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Photosynthetic production of boreal ground vegetation after a forest clear-cut

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Abstract

Heather (*Calluna vulgaris*), rosebay willowherb (*Epilobium angustifolium*), wavy hair-grass (*Deschampsia flexuosa*) and raspberry (*Rubus idaeus*) are typical species on boreal clear-cut sites. According to our study, they all had clear and species-specific annual cycles of photosynthetic activity (P_{max}). The maxima of *C. vulgaris* and *E. angustifolium* occurred around June and July, while that of *R. idaeus* occurred as late as in August. The photosynthetic activity of *C. vulgaris* followed the temperature history closely when the soil moisture was high. Deciduous *D. flexuosa* also followed the temperature history, unlike *E. angustifolium* and *R. idaeus*. During a short drought, some shoots decreased their P_{max} levels but none of the species showed congruent reactions within individuals. In general, we noticed that the comparison of P_{max} or respiration of different shoots caused less discrepancy when based on ground area than on leaf mass. Using species composition and continuous temperature and light measurements, we upscaled the species-specific process rates and integrated fixed and respired CO_2 of ground vegetation during an entire growing season 2005. The photosynthetic production of ground vegetation was 760 g C m^{-2} y^{-1} at the fertile site and 300 g C m^{-2} y^{-1} at the infertile site. During the snow-free period (18 April–21 November), *C. vulgaris* respired 68 g C m^{-2} y^{-1} and *E. angustifolium* 7 g C m^{-2} y^{-1} at the infertile site. At the fertile site, *E. angustifolium* and *R. idaeus* respired 22 and 12 g C m^{-2} y^{-1}, respectively.

1 Introduction

Current climate scenarios suggest that the global mean temperature will increase in the 21st century, due to increased concentrations of greenhouse gases such as carbon dioxide (CO_2) in the atmosphere (IPCC, 2007). The increase is predicted to be largest in the highest latitudes. Precipitation patterns are also expected to change dramatically, which may result in serious consequences to the present vegetation. These scenarios have resulted in several studies on vegetation and plant processes related to CO_2

exchange, i.e. photosynthesis and respiration.

Until recently, research on CO_2 fixation has mainly focused on photosynthetic production of trees. However, due to timber harvesting 282 000 ha (1.4%) of forests in Finland are completely treeless and 3 264 000 ha (16.1%) of forests are younger than 20 y. (Metla, 2004). Therefore, a significant part of these forests is in the early phase of succession.

During the first phases of succession, the number of vascular plant species is high (e.g. Pykälä, 2004) and the irradiation environment is unshaded. Opportunistic, shade-intolerant, nutrient-demanding, fast-growing and well-dispersed vascular plant species predominate before more competitive trees eliminate or reduce the role of opportunistic species at ground level. The rapid growth of ground vegetation after clear-cutting heavily affects nutrient cycling, because the ground vegetation biomass is high as well as the nutrient concentration in the tissues of the opportunistic species (Palviainen et al., 2005). The succession patterns and ecology of ground vegetation are well studied, but the photosynthetic production of the ground vegetation is still poorly known.

Different species have species-specific strategied for competing and surviving in their natural growing environments. For example, perennial leaves require longer periods to produce benefit due to slow development, costly production and low photosynthetic production (Chabot and Hicks, 1982). Deciduous species are effective assimilators, but their growing seasons are shorter. In contrast, a considerable fraction of the carbon fixed in photosynthesis is lost as CO_2 during respiration. Respiration serves many important functions, such as supply of energy for maintenance of membranes, proteins, and ion gradients and the structural building blocks for new biomass. Van't Hoff already noted in 1884 that the chemical reactions in a plant are dependent on temperature. The temperature dependence of respiration is also influenced by many factors such as species, growth habit, age, nutrients and water supply (Taiz and Zeiger, 2002). For reliable estimations of photosynthetic production from large areas, we need to study the effects of different environmental factors on species-specific activity in fixing and releasing CO_2.

In traditional studies of CO_2 exchange, chamber measures over a small area with natural species composition and the role of different species are unobtainable. These studies face uncertainties in averaging the measurement over a single spot to a larger area because the ground vegetation usually is spatially very heterogeneous and changes substantially, even in a small area (Jalonen et al., 1998; Palviainen et al., 2005; Riutta et al., 2007; Kulmala et al., 2008). Some ecosystem scaling net CO_2 flux studies at young forests of various types has been carried out with the eddy covariance (EC) technique. These studies have mainly concerned the size of the carbon sink or source. However, the detailed analysis of the flux components indicate that the photosynthetic production of ground vegetation is substantial (e.g. Rannik et al., 2002; Kolari et al., 2004; Humphreys et al., 2006; Fredeen et al., 2007). Again, the EC measurements are unable to detect exactly the role of different species and small changes in photosynthetic activity. Therefore, we aimed at studying the processes and species-specific environmental responses. We quantified the yearly production by upscaling all the processes with species composition and environmental factors.

In the present study, we (1) measured the net CO_2 exchange and its components, photosynthesis and respiration, of common species separately during one growing season and (2) studied the relationship between the exchange processes and environmental factors on two 5-y-old clear-cut sites in southern Finland. One of the studied sites was very fertile, with fast-growing and opportunistic dominant species having rapidly reproducing new tissues. The other site is nutrient-poor, and the dominated species are evergreen and grow slowly. At both sites, we (3) upscaled fixed and respired CO_2 of ground vegetation for an entire growing season to estimate the potential range of CO_2 production present at any young site.

2 Materials and methods

2.1 Study site

We measured the CO_2 exchange of the most common forest floor species on two clear cut sites located approx. 7 km from the station for measuring ecosystem-atmosphere relations (SMEAR II, Hari and Kulmala, 2005) in Hyytiälä, southern Finland (61.52° N, 24.17° E). During the time period from 1960 to 2000, the annual mean temperature in the area was +2.9 °C and precipitation 709 mm. January was the coldest month (mean −8.9°C) and July the warmest (mean +15.9°C) (Drebs et al., 2002).

The parent material of the soil at the infertile site is glaciofluvial deposits and at the fertile site, the soil is glacial till. In the Food and Agriculture Organization – United Nations Educational, Scientific and Cultural Organization soil classification system, the soil type at both of the sites is a Haplic podzol (FAO-Unesco, 1990). The bedrock is mainly acidic granite, granodiorite and mica-gneiss with some small intrusions of gabbro and peridotite.

The sites had been clear-cut and sown earlier. Tree seedlings were approx. 5 years old at both sites in summer 2005 when we performed the fieldwork. One of the sites studied was very fertile, with fast-growing and opportunistic dominant species having rapidly reproducing new tissues, such as wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.), rosebay willowherb (*Epilobium angustifolium* (L.) Holub), raspberry (*Rubus idaeus* L.) and mosses (mainly *Pleurozium schreberi* (Willd. ex Brid.) Mitt.). The available nitrogen in the soil can be observed by the appearance of nitrogen indicators such as *D. flexuosa* and *E. angustifolium*. The other site is nutrient-poor, and the dominant species are evergreen and grow slowly. At this infertile site, heather (*Calluna vulgaris* (L.) Hull), mountain crowberry (*Empetrum nigrum* L.) and mosses (mainly *P. schreberi*) dominated the ground vegetation, with some sparse growth of *E. angustifolium*.

In 2005, the mean tree height of Scots pine (*Pinus sylvestris* L.) was 0.9 m and density 1200 ha^{-1} while the mean tree height of birch (mainly downy birch *Betula pubescens* Ehrh.) was 1.5 m and density 710 ha^{-1} at the infertile site. At the fertile site, the average tree height of Norway spruce (*Picea abies* (L.) H. Karst.) was 0.4 m and density 5000 ha^{-1} and the average tree height of birch (mainly *B. pubescens*) 1.5 m and density 16 000 ha^{-1}.

To upscale the measured activity of photosynthesis, we continuously measured PAR (photosynthetically active radiation) with an LI-190 (LI-COR Biosciences, Lincoln, NE, USA) at the SMEAR II station above the canopy. Due to lack of shade and close distance, it is similar to the average radiation at the clear-cut sites. Soil water suction was measured manually at app. 2-week intervals, using eight tensiometers (Soil Measurement Systems (TX), Tuscon, AZ, USA) and a Tensicorder (Soil Measurement Systems) at a depth of 3 cm in mineral soil.

We measured the air temperature at 2-m height at the open Siikaneva fen in southern Finland (61.48° N, 24.09° E.) at the same altitude from sea level as the clear cut sites. Siikaneva is approx. 5 km west of the SMEAR II and 4 km from the clear-cut sites. There were some gaps (26 May–1 June, 7 July–5 August, 9 August–18 August, 30 August–16 September) in the measured temperature series that were filled with temperature readings from a 16-m height at the SMEAR II station. In general, the temperatures at the SMEAR II and at the Siikaneva fen were very similar except for spring and early summer when the night temperatures were cooler at the open fen than at the SMEAR II.

2.2 Sampling of vegetation

We estimated the average biomass of ground vegetation at the sites by systematically collecting aboveground samples of forest floor vegetation from an area of 300 m^2. The sample numbers were 20 and 19 at the infertile and fertile sites, respectively. The samples were collected systematically at 5-m intervals on four lines 5 m apart. One sample was 0.090 m^2 in size. We separated each sample into different species and each species into leaves and stems if possible. These segments were weighed after drying at 60°C for 24 h.

2.3 Chamber measurements of CO_2 exchange

A manual chamber, based on the closed static chamber technique, was used for measuring the light response curves of CO_2 exchange. The measurements were begun on 2 June and ended on 24 October 2005. All of the measurements were carried out between 08:00 and 13:00 but we varied the measurement order among shoots. We repeated the measurements at app. 2-week intervals on two shoots of *Epilobium angustifolium* and *Calluna vulgaris* on the infertile site and two shoots of *Epilobium angustifolium* and *Rubus idaeus* and two populations of *Deschampsia flexuosa* at the fertile site.

The chamber was made of 5-mm-thick transparent Plexiglas 0.30 m in diameter, 0.30 m in height and open towards the ground. During the measurements, the chamber was placed on a polyvinylchloride (PVC) collar that was perforated to allow air to circulate freely under the chamber. 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 to the environmental factors or disturbance to the shoots. Some of the shoots grew taller than 30 cm and in this case, we used an otherwise identical chamber but 0.40 m in height. *Deschampsia flexuosa* was measured with a higher chamber but no cellular plastic was used as a bottom. A solid, plastic collar was placed in the soil and the shoots freely entered the chamber. The measurement signal was then a sum of the soil CO_2 efflux and photosynthesis of *D. flexuosa*.

The CO_2 concentration inside the chamber was monitored during the measurement with a CO_2 probe based on a nondispersive infrared sensor (NDIR) technique (GMP343; Vaisala Corporation, Vantaa, Finland) attached inside the chamber. The CO_2 concentration readings were recorded at 5-s intervals and corrected automatically for humidity, temperature and pressure with a data recorder (MI70; Vaisala Corporation). The humidity and temperature values used in the correction were obtained from a temperature and humidity probe (HMP75; Vaisala Corporation) attached inside the chamber and connected to the MI70 data recorder. A small fan was used to mix the air inside. Instantaneous irradiation was measured with a PAR sensor (LI-190, LI-COR Biosciences) attached outside the chamber. Atmospheric pressure was continuously monitored at the SMEAR II station. The rate of CO_2 exchange was estimated from a linear regression fitted to CO_2 readings over a 3-min time. During high photosynthetic activity in summer, the measuring period in high light intensity was shortened to 1 min to avoid heating of the chamber.

One set of measurements consisted of four to six measurements with different light intensities and one dark measurement. 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. During the dark measurement the chamber was fully darkened with an aluminium cover. After the campaign the aboveground parts of the measured plants were collected, dried for 24 h at 60°C and weighed to obtain the leaf and total biomasses.

Photosynthesis is driven by light but the relationship between light and photosynthetic rate is saturating because the availability of CO_2 begins to limit in high light intensities. Respiration accompanies the observable CO_2 exchange during daytimes. Therefore we fitted a Michaelis-Menten-type equation (Michaelis and Menten, 1913) for each set of our measurements as follows:

$$NE_i(I) = \frac{P_{\max,i}\, I}{b_i + I} - r \tag{1}$$

In the equation, $NE_i(I)$ is the species-specific leaf mass-based ($\mu\mathrm{mol\,g^{-1}\,s^{-1}}$) or the ground area-based rate of CO_2 exchange ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), I is the light intensity ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), b is the light intensity ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) when the assimilation rate is half the rate of light-saturated assimilation, r is the rate of dark respiration and $P_{\max,i}$ is the rate of light-saturated assimilation per leaf mass ($\mu\mathrm{mol\,g^{-1}\,s^{-1}}$) or per ground area ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), i.e. photosynthetic activity. The photosynthetic activity indicates the amounts and catalytic activities of photosynthetic enzymes (Pearcy et al., 1987).

Respiration is strongly influenced by temperature and the dependence is often described as a exponential function. Therefore, we fitted an exponential model of species-specific temperature dependence, $r_i(T)$, into the r parameters (Eq. 1) and instantaneous temperature measured during the photosynthesis measurement, T, as follows:

$$r_i(T) = r_{0,i} Q_{10,i}^{\frac{T}{10}} \tag{2}$$

where $Q_{10,i}$ and $r_{0,i}$ are species-specific parameters.

In Boreal region, there is a clear annual cycle in photosynthesis. To study the changes in the rate of photosynthetic, we used a function called state of development, S (°C, Pelkonen and Hari, 1980; Mäkelä et al., 2004). S follows temperature with a time constant τ:

$$\frac{dS}{dt} = \frac{T(t) - S}{\tau} \tag{3}$$

where $T(t)$ is temperature in °C at moment t. As the temperature, we used hourly averages that were measured at Siikaneva. The initial value of S was set to be the first value of temperature when the estimation was begun on 1 April 2005.

The estimated daily $P_{\max,i}$ values, $\bar{P}_{\max,i}$, were assumed to follow the S values. The highest estimated $\bar{P}_{\max,i}$ was set to the highest measured species-specific $P_{\max,i}$ value on the measuring date ($t_{\max,i}$). Other daily values were estimated by the relationship between the estimated daily $S(t)$ value and the $S(t_{\max,i})$:

$$\bar{P}_{\max,i}(t) = \frac{S(t)}{S(t_{\max,i})} P_{\max i}(t_{\max,_i}) \tag{4}$$

If $S(t)$ was smaller than 0°C, $\bar{P}_{\max,i}(t)$ was set to zero.

The above model of state of development described properly only the measurements of *Calluna vulgaris* and *Deschampsia flexuosa*. Therefore we estimated the species-specific daily $\bar{P}_{\max,i}(t)$ parameters for *Epilobium angustifolium* and *Rubus idaeus* by interpolating the intermediate values from the measured average $P_{\max,i}$ values.

2.4 Upscaling

We upscaled the mass-based and species-specific parameters of photosynthesis (Eq. 1) over the whole site using plant biomasses from the sampling. To estimate the assimilation over the entire season, P_e, we integrated the momentary rates by continuous PAR measurements above the SMEAR II canopy:

$$P_e = \sum_i \int_{t_1}^{t_2} m_i \frac{\bar{P}_{\max,i}(t) I(t)}{b_i + I(t)} dt \tag{5}$$

where i is the species measured (*Deschampsia flexuosa*, *Calluna vulgaris*, *Epilobium angustifolium, Rubus idaeus*), m_i is the areal average leaf mass of species i, $\bar{P}_{\max,i}(t)$ and b_i the species-specific parameters and $I(t)$ the PAR intensity (30-min average) measured at the SMEAR II station. The upscaling was begun on 18 April (t_1) and lasted until 21 November (t_2).

For the estimation of released mass of carbon dioxide, R_e, we integrated and summed the species-specific respiration rates

$$R_e = \sum_i \int_{t_1}^{t_2} m_{\text{tot},i} R_i(T(t)) dt \tag{6}$$

where $m_{\text{tot},i}$ is the species-specific total aboveground mass, also including the stems of small shrubs, $R_i(T(t))$the model of temperature dependence (Eq. 2) and T the temperature.

3 Results and discussion

3.1 Weather

The weather was fairly typical during the snow-free period in 2005. The snow had melted entirely by 18 April 2005 at the SMEAR II site. The daily average air temperatures began to fluctuate above zero in late March after being below zero for several months (Fig. 1a). This cool period lasted until early May when the daily average temperatures began to increase, remaining above 10°C for 1 week. Thereafter followed another cool period. The daily average temperature crossed 10°C steadily in early June. In late June to early July, there was again a colder and rainy week, after which the average and maximum temperatures increased again, but the minimum temperatures were as low as 2°C on 2 July. The average temperature began slowly decreasing in mid-July but crossed 0°C for the first time as late as 19 October. However, the minimum temperatures had already been very close to zero in mid-September and crossed it for the first time on 29 September. The first snow appeared on 24 October and became permanent on 21 November. During snow-free period, the modelled state of development (Eq. 4, τ=150, Fig. 1c) followed the air temperature.

Soil temperatures affect biomass allocation (DeLucia et al., 1992), root growth (Ryyppö et al., 1998) and nutrient uptake. At the sample sites, the soil temperature closely followed the average air temperature attaining a maximum (17°C) in the mid-July (Fig. 1b) slightly after maximum air temperature. There were no clear differences in the soil temperatures at the sites; However, the temperatures were generally 5°C higher in the clear-cuts than in their surrounding forests. The peat temperature readings in the Siikaneva fen began to increase on 14 April 2005, which suggests that the snow had already melted by then in the open areas. However, Bergeron et al. (2008) noticed that the photosynthetically active growing season began about 1 week later and ended 1 week earlier at a clear cut site compared with the mature site. Therefore we can assume that the growing season had not started much earlier than our measurements. The small sizes of the deciduous shoots in the beginning of our measurement campaign similarly suggest that the growing season was in its early phase.

There were two rain-free warm periods (Fig. 2b) that caused the soil water tension to increase for a short period of time (Fig. 2a) after mid-June and in early July. Except for these short droughts, the soil was fairly moist.

3.2 Vegetation at the sites

The results of the vegetation inventory are shown in Table 1. The total biomass of the above ground parts of the vegetation was approx. 360 g m^{-2} and 240 g m^{-2} at the infertile and fertile sites, respectively. The high value of the infertile site can be explained mainly by the wooden parts of *Calluna vulgaris*. In general, 94% of the vegetation at the infertile site comprised species with perennial leaves, while the same value for the fertile site was only 27%, if mosses are considered perennial. At the infertile site, *C. vulgaris*, lingonberry (*Vaccinium vitis-idaea* L.), *Empetrum nigrum* and *E. angustifolium* had the highest biomass of the vascular species. At the fertile site, the species were *D. flexuosa*, *E. angustifolium*, *V. vitis-idaea* and *R. idaeus*. *V. vitis-idaea* and mosses of different kind were found most frequently from different sample plots on the infertile site. On the fertile site, the most frequent species were grasses (most commonly *D. flexuosa* and *Calamagrostis sp.*) and *R. idaeus* and *E. angustifolium*.

Mosses were denser at the infertile site. *Pleurozium schreberi* and *Dicranum polysetum Sw.* were the most common species at the infertile site and an the fertile site, *D. polysetum* and *Polytrichum* Hedw. Sp. were the most typical species.

3.3 Photosynthesis

3.3.1 Initial slope of the light response curve

Parameter b_i in Eq. (1) describes the light level at which photosynthesis is half the maximum rate of photosynthesis. The smaller parameter b is, the more rapidly photosynthesis saturates in the increasing light. The parameters $P_{\max}$ and b are closely related and the values of the parameter b tend to be too high at low light levels. In addition, a small number of measurements in one light response curve made the parameter estimation unstable. Therefore, we assumed that the species-specific b values were constant over the season. The b values used for *R. idaeus*, *E. angustifolium*, *C. vulgaris* and *D. flexuosa* were 221, 280, 216 and 259 $\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-2}$, respectively. *Calluna vulgaris* had slightly lower values at the SMEAR II station under canopy than the values we measured, although within the same range. Kolari et al. (2006) estimated the parameter b value to be 240 and Kulmala et al. (2008) to be 208 $\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-2}$.

However, parameter b of *Calluna vulgaris* appears to be maximal early in the year and decreases towards the end of the season (not shown). *Epilobium angustifolium* did not have a very clear trend in the estimated b values, except for one of the four shoots which showed a trend towards increase in late summer. One other shoot had secondary growth that clearly decreased its b values. The b values of *Deschampsia flexuosa* did not show a clear trend, except for late autumn when the b values were very low. The b values of the *Rubus idaeus* shoots followed the P_{max} values loosely. One was maximal at the same time as the P_{max} values in the middle of the season and the other somewhat after the peak in P_{max}.

3.3.2 Saturation level of the light response curve, P_{max}

3.3.3 Individual characteristics

The P_{max} values of *Epilobium angustifolium Calluna vulgaris*, *Rubus Idaeus* and *Deschampisa flexuosa* had very clear annual patterns (Fig. 3). In early June, the shoots of *E. angustifolium* and raspberries were still approx. 10 cm in height and the shoots of *D. flexuosa* were still fairly short. *Calluna vulgaris* has perennial leaves but the photosynthetic capacity was still quite low (Fig. 3b) due to cold temperatures. However, *C. vulgaris* recovered from winter very rapidly and its P_{max} values increased to more than double in the first half of June.

The leaf mass-based P_{max} values (Eq. 1) of four *E. angustifolium* shoots (Fig. 3e) varied widely. The ground area-based values (Fig. 3a) throughout the measuring period were more similar. There were no clear differences in the values at the two clear-cut sites. The shoots at the fertile site were taller, causing the ground area based values to be higher than those at the poor site. However, the status was reversed in the mass-specific inspection – probably a result of higher self-shading due to higher leaf mass (Fig. 3e). The shoots were quite identical at the poor site (masses 4.6 g and 5.4 g). However, the smaller shoot already showed significantly lower P_{max} values early in the campaign before it accidentally died in early July. At the fertile site, the shoots were of different sizes (18.0 g and 8.1 g) late in the campaign, due to secondary growth which began in early July in the larger one. The leaf mass-based P_{max} values of the dense shoot were very low probably due to high levels of self-shading. The self-shading or other limitations apparently had such a significant effect that the ground area-based results were more similar than the mass-based results.

Calluna vulgaris had substantially lower P_{max} values than the *E. angustifolium*, based both on individual and leaf mass. The dense *C. vulgaris* shoot (biomass 27.8 g) had substantially lower leaf mass-based P_{max} values than the sparser shoot (8.6 g, Fig. 3f) while the dense shoot assimilated per ground area more than the sparse shoot (Fig. 3b). Accordingly, we again observed that the shoots had more similar levels of photosynthesis when compared as shoots than as mass-based. *Rubus idaeus* did not show this type of phenomenon, but the shoots did not differ greatly. They had 3.0 g and 3.4 g of leaves, the smaller having slightly less ground-based photosynthesis (Fig. 3d) as well as higher leaf mass-specific P_{max} values (Fig. 3h).

Comparison between the mass-specific measurements of *D. flexuosa* indicates that grass populations also have some self-shading. The sparser population occasionally showed leaf mass-based P_{max} values twice as high as those of the denser population (Fig. 3g), except for the autumn measurements when the sparser population showed earlier senescence. On the other hand, we again observed that there is less variation between the results per ground area than per leaf mass (Fig. 3c and g). Unfortunately, the photosynthetic signal was very noisy during the hottest weeks in midsummer. Therefore, we rejected several measurements, thus obtaining a more than 1-month gap in the data that made the comparison more challenging. The reason behind the clearly weaker observations with the grasses was the different measuring setup as described earlier. High and fluctuating soil CO_2 fluxes could have disturbed the photosynthetic signal.

These results indicate that ground-based levels of photosynthesis is quite equal whereas mass-based values differ. Therefore the amount of shoots would be a more informative quantity than the actual leaf mass that is often used in scaling up the chamber fluxes over a larger area. The effect of self-shading could be one explanation for the various leaf mass-specific levels of photosynthesis. On the other hand, there could be a physiological factor that limits photosynthesis with high leaf mass. In addition, the water transport or root system may not be capable of efficiently supplying shoots with high leaf mass.

3.3.4 Environmental effects on $P_{\max}$ values

Epilobium angustifolium was the only species that grew at both the fertile and infertile sites in this study. At the fertile site, the shoots had higher leaf mass; however, photosynthesis of the entire plant was not substantially higher at the fertile site than at the poor site, but actually lower per leaf mass, as highlighted earlier (Fig. 3e). Erley et al. (2001) found that under 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 different composition and density of leaves may also explain the unexpected differences in the mass-specific expression of our results with *E. angustifolium*. In contrast to this study, several others found that the rates of photosynthesis and leaf respiration per leaf weight, specific leaf area and leaf mass ratio are higher in plants grown in high N soils (Field et al., 1983; Field and Mooney, 1983; Masarovicova et al., 2000; Poorter et al., 1995). Nevertheless, the difference in available nutrition did not significantly affect the rate of photosynthesis in this study.

Erley et al. (2002) found that N supply extends the life span of the leaf. All of our shoots showed signs of approaching senescence, but the $P_{\max}$ values of the shoots at the fertile site did not decrease, in contrast to in the living shoots at the infertile site (Fig. 3a and e). However, our results cannot confirm the results of Erley et al. (2002), due to early ending of the campaign for *E. angustifolium*.

The leaf mass-based average of the measured $P_{\max}$ values of *Calluna vulgaris* fits well with the estimated $\bar{P}_{\max,i}(t)$ based on stage of development (Fig. 4a, Eq. 4, τ=150). However, in early spring $\bar{P}_{\max,i}(t)$resulting in underestimation of the estimated $P_{\max}$ and on 7 October the estimated values were higher than the measured values. The difference in autumn may be explained by the frost events occurring during the previous night which temporarily decreased the capacity.

When the shoots were examined separately, we noted that the measurements of the sparse shoot followed $\bar{P}_{\max,i}(t)$ more closely than the measurements of the dense shoot which showed an early peak in the measured $P_{\max}$ values before a decrease in midsummer (Fig. 4b) at the same time that the short drought appeared (Fig. 2). Due to the decrease, we fitted the model based on the measurements before the drought, noting a close fit between the estimation and the measurements except for the drought period and for the second last measurement in autumn. The overestimation in the model was presumably again a result of the frost that occurred the previous night.

Deschampsia flexuosa, which has a relatively low growth rate for a grass, also followed $\bar{P}_{\max,i}(t)$ even though its leaves are deciduous (Fig. 5a, Eq. 4, τ=150). Here, we had to perform the fitting based on the measurement in late June, because the midsummer values were missing. The average leaf mass-based $P_{\max}$ fits with the state of development better than any of the individual shoots (Fig. 5b). Again, there was an overestimation in the autumn, similar to that observed in *C. vulgaris*. The measured $P_{\max}$ in the sparser population was higher than the estimation early in the campaign, having the highest measured photosynthetic activity in August.

The measured $P_{\max}$ values of *Rubus idaeus* and *Epilobium angustifolium* did not follow the modelled $\bar{P}_{\max,i}(t)$. Early in the campaign, the shoots of *R. idaeus* were short and the leaves small. The P_{max} values increased until as late as on 22 June (Fig. 3). The daily average temperature had been then over 10°C for 10 days and the 5 days running average had been over 13°C for six clear and sunny days. The first decrease in the P_{max} values was observed on 9 September when the length of the light hours (PAR >10 μmol m^{-2} s^{-2}) had decreased from 15.5 to 13.5 h day^{-1} and the daily minimum temperatures had decreased since the previous measurement (from 13.5°C to 9.5°C). However, the temperatures had already decreased since mid-June (Fig. 1A). Nevertheless, temperature, temperature history or radiation cannot be the main factor alone for the annual pattern of *R. idaeus*.

The photosynthetic and growth responses of trees are widely studied, due to their universality. *Rubus idaeus* is the only species studied here that has a long history of manipulation and follow-up studies, since it is commercially valuable. For example, Carew et al. (2003) found that photoperiod did not significantly affect the growth rate, but increased temperature resulted in an increased rate of vegetative growth the optimum temperature being approx. 25°C or below. Sonsteby and Heide (2008) also studied *R. idaeus* under natural summer daylight conditions and found that temperature clearly affects positively shoot growth.

Early in our campaign, the temperature sum was 390°C and all of the shoots of *Epilobium angustifolium* were small. The highest P_{max} values of *E. angustifolium* occurred in early June (Fig. 3) at the same time that the nights were shortest. On the other hand, there was simultaneously a short cold week with average temperatures below 15°C (Fig. 1). We already had to end the measurement campaign with *E. angustifolium* in mid-July because the shoots began to show visible signs of senescence and we did not want to lose the leaf mass information. We observed, however, that there is a wide variety in the individual timing of senescence and some shoots can to a degree be photosynthetically active even relatively late in autumn.

Both *R. idaeus* and *C. vulgaris* showed individual reaction to drought. One of the shoots of both species at the fertile site showed a decreasing photosynthetic capacity with increasing soil water tension in July (Fig. 3b and c). At the same time, the other shoots showed no particular decrease. Two of the *E. angustifolium* shoots were affected by the drought its maximal on 13 July (Fig. 2). The other at the infertile site did not recover from the drought, but the one at the fertile site again increased its $P_{\max}$ value after the drought was over on 20 July. The drought that affected of these two shoots slightly decreased also the mass-based average of *E. angustifolium* (see Fig. 7). The individual reactions to the drought might be due to diverse allocation to roots or microsite variation in soil.

3.4 Respiration

Leaves with high nitrogen content have high maintenance requirements, and consequently they typically have higher dark respiration than low-nitrogen leaves and therefore lose more carbon in respiration (Chapin et al., 1987). In addition, *Calluna vulgaris* is a small shrub with abundant wooden biomass and perennial leaves. As a result, *C. vulgaris* has the lowest mass-specific level of respiration but the temperature response was similar to that of the other species (Q_{10} in Table 2). *Epilobium angustifolium* and *Rubus idaeus* showed wide variation in respiration values, but no temperature sensitivity (Fig. 6b and d). Frantz et al. (2004) found that whole-plant respiration of rapidly growing plants had low sensitivity to temperature. However, the narrow temperature range and the two low values near 30°C might be as well the reason for the week response.

Reich et al. (1998) found that mass-based leaf dark respiration rate (R_{mass}) was positively related to specific leaf area and mass-based net photosynthetic capacity as well as to leaf nitrogen mass, while the respiration rate decreased sharply with increasing leaf life span. Larsen et al. (2007) found that even the whole ecosystem respiration depends on the photosynthesis of *C. Vulgaris* on a temperate heath. Our results indicate the same: the measured respiration rates of above ground parts closely followed to the photosynthetic rate and *C. vulgaris*, with the longest life span, had the lowest respiration rates.

However, averaging of the species-specific respiration was again problematical because the individual shoots had a different mass-based level of respiration. The shoots of *Calluna vulgaris* had a similar type of response to temperature, but the R_{mass} level was different (Fig. 6c), while the respiration per ground area (R_{ground}) gave less variation in the results (Fig. 6A). The temperature dependence that was somewhat seen in the ground-based results (Fig. 6b) was lost, when the respiration of *E. angustifolium* is based on above ground mass (Fig. 6d).

3.5 Upscaling

For upscaling, we used the estimated daily P_{max} values of *Calluna vulgaris* and *Deschampsia flexuosa* that followed the state of development (Eq. 4, Fig. 7). We did not measure the photosynthesis of *D. flexuosa* before early June, but we assumed that it remained zero for a time after the snow melted even as the temperature increased. Therefore, we set the P_{max} values to increase linearly from zero, starting from 9 May until 20 May and thereafter to follow the temperature. *Rubus idaeus* was set to increase linearly from 1 May to the first measurement (2 June) when P_{max} was still very low. In the autumn, the shoots of *Epilobium angustifolium* already began to senescence in midsummer, but in some individuals the leaves may have remained partly green until late autumn. We extrapolated the P_{max} values for *E. angustifolium* linearly from the last measurement on 2 July to be zero on 12 September and thereafter. Using these daily P_{max} values, average leaf mass and hourly average PAR measurements we upscaled (Eq. 5) the photosynthetic production to be 2800 g CO_2 m^{-2} y^{-1} (760 g C m^{-2} y^{-1}) at the fertile site and 1100 g CO_2 m^{-2} y^{-1} (300 g C m^{-2} y^{-1}) on the infertile site (Fig. 8). If we consider only the time between the first and last species-specific measurement without any assumptions for early spring and late autumn, we obtain 2500 g and 930 g CO_2 m^{-2} y^{-1} (680 and 250 g C m^{-2} y^{-1}) at the fertile and infertile site, respectively.

The result is within the range of other results published. Herbaceous plants and woody shrubs were estimated to uptake 315 and 172 g C m^{-2}, respectively at a 5-y-old vegetated clear-cut in subboreal British Columbia in 2000 (Pypker and Fredeen, 2002).

Using EC measurements, gross ecosystem production (GEP) was 316 g C m^{-2} y^{-1} in Québec (Bergeron et al., 2008), 435 g C m^{-2} y^{-1} in Vancouver (Humphreys et al., 2006) and gross primary production (GPP) 323 g C m^{-2} y^{-1} in southern Finland (Kolari et al., 2004) at young clear-cut sites. In the southwestern United States, the GPP was 858 g C m^{-2} a^{-1} after fire (Dore et al., 2008). Noormets and colleagues (2007) showed that time-integrated fluxes from May to October in managed forests in northern Wisconsin (USA) in 2002 were 699, 1052, and 460 g C m^{-2} at 3-, 8-, and 12-year-old sites, respectively.

Our measurements showed that *Calluna vulgaris* released 68 g C m^{-2} at the infertile site during the snow-free period (18 April–21 November), when modelled with the temperature dependence curve (Eqs. 2 and 6), hourly average temperatures and the average aboveground biomass (Table 1). *Epilobium angustifolium* released 7 g C m^{-2} at the infertile site and 22 g C m^{-2} at the fertile site, using the same calculation method. *Rubus idaeus* released 12 C m^{-2} at the fertile site. The value of *C. vulgaris* seems very high in comparison to that value of fixed carbon based on leaf mass (33%) and was probably caused by the fitting of the respiration values: the model apparently results in overestimation of the respiration at lower temperatures (below 12°C). In addition, the model might estimate the respiration of all species during night time because respiration has been observed to be highest after photosynthesis and decreasing in prolonged darkness (Azcón-Bieto and Osmond, 1983).

Climate change will most probably shorten the snow-covered period which will increase the photosynthetic production of *Calluna vulgaris* and other perennial species. The species with perennial leaves and seedlings at a clear-cut site may competitively benefit from the warm and snow-free springs and winters.

4 Conclusions

Common ground vegetation species in early succession, *Epilobium angustifolium*, *Deschampsia flexuosa Rubus idaeus* and *Calluna vulgaris*, have clear, species-specific annual cycles in their $P_{\max}$ levels. The maxima of *C. vulgaris* and *E. angustifolium* were near June and July while *R. idaeus* was maximal as late as in August. The photosynthetic capacity of *C. vulgaris* followed the state of development estimated from the temperature history closely when the soil moisture conditions were normal. *Deschampsia flexuosa* with its deciduous leaves followed the estimated state of development as well within the time frame of our measurement campaign.

Environmental conditions are usually not optimal for photosynthesis, due to water stress, too high or too low temperatures or light intensities and individuals can be affected differently as well. For example, some shoots of *C. vulgaris* and *R. idaeus* decreased their photosynthetic capacity during drought, while the drought did not affect the other shoots. There might be also some small microsite variation in environmental factors. *Epilobium angustifolium* also showed differences in the reaction to drought.

Calluna vulgaris is a small shrub with abundant wooden biomass and perennial leaves. As a result, *C. vulgaris* has the lowest mass-specific level of photosynthesis and respiration. However, temperature response of respiration was similar to that in the other species. Whole-plant respiration of *R. idaeus* and especially *E. angustifolium* did not show a clear sensitivity to temperature.

This study showed that some species apparently have such characteristics that comparison of photosynthesis or respiration of different shoots results in less inconsistency when based on ground area rather than on mass. This may be the result of self-shading that increases with leaf mass.

By species composition, we upscaled the species-specific process rates and by continuous temperature and radiation measurements, we integrated fixed and respired CO_2 of ground vegetation during an entire growing season. The results show that from very poor and very fertile clear-cut site, the potential present range of photosynthetic production is 300–760 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$. During the snow-free period (18 April–21 November), *Calluna vulgaris* released 68 $\mathrm{g\,C\,m^{-2}}$ at the infertile site. *Epilobium angustifolium* released 7 $\mathrm{g\,C\,m^{-2}}$ at the infertile site and 22 $\mathrm{g\,C\,m^{-2}}$ at the fertile site. *Rubus idaeus* released 12 $\mathrm{C\,m^{-2}}$ on the fertile site.

The process-based upscaling used in this study functions in extrapolating and estimating the future CO_2 exchange of the ground vegetation. However, the method is still not without its drawbacks: it is very sensitive to biomass, it does not take shading into account, there are differences in the level of and reactions to environmental factors between individuals in single species and measuring all of the species and variation in individuals is difficult. To decrease the effect of these possible causes of error is very laborious and therefore integrated use with EC technique would be advantageous.

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Table 1. Density (g m^{-2}) and occurrence (%) of different species or vegetation types on the sites. The species with site-specific gas exchange measurements are in bold face. The occurrence indicates the fraction of the sample plots in which the species were present.

	Infertile site		Fertile site	
	Density (g m^{-2})	Occurrence (%)	Density (g m^{-2})	Occurrence (%)
Calluna vulgaris	**221.0**	**45**	0.0	0
Vaccinium myrtillus	0.0	0	4.8	32
Vaccinium vitis-idaea	29.6	90	39.4	53
Empetrum nigrum	26.3	25	0.0	0
Rubus idaeus	0.0	0	**19.9**	**63**
Epilobium angustifolium	**19.7**	**35**	**58.4**	**63**
Deschampsia flexuosa	0.1	5	**73.2**	**74**
Other grasses	0.0	0	0.8	21
Melanpyrum pratense	0.0	0	6.1	47
Trientalis europea	0.0	0	4.3	26
Other herbs	0.0	0	0.1	5
Mosses	63.8	90	34.2	79
Total	**360.5**		**241.2**	

Table 2. Fitted parameter values for the temperature dependence of respiration.

	R_0 $\mu g\,g^{-1}\,s^{-1}$	Q_{10}
Calluna vulgaris	0.022	2.3
Epilobium angustifolium	0.017	3.0
Rubus idaeus	0.038	2.5

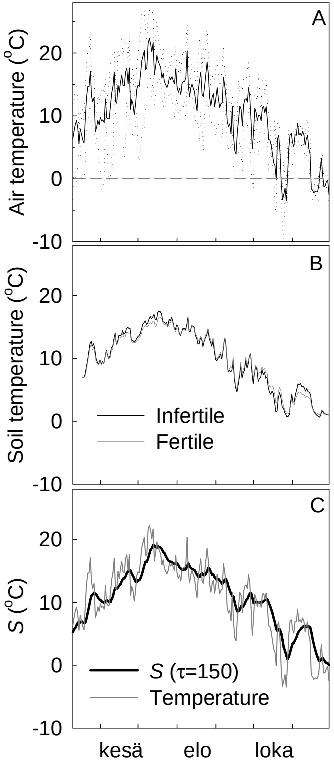

Fig. 1. (A) Daily average (black line), minimum and maximum air temperatures (dashed lines) measured at neighbouring Siikaneva fen between 10 May and 1 December 2005. **(B)** Daily average soil temperatures measured between the H and A horizons at the clear cut sites. **(C)** State of development (S, bold line) follows temperature (thin line) with a time constant of (here=150 h).

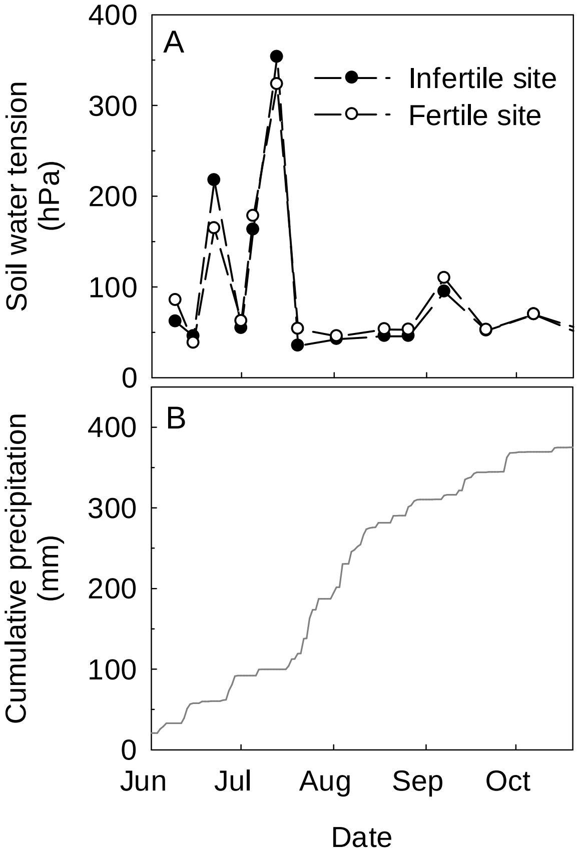

Fig. 2. Soil water tension at both clear-cut sites **(A)** and cumulative precipitation **(B)** measured at the SMEAR II station above the canopy between 1 May and 1 December 2005.

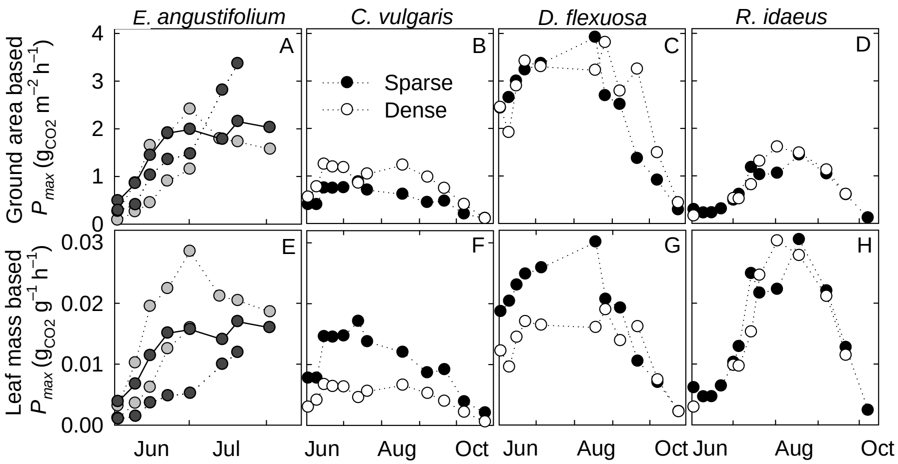

Fig. 3. Measured P_{max} values of four individual shoots of *E. angustifolium*, *C. vulgaris*, *D. flexuosa* and *R. idaeus* **(A–D)** and the same values divided by their shoot-specific leaf masses **(E–H)**. The measured E. angustifolium shoots at the fertile site are marked with dark grey. Light grey indicates to the infertile site (A and E). The experimental shoots of *C. vulgaris* and *D. flexuosa* were different in size. The leaf mass-based result of the smaller shoots are marked with black spheres ("Sparse") and of the larger shoots with empty spheres ("Dense").

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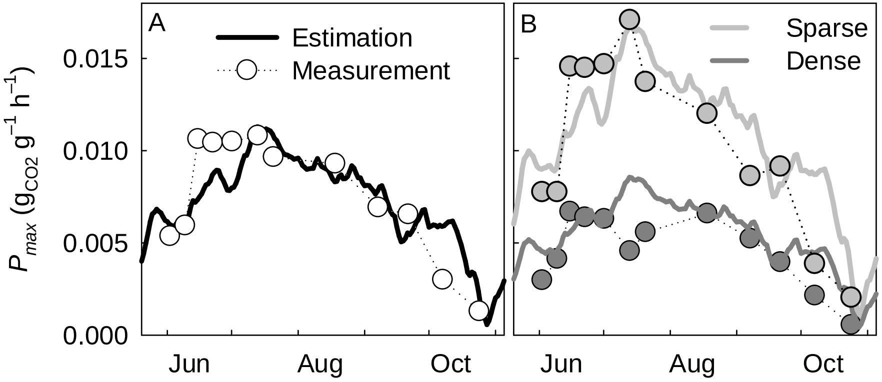

Fig. 4. Mass based $\bar{P}_{\max}(t)$ values (lines) estimated from the state of development (Eq. 4) and measured $P_{\max}$ values (spheres) of *C. vulgaris*. **(A)** The average values **(B)** both measured shoots and separately estimated $\bar{P}_{\max}(t)$ values. The dense shoot (dark grey) is shows a drought effect in July.

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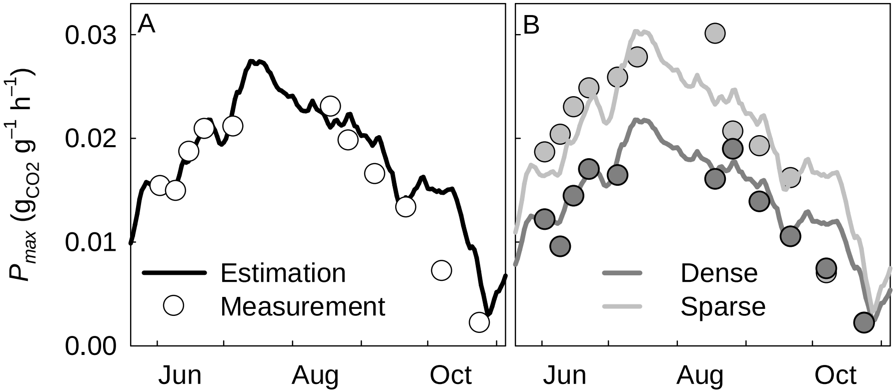

Fig. 5. Mass-based $\bar{P}_{\max}(t)$ values (lines) estimated from the state of development (Eq. 4) and measured $P_{\max}$ values (spheres) of *D. flexuosa*. **(A)** The average values and **(B)** both measured shoots and separately estimated $P_{\max}$ values.

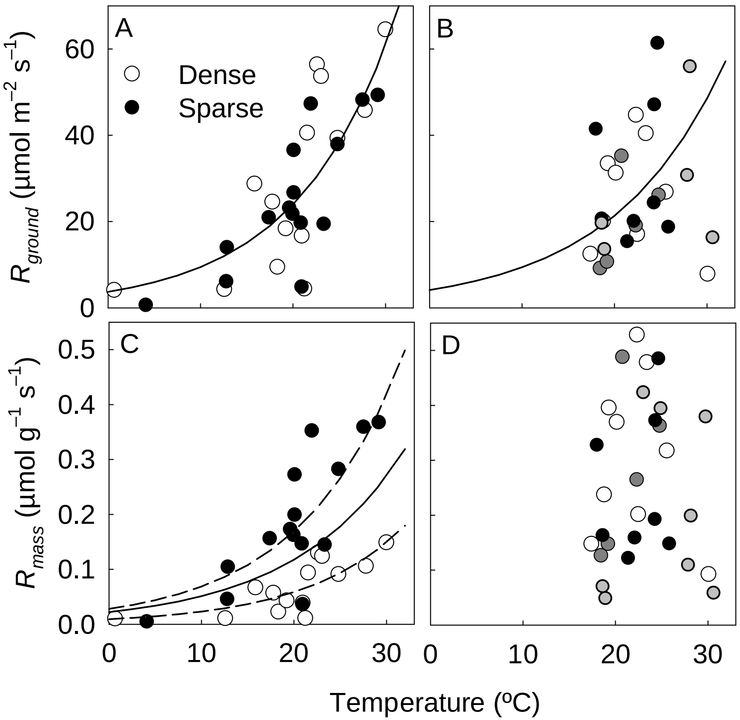

Fig. 6. Respiration against temperature of *C. vulgaris* (**A** and **C**) and *E. angustifolium* (**B** and **D**) per ground area (upper panels) and per above ground mass (lower panels). Individual shoots are marked with spheres of different colours. The fittings for both shoots are marked with the dashed lines and the average fitting with solid line in panel C.

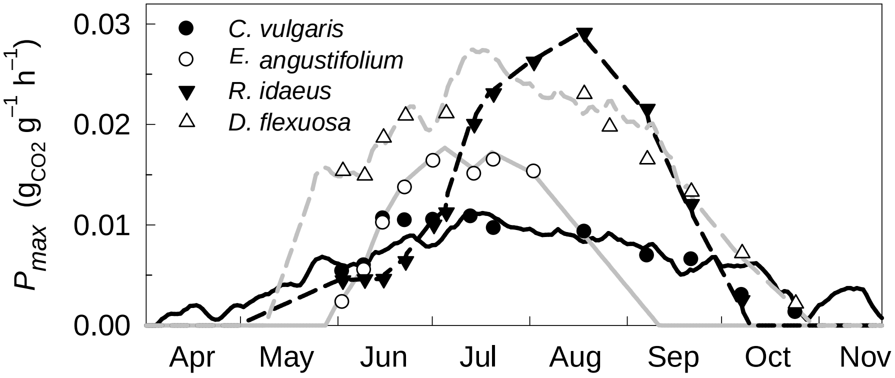

Fig. 7. Measured average P_{max} values for *C. vulgaris*, *E. angustifolium*, *D. flexuosa* and *R. idaeus* are marked with symbols. The daily P_{max} values used in the upscaling (lines) of *E. angustifolium* and *R. idaeus* are linearly interpolated from the measurements, whereas values of *C. vulgaris* and *D. flexuosa* follow the state of development (Eq. 4).

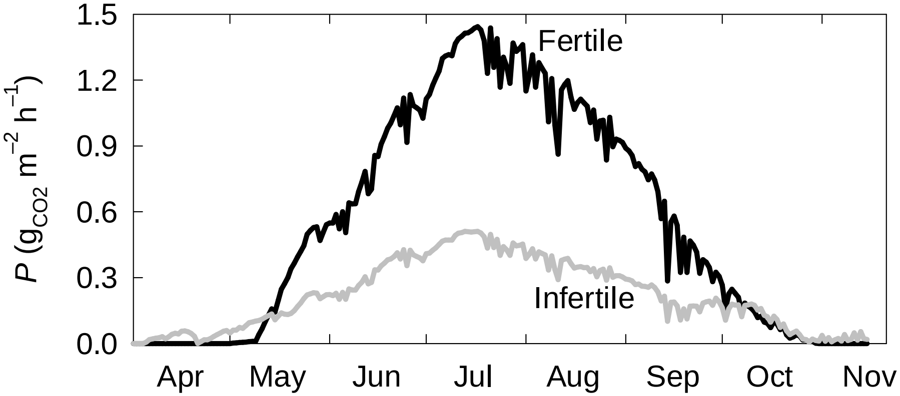

Fig. 8. Upscaled daily maximum photosynthesis rate at the infertile and fertile sites.