhausser et al. (1997) showed that the adaptation is likely to be related to the ability of evergreen species to function at low temperatures. Goulden et al. (2006) revealed that the length of the growing season in Manitoba changed markedly with stand age, being approximately twice as long at the old sites as at the young sites. Welp et al. (2006) also found a shorter growing season in a 15-year-old stand than in an 80-year-old stand.

The process-based upscaling procedure used is very sensitive to leaf mass, which is very laborious to estimate, precisely due to the high spatial heterogeneity of ground vegetation. In addition, the biomass involves a factor of self-shading that is high in dense growth populations (II, III). Measuring all the species present is very laborious and there are differences in the level of and in the reactions to environmental factors, even within species. In addition, the model used, e.g. the time constant (τ , Eq. 2), also needs further testing.

The light-response curves of mosses were measured with no shading from other vegetation. An approximation of the light attenuation in the upper vascular vegetation with frequency estimation of uncovered and mixed populations would improve the model in theory. In practice, however, the density and composition of the predominating vegetation are varying and unpredictable in detail and, therefore, developing the P_{max} model towards such details would demand much fieldwork.

Due to these several sources of inaccuracy, it is difficult to set an exact confidence interval for the site-specific annual sums of photosynthetic production. Simultaneous measurements of CO₂ exchange on an ecosystem scale would increase the reliability of the determination of GPP at the stand level. However, the results obtained with chamber measurements give information on the role of different species in the CO₂ exchange and are in the same range as other net exchange studies.

Table 5. Reported annual GPP of ground vegetation (g C m^{-2}), percentage (P) of ground vegetation of the total GPP of the forest, tree age, predominating tree species, location and reference

GPP	P	Age	Tree species	Loc.	Reference
172 ^a	-	5		Ca-Bc	Pypker and Fredeen (2002)
315 ^b	-	5		Ca-Bc	Pypker and Fredeen (2002)
300	-	5	Scots pine	Fi	III
760	-	5	Spruce	Fi	III
352	-	6	Scots pine	Fi	V
349	-	12	Scots pine	Fi	V
168	-	20	Scots pine	Fi	V
90–135	9–13%	45	Scots pine	Fi	Ilvesniemi et al (2009)
83/131	13%	45	Scots pine	Fi	Kolari et al. (2006)
146	-	45	Scots pine	Fi	V
130–210	-	70	Mix. conifer	S	Widen (2002)
190	-	70	Mix. conifer	S	Moren and Lindroth (2000)
170	3–12%	112	Spruce	De	Subke and Tenhunen (2004)
108 ^c	13% ^d	120	Black spruce	Ca-Sk	Swanson and Flanagan (2001)
41	-	120	Scots pine	Fi	V
-	10–50%	120	Black spruce	Ca-Mb	Goulden and Crill (1997)
105–137 ^e	13–24%	-	Black spruce	Ca-Qc	Bergeron et al. (2009)

^a Woody shrubs

^b Herbaceous plants

^c Feather mosses in May–Oct

^d Sphagnum and feather moss

^e May–Oct

CONCLUDING REMARKS

The ground vegetation comprises only a small fraction of the total ecosystem carbon content, and therefore, it has been widely neglected in previous research on CO_2 exchange. However, the ground vegetation greatly influences the functioning and carbon cycling of the ecosystem.

Ground vegetation species form a diverse group of vascular and nonvascular, annual and perennial, deciduous and evergreen species with different types of strategies for growing and photosynthesizing. The environmental factors cause varying response in different species, and therefore the species-specific reactions to changes in the environment need to be identified to estimate the level of photosynthetic production in a variety of forests with diverse species composition and environmental factors.

The photosynthesis of low shrubs and also partly the changes in photosynthesis of deciduous species can be explained by light, temperature history, soil moisture and recent

possible frosts. Light and air temperature play the biggest role, but drought also decreases the photosynthetic activity although intraspecific variation occurs as well. Light and the occurrence of rain events explain most of the variation in the biomass-based photosynthesis of mosses.

Leaf mass-based photosynthesis is highest in deciduous species and, therefore, photosynthetic production was notably higher at a fertile site with high occurrence of grasses and herbs than at a poor clear-cut site. In general, the occurrence of evergreen species is highest at poor sites and below canopies, whereas grasses and herbs predominate at fertile sites and open areas. As a result, the photosynthetic production of ground vegetation decreases with stand age. In addition, the leaf mass-based photosynthetic activity of *Calluna vulgaris* decreased with the age of the surrounding trees. The photosynthetic activity of *Vaccinium vitis-idaea* did not decrease until the latest phases of succession. On the other hand, the growing season was prolonged below canopies.

The photosynthetic productions of ground vegetation obtained include uncertainties from intraspecific variation and self-shading. The result of the species-specific method is also very sensitive to biomass. Nonetheless, the method used is crucial to finding detailed species-specific responses of photosynthetic activity to environmental changes. In general,

Measuring CO₂ fluxes has many other potential sources of error, starting from CO₂ concentration readings. Users should be familiar with their analysers and measurement setups and test the performance with varying environmental factors. Different measuring methods for CO₂ exchange should not be considered as exclusionary or competing, but rather as complementary approaches. They all have advantages as well as shortcomings and simultaneous use of all would be most informative. If this is not possible, the aim of the study should guide the choice of the method used. For instance, to simulate the photosynthesis of ground vegetation under different environmental conditions or in areas other than those near the measuring site requires detailed understanding of the underlying processes. Measurements of the photosynthesis of individual species provide precise information on the photosynthetic capacity and separate responses of different species. Therefore, shoot measurements are likely very useful for model parameter development. On the other hand, due to upscaling difficulties, a large-scale method would be the choice if the aim is to achieve representative average values for CO₂ exchange of the particular site.

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