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ORIGINAL PAPER

Ecosystem respiration depends strongly on photosynthesis in a temperate heath

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Abstract We measured net ecosystem CO_2 flux (F_n) and ecosystem respiration (R_E), and estimated gross ecosystem photosynthesis (P_g) by difference, for two years in a temperate heath ecosystem using a chamber method. The exchange rates of carbon were high and of similar magnitude as for productive forest ecosystems with a net ecosystem carbon gain during the second year of 293 ± 11 g C m^{-2} $year^{-1}$ showing that the carbon sink strength of heather-dominated ecosystems may be considerable when *C. vulgaris* is in the building phase of its life cycle. The estimated gross ecosystem photosynthesis and ecosystem respiration from October to March was 22% and 30% of annual flux, respectively, suggesting that both cold-season carbon gain and loss were important in the annual carbon cycle of the ecosystem. Model fit of R_E of a classic, first-order exponential equation related to temperature (second year; $R^2 = 0.65$) was improved when the P_g rate was incorporated into the model (second year; $R^2 = 0.79$), suggesting that daytime R_E increased with increasing photosynthesis. Furthermore, the temperature sensitivity of R_E decreased from apparent Q_{10} values of 3.3 to 3.9 by the classic equation to a more realistic Q_{10} of 2.5 by the modified model. The model introduces R_{photo}, which describes the part of respiration being tightly coupled to the photosynthetic rate. It makes up 5% of the assimilated carbon dioxide flux at 0°C and 35% at 20°C implying a high sensitivity of respiration to photosynthesis during summer. The simple model provides an easily applied, non-intrusive tool for investigating seasonal trends in the relationship between ecosystem carbon sequestration and respiration.

Keywords *Calluna* heath · Carbon balance · Modelling ecosystem respiration · Photosynthesis-related respiration · Q_{10}

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Introduction

The carbon (C) exchange of terrestrial ecosystems is a key factor in the prediction of the future global climate because these ecosystems contain significantly more carbon than is present in the atmosphere (Davidson and Janssens 2006) and sequester 1/6 of the global atmospheric CO_2 annually (IPCC 2001). Consequently, they have a high potential for creating negative or positive feedbacks to climate change. The net exchange of carbon in most terrestrial ecosystems

is a relatively small difference between large fluxes of C sequestration by plants and release of C through respiration by plants, soil microbes and animals. Small errors in the estimation of photosynthesis and respiration may therefore lead to relatively large errors in the estimate of net ecosystem exchange.

All current methods for estimating ecosystem carbon balance, including the two most frequently applied techniques, eddy co-variance and the chamber method, depend on models of photosynthesis and respiration or gap filling methods, because measurements are not continuous. Furthermore, the eddy covariance technique only provides the net ecosystem carbon exchange, and other methods are required to estimate the components of the net balance, i.e., photosynthesis and respiration. Models of photosynthesis and respiration are therefore important tools in studies of carbon cycling and play a fundamental role for the estimation of ecosystem carbon exchange.

The enzymatic processes involved in photosynthesis vary only little across taxa (Davidson et al. 2006), and the theoretical understanding of photosynthesis is well-established (Trumbore 2006). Unless plants are drought stressed, temperature and solar radiation are by far the most important drivers of instant ecosystem photosynthetic rates. Consequently, ecosystem photosynthesis can be modelled with relatively high confidence using well-known empirical temperature and light response equations given that the number of photosynthesis measurements and their distribution in space and time are sufficient.

In contrast, respiration processes span over many different enzymatic systems across taxa (Davidson et al. 2006). Still, ecosystem respiration (R_E) has traditionally been modelled based on thermodynamic principles by using simple, first-order exponential equations with temperature as the only determinant (Craine et al. 1999). Their use and appropriateness are currently being questioned, because the simple temperature-dependency of these models poorly reflects the complex nature of the different components of ecosystem respiration and the drivers that control them (Craine et al. 1999; Davidson et al. 2006).

Especially the relative contribution from autotrophic (R_a) and heterotrophic (R_h) respiration has recently been intensely studied (Subke et al. 2006). However, the complex structure of the soil environment impedes the separation of the various sources of R_E. Many different approaches have been used including destructive methods like root exclusion (e.g., clipping, trenching, and girdling) and physical separation of components, as well as non-destructive methods like isotope techniques and modelling; see reviews of Hanson et al. (2000), Subke et al. (2006), and Kuzyakov (2006). It has been argued that R_a and R_h are likely to respond differently to the major ecosystem conditions (e.g., temperature and water availability) because R_a is tightly coupled to the carbon input from the canopy while the resulting carbon storage and nutrient turnover in the soil depend on the activity of the heterotrophic soil community (Binkley et al. 2006).

The evidence of a strong coupling between the photosynthetic rate and R_E has increased in the recent years (Hogberg et al. 2001; Tang et al. 2005; Irvine et al. 2005; Knohl et al. 2005) and this interaction needs to be incorporated into the models (Craine et al. 1999). Still, most studies focusing on partitioning or modelling respiration at either soil or ecosystem level do not include this interaction, possibly because the empirical modelling of respiration by classic, temperature-dependent exponential equations often fit well with observed respiration rates. The good fit of the model may, however, be misleading because several factors like phenology, photosynthesis, substrate supply or soil water content often co-vary with temperature (Trumbore 2006; Davidson et al. 2006) and mask other important drivers of the respiration. Furthermore, despite the often high model fit of the classic Q_{10} equation, the resulting temperature sensitivities often become unrealistically high with Q_{10} values exceeding 2.5, which suggests that other factors than temperature are affecting the respiration (Davidson et al. 2006).

In the present study we investigated the CO_2 exchange of a semi-natural, temperate heath ecosystem for two years with a focus on seasonality of carbon fluxes and the interaction between photosynthesis and respiration. The low-statured vegetation enabled us to estimate the carbon fluxes at the ecosystem level with a chamber technique. The major aims were to (a) determine the important drivers of ecosystem respiration and photosynthesis, (b) model ecosystem photosynthesis using well-established models, (c) incorporate photosynthesis into a respiration model and evaluate the model performance

compared to a classic, first-order temperature-dependent model, and (d) use the models to estimate seasonal and annual ecosystem exchange rates of CO_2.

Materials and methods

Study site and experimental setup

The experimental area is a heath close to the CLIMOOR site (Beier et al. 2004) at Mols Bjerge, Eastern Jutland, Denmark (56°23′ N, 10°57′ E), 58 m above sea level. Annual mean air temperature is 9.4°C (1.6°C in January and 18.1°C in July) and mean annual precipitation (1998–2000) is 758 mm. The soil is a sandy podzol with a pH of 4.6 (Jensen et al. 2003). The heath has an approximately 3 cm thick organic top layer with a mean soil organic matter (SOM) content of 19.3 ± 1.7%, and the upper 7 cm of the mineral soil has a SOM content of 3.2 ± 0.3%, Together, the two soil layers have 5.6 ± 0.1 kg SOM m^{-2} in the top 10 cm. The vegetation is dominated by the evergreen dwarf shrub *Calluna vulgaris* (L.), various mosses and the grass *Deschampsia flexuosa* (L.). The area is grazed extensively and mostly during winter by Galloway cattle.

In fall 2003, 6 replicate plots of 2 × 2 m^2 were randomly selected within the experimental site, and a soil collar of 30 × 30 cm^2 was installed within each plot reaching 2 to 10 cm into the soil. Rather than placing the soil collars randomly, we made sure that all of them contained a patch of *C. vulgaris* small enough to fit into the collar, as well as a substantial cover of mosses and *D. flexuosa*. Tinytags (Gemini Data Loggers, Chichester, England) were installed ca. 30 cm outside each soil collar, logging the temperature at the soil surface (T_{surf}) and at 3 cm soil depth (T_{soil}). From 27 September 2004, a Campbell CR10X datalogger (Campbell Scientific Inc., Logan, USA) also recorded the volumetric soil water content (SW) at two points within the experimental area using Campbell CS616 water content reflectometers, as well as the incident photosynthetic active radiation (PAR) at one point in the middle of the experimental site (Campbell quantum sensor). PAR was recorded once per minute, temperatures every 10 min, and SW every hour. All data was stored by the loggers as 1-h averages. From 24 February 2004 to 26 September 2004, PAR flux densities were extrapolated from measurements of global radiation (2 h intervals) from the weather station at the Mols Laboratory approximately 200 m from the site. To avoid animal disruption of equipment, the experimental area had to be fenced and was therefore not grazed after 1 October 2004 until the end of the observation period.

Vegetation biomass and height

Four times during the cold season of 2004 and 2005, we collected 20 × 20 cm^2 cores of soil with vegetation to a depth of 10 cm within each plot. The cores were taken at a minimum distance of 30 cm from the soil collars and brought to the laboratory, where the plants were carefully separated from the soil with as many roots as possible attached. The plants were subsequently sorted into five fractions: Evergreens (shoots and roots), graminoids and herbs (shoots and roots) and mosses. Dead plants were discarded except for partly senesced grass leaves. *C. vulgaris* was the sole evergreen, and the grass *D. flexuosa* accounted for more than 90% of the graminoid/herb fraction of each sample. A subsample of about 100 cm^3 of the soil was sorted for a maximum of 30 min in order to extract remaining roots for determination of total root biomass. The mean vegetation height within each soil collar was measured during spring (March) and fall (September) each year as an average of six point measurements.

CO_2 flux measurements

From 30 September 2003 to 20 September 2005, CO_2 fluxes were measured 58 times at each soil collar, summing up to a total of 348 measurements. The flux observations include nine diurnal measurement campaigns, usually with four measurements per plot within 24 h and 25 additional measurement dates with fluxes measured between 10 a.m. and 2 p.m. CO_2 fluxes were measured with a LI-6400 infrared gas analyzer (IRGA, LI-COR, Lincoln, NE, USA) attached to a rebuilt LI-6400-09 soil chamber where the dark, standard chamber had been replaced by a 33.5 L transparent Perspex chamber. The Perspex chamber was installed with a fan as well as a temperature probe (LI-6400-09 temperature probe) and a PAR sensor (LI-COR quantum sensor). A water-filled channel on the sides of the soil collars

ensured a tight seal of the chamber atmosphere during measurements.

The net ecosystem CO_2 exchange rate (F_n) was measured during three consecutive 1-min intervals after allowing the chamber to equilibrate for about 20 s from the time when the chamber was placed on the soil collars. In most cases, F_n decreased from the first to the third minute of measurement, indicating an effect of the chamber by the decreasing CO_2 concentration as photosynthesis progressed. We therefore use the fluxes during the first minute of measurement as an estimate of F_n.

After the F_n measurements, the chamber was vented and repositioned, followed by measurements of the ecosystem respiration rate (R_E) with the chamber covered by a thick layer of black plastic. In this way, F_n and R_E could be measured in the six plots within 1 h. Similar approaches of measuring ecosystem respiration during the daytime have been used by e.g., Christensen et al. (2000), Olsrud and Christensen (2004) and Illeris et al. (2004), and although respiration for some plants has been shown to be partly inhibited on the leaf level when leaves are photoactive, we believe that this effect is insignificant at the ecosystem level and may even be cancelled out due to higher respiration in plant roots and soil rhizosphere as photosynthate is translocated here and respired. As for the F_n measurements, we observed a chamber effect of decreasing rate of CO_2 flux into the chamber with time, presumably because of reduced diffusion from the soil as the chamber CO_2 concentration increased. In order to avoid bias due to disturbance when the chamber was repositioned and the effect of reduced diffusion with time, we use the flux during the second of three consecutive 1-min measurements for the estimate of R_E. The gross photosynthetic rate (P_g) was estimated as $F_n - R_E$ and has a negative sign, while R_E is positive.

Statistical analysis and data processing

Changes over time in plant biomasses of the plant fractions and their sum (*C. vulgaris*, mosses and *D. flexuosa* and their sum) and in mean height of the vegetation were tested using one-way ANOVA followed by Tukey's test (SAS Enterprise Guide 3.0, SAS Institute, Cary, NC, USA).

Model parameters of photosynthesis and respiration models were fitted by multiple, nonlinear regression (*Proc Model*, SAS v. 8.1, SAS Institute).

We first modelled P_g (μmol CO_2 m^{-2} s^{-1}) using the non-rectangular hyperbola (Thornley 1976):

$$P_g = \frac{(\alpha \cdot I + P_m) - \sqrt{(\alpha \cdot I + P_m)^2 - 4\alpha \cdot I \cdot P_m \cdot \theta}}{2\theta} \quad (1)$$

where α is the PAR use efficiency (mol CO_2 mol photon^{-1}), I is photosynthetic active radiation (PAR) measured in μmol photons m^{-2} s^{-1}, P_m is maximum P_g at a certain leaf temperature, and θ is a dimensionless curvature parameter. Temperature dependency of P_g was described using an equation similar to the equation used by dePury and Farquhar (1997) for electron transport enzyme kinetics:

$$P_m = P_{mr} \cdot e^{\frac{E_a(T-T_r)}{RTT_r}} \cdot \frac{1 + e^{\frac{\Delta ST_r - E_d}{RT_r}}}{1 + e^{\frac{\Delta ST - E_d}{RT}}} \quad (2)$$

where $P_{m\,r}$ is P_m at the reference temperature (T_r) of 298 K, T is temperature in K, E_a is the activation energy (kJ mol^{-1}), R is the universal gas constant (8.341 J mol^{-1} K^{-1}), ΔS is an entropy term (J mol^{-1} K^{-1}), and E_d is the energy of deactivation (kJ mol^{-1}). We fitted models with T_{soil} (−3 cm), T_{surf} (0 cm) and their mean (T_{mean}), and found the closest model fit when using the T_{mean}, which therefore is reported here.

In order to model R_E (μmol CO_2 m^{-2} s^{-1}) we first used a classic, first-order exponential equation by van't Hoff (1898):

$$R_E = R_0 e^{bT} \quad (3)$$

where R_0 represents the ecosystem respiration at 0°C depending on substrate availability, b is the temperature sensitivity of respiration (°C^{-1}), and T is temperature (°C). To investigate the possible dependency of respiration on photosynthesis we modified the classic exponential equation while making the following assumptions:

$$R_E = R_{base} + R_{photo} \quad (4a)$$

$$R_{base} = R_{0m} e^{b_m T} \quad (4b)$$

$$R_{photo} = \lambda P_g e^{b_m T} \quad (4c)$$

R_{base} is the basal ecosystem respiration rate independent of the P_g rate with R_{0m} representing

R_{base} at 0 °C. R_{photo} is the part of R_E depending on P_g where λ is the fraction of P_g being instantly respired at 0°C. R_{base} and R_{photo} describe the mitochondrial respiration of two different sources of carbon, with the assumption that they have identical temperature sensitivities (b_m). It follows that $\lambda e^{b_m T}$ in Eq. 4c is the fraction of P_g being instantly respired at any given temperature, comprising both above-ground effects of enhanced assimilate metabolism and transport, and/or enhanced soil respiration, e.g., through increased autotrophic respiration, mycorrhizal and rhizosphere respiration. Inserting Eqs. 4b and 4c in Eq. 4a leads to the modified model, which was tested:

$$R_E = (R_{0m} + \lambda P_g)e^{b_m T} \quad (4d)$$

The observed R_E and P_g rates were used for the model fitting. As for the photosynthesis model, we fitted the model based on temperatures of the soil, the soil surface and their mean and found the closest fit using the T_{soil}, which is reported here.

Because the grazing stopped in October 2004, we evaluated the model parameters for ecosystem CO_2 fluxes separately for the first and second year of the study. Hence, measurements from 30 September 2003 to 13 September 2004 were used to model the fluxes the first year, while measurements from 27 September 2004 to 20 September 2005 were used to model the fluxes the second year. All six replicate plots were included in the same model.

The models were used to extrapolate from the measurements to the whole period using the continuous climate data and using the modelled P_g in the modified R_E model. When applying the models to the climate data, the models were run on the temperature recorded by each temperature logger individually and then corrected for seasonal residuals to include potential seasonal differences in the physiological response of the ecosystem. Standard errors of the reported monthly estimates therefore represent the variability in temperatures as well as the residuals caused by variations over the seasons.

Results

Biometrical measurements of vegetation

The vegetation was dominated by *C. vulgaris*, which constituted on average 52 ± 4% of the aboveground biomass (AGB), followed by mosses (29 ± 3%) and *D. flexuosa* (18 ± 2%). The mean total AGB over the four samplings during the cold season 2004/2005 was 980 ± 43 g m^{-2}, and did not change significantly with time ($ANOVA_{3,20}$, $F = 0.85$, $P = 0.48$). However, the AGB of *D. flexuosa* was low from November to March and then increased significantly from March to May (One-way $ANOVA_{3,20}$, $F = 17.3$, $P < 0.0001$). Total belowground biomass (BGB) was on average 768 ± 64 g m^{-2}, resulting in a mean ratio of 1.3 between AGB and BGB.

The mean vegetation height (Fig. 1) was 14 ± 2 cm in fall 2003 and decreased significantly (Tukey's test, $P < 0.05$) over the cold season due to cattle grazing, reaching only 8 ± 1 cm in spring 2004. As expected, the vegetation height tended to increase over the following growing season, although this was not statistically significant. In the second winter, when the area was un-grazed, the vegetation height was constant, but doubled during the subsequent growing season.

Observed and modelled CO_2 fluxes

The observed P_g and R_E rates (Fig. 2a) showed the expected seasonal pattern decreasing from late September until the winter months (December–February), when R_E rates were low and relatively constant between 0.59 µmol and 0.99 µmol CO_2 m^{-2} s^{-1} during the first winter. The R_E rates fluctuated more during the second winter ranging

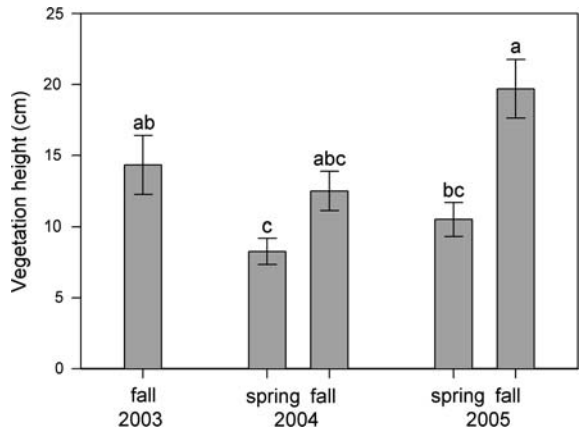

Fig. 1 Mean vegetation height in fall (September) and spring (March) during the experiment. Data are means ± SE, $n = 6$. Results of Tukey's test following a one-way Anova are shown. Bars, which do not share letters, are significantly different ($P < 0.05$)

between 0.43 μmol and 1.77 μmol CO_2 m^{-2} s^{-1}. Considerable mid day P_g rates were measured even during mid winter with e.g., −5.0 ± 0.4 μmol CO_2 m^{-2} s^{-1} in January 2005, leading to a negative mid day net carbon exchange (i.e., ecosystem sequestration of C) at all occasions of measurement. From the beginning of April, P_g and R_E rates increased rapidly with time, especially during the second year when there was no cattle grazing, reaching peak mid day rates of P_g of −30.6 ± 1.9 μmol CO_2 m^{-2} s^{-1} in June 2005. In comparison, R_E rates peaked at 12.2 ± 1.0 μmol and 11.7 ± 1.3 μmol CO_2 m^{-2} s^{-1} in June and July, respectively.

The seasonal pattern of the observed P_g and R_E rates followed closely the seasonal development in temperatures and solar radiation (Fig. 2b, c). For instance, during the second year P_g correlated more with PAR (R^2 = 0.62) than with T_{mean} (R^2 = 0.39) and soil water content (R^2 = 0.20) while R_E correlated most strongly with T_{soil} (R^2 = 0.65) and more moderately with the soil water content (Fig. 2d, R^2 = 0.39).

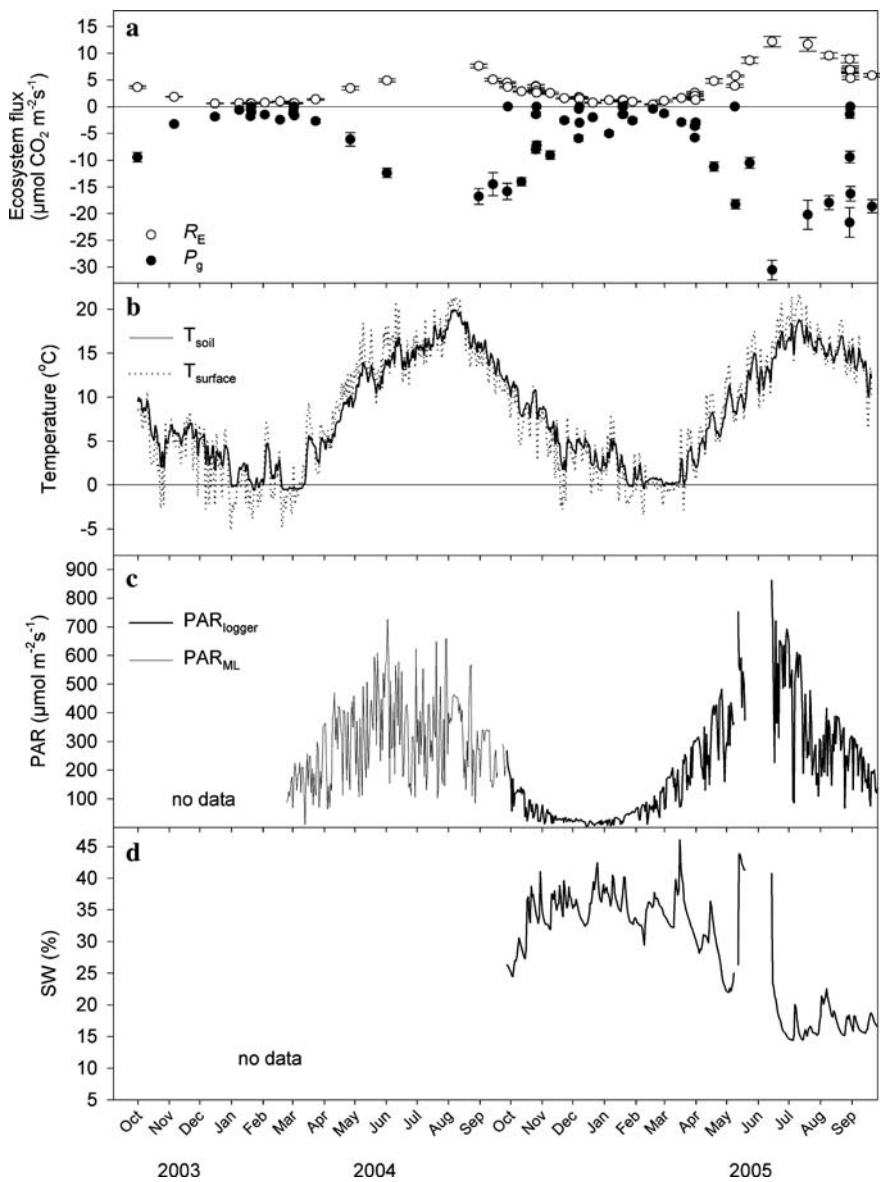

Fig. 2 Observed mid day flux rates (from 10 a.m. to 2 p.m.) of gross ecosystem photosynthesis (P_g) and ecosystem respiration (R_E) from 30 September 2003 to 20 September 2005 (**a**). Several circles at the same point in time represent the diurnal variation in flux rates including night-time measurements. Data are means ± SE, n = 6 and the number of measurements per plot is 58. Also shown are (**b**) temperatures at 3 cm soil depth (T_{soil}) and at the soil surface ($T_{surface}$), (**c**) photosynthetic active radiation (PAR) and (**d**) volumetric soil water content (SW). No data on PAR was available prior to 24 February 2004 and SW was logged with start on 27 September 2004. From 24 February to 26 September 2004, PAR data are extrapolated from global radiation data measured at the Mols Laboratory weather station situated about 200 m from the site (PAR_{ML}). From 27 September 2004, the data are from a data logger placed within the site (PAR_{logger})

The P_g models yielded high R^2-values of 0.87 during both years (Fig. 3, Table 1), clearly indicating that temperature and solar radiation were the major determinants of the photosynthetic rates, as also shown by the linear regression analyses. Using the classic, first-order exponential equation, the best model fit for R_E was found using T_{soil}, which resulted in $R^2 = 0.91$ during the first year and $R^2 = 0.65$ during the second year (Fig. 4 upper panel, Table 2). Interestingly, the model fit was improved to $R^2 = 0.93$ and $R^2 = 0.79$, respectively, when R_{photo} was included in the modified R_E model (Fig. 4 lower panel, Table 2).

In the modified R_E model, λ was significant in both years ($P < 0.0001$), showing that R_E increased considerably concomitant with increasing P_g rate. λ reached about -0.05 in both years, i.e., the reference respiration at 0°C increased by 5% of the instant P_g rate. At higher temperatures, however, the proportion increased with temperature to e.g., 14% of the instant P_g rate at 10°C and 35% at 20°C (Fig. 5).

Due to the pronounced sensitivity of R_E to the P_g rate, the modified R_E model estimated significantly lower temperature sensitivities (b_m) than the classic model (Student's t-test, $P < 0.01$ in both years), resulting in annual Q_{10} values of 2.5 in both years as compared to 3.3 or 3.9 by the classic model. Consequently, the slopes of temperature response curves generally were lower than for the classic R_E model, except at high P_g rates (Fig. 6).

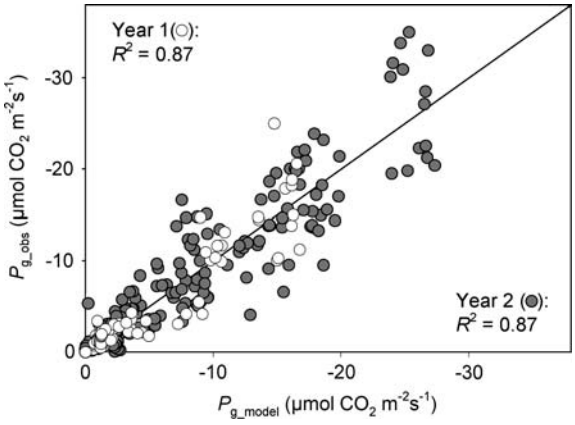

Fig. 3 Modelled (P_{g_model}) and observed (P_{g_obs}) flux rates of ecosystem photosynthesis (P_g). Explained variances (R^2) of regressions for each year are shown as well as the ideal 1 to 1 line. See text for model equations and Table 1 for the parameter estimates

The model fit improvement by the modified R_E model compared to the classic model, and the resulting high R^2 values indicates that temperature and P_g rates were the major drivers of R_E. In a similar way, we also investigated the effect of the soil water content on R_E during the second year, using a similar modification of the classic model with soil water content instead of the P_g rate. This improved the model fit only marginally ($R^2 = 0.68$, data not shown) compared with the classic model ($R^2 = 0.65$), and the constant related to the water content in this model (similar to λ in Eq. 4c) only tended to be significant ($P = 0.08$).

The close model fit of both the P_g and R_E rates is reflected by small residuals between observed and modelled fluxes (Fig. 7) relative to the level of the measured flux rates. Often, the residuals were not significantly different from zero. Still, both R_E models showed a seasonal trend of slightly overestimated model fluxes during fall and winter and underestimation during spring. This trend tended to be decreased, although not significantly, by the modified R_E model. Similarly, the residuals of P_g generally were not significantly different from zero, except during spring, when the model slightly overestimated the photosynthetic rates.

In general, the low residuals and high R^2-values give considerable confidence in the estimates of the gas fluxes. We therefore ran the modified R_E model (Eq. 4d) and the P_g model (Eqs. 1 and 2) on the available temperature and radiation data (Fig. 2b, c) in order to extrapolate from our measurements to the entire time period. We estimated R_{photo} (Eq. 4c) using the parameter estimates of λ and b_m from the model fit of Eq. (4d). We modelled R_E by the classic model (Eq. 3) during the first six months of the study period, when P_g could not be modelled due to the lack of radiation data.

The modelled monthly estimates of ecosystem respiration and photosynthesis revealed a seasonal pattern of 70% of annual respiration taking place during April to September, while the remaining 30% occurred during the cold season from October to March (Fig. 8a). The lowest rates were in January and February during both years, which together accounted for 4% to 6% of the annual respiration, while monthly respiration peaked in August during the first year and in June/July during the second year. However, the respiratory carbon loss was almost

Table 1 Fitted parameters and standard errors (in brackets) from model estimation of gross ecosystem photosynthesis (P_g, Eq. 1 and 2). See text for equations and parameter explanations

Year	α	θ	$P_{m\ r}$	E_a	E_d	R^2	N
2003–2004	0.030 (0.003)	0.996 (0.02)	14.2 (1.2)	143,929 (21,329)	202,826 (1,543)	0.87	114
2004–2005	0.055 (0.015)	−0.795 (1.70)	46.3 (18.1)	153,940 (25,177)	201,615 (1,555)	0.87	234

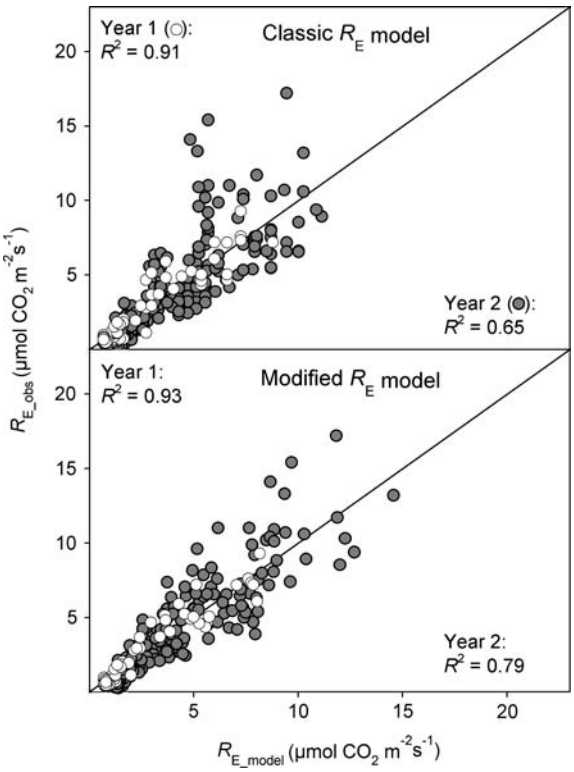

Fig. 4 Modelled (R_{E_model}) and observed (R_{E_obs}) flux rates of ecosystem respiration (R_E), using classic (upper panel) and modified (lower panel) first-order exponential equations. Explained variances (R^2) of regressions for each year are shown as well as the ideal 1 to 1 line. See text for model equations and Table 2 for the parameter estimates

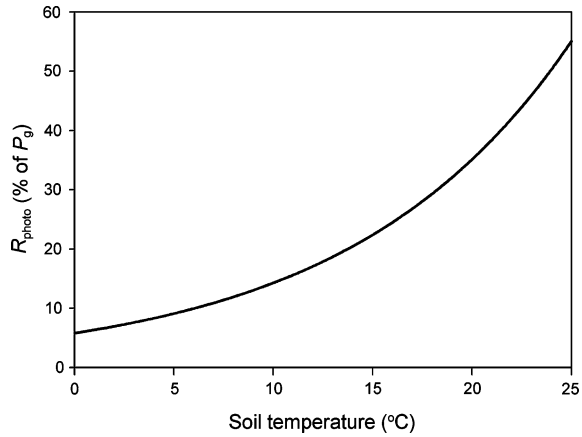

Fig. 5 R_{photo} in percentage of P_g as function of soil temperature using fitted values of λ and b_m from the second year (see Table 2)

entirely cancelled out by similar or higher photosynthesis rates at all times, except in March 2005 (Fig. 8b, c). As a result, cold-season photosynthesis accounted for 22% of the annual C uptake. Total annual respiration of the second year was estimated to 1481 ± 11 g C m^{-2} $year^{-1}$ when using the modified R_E model (Eq. 4d) compared to 1662 ± 16 g C m^{-2} $year^{-1}$ if using the classic model (Eq. 3). R_{photo} was close to zero from November to March in both years, i.e., the plants had a constant respiration

Table 2 Fitted parameters and standard errors (in brackets) from model estimation of ecosystem respiration (R_E) using two first-order exponential equations; a classic R_E model (Eq. 3) and a model including a dependency of R_E on gross ecosystem photosynthesis (P_g, modified R_E model, Eq. 4d). See text for equations and parameter explanations

Year	Model	R_0/R_{0m}	B	Q_{10}	λ	R^2	N
2003–2004	Classic	0.738 (0.05)	0.137 (0.005)	3.9	–	0.91	114
	Modified	0.738 (0.05)	0.093 (0.009)	2.5	−0.048 (0.013)	0.93	114
2004–2005	Classic	1.291 (0.12)	0.118 (0.007)	3.3	–	0.65	234
	Modified	1.217 (0.09)	0.090 (0.006)	2.5	−0.058 (0.007)	0.79	234

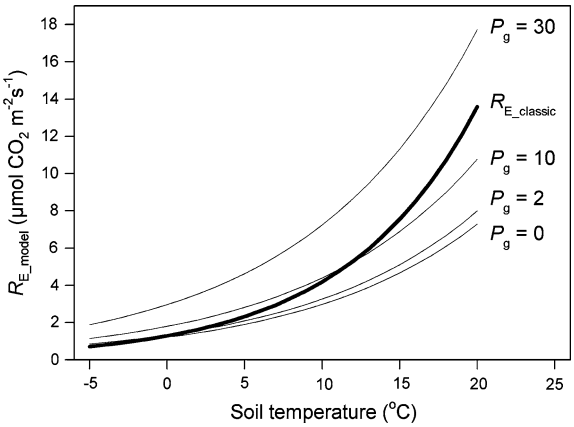

Fig. 6 Temperature response curves for the ecosystem respiration (R_E) models from the second year of the study. The solid line represents the classic R_E model ($R_{E\_classic}$) and thin lines represent the response to temperature by the modified R_E model at different rates of gross ecosystem photosynthesis (P_g). See Table 2 for parameter estimates

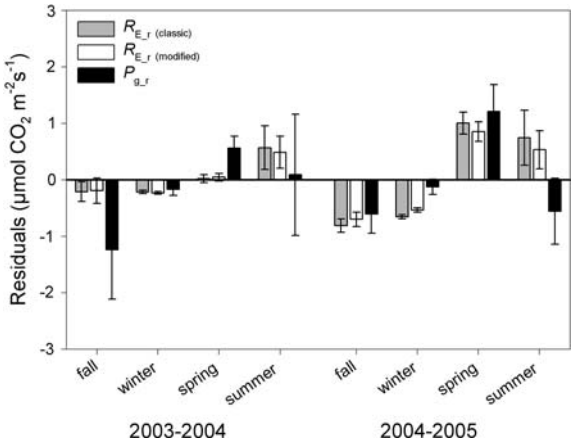

Fig. 7 Seasonal residuals (_r) of ecosystem respiration (R_E, classic and modified models) and photosynthesis (P_g). Data are means ± SE, n = 3. Residuals were calculated as observed minus modelled fluxes; i.e., positive residuals means model overestimation of P_g and underestimation of R_E. The seasons were defined as fall (Sep–Nov), winter (Dec–Feb), spring (Mar–May) and summer (Jun–Aug)

over the day in spite of considerable observed P_g-rates during mid day (Fig. 2a). From March to June, P_g increased strongly and so did the R_{photo}, thereby accounting for 34% and 38% of R_E in June 2004 and June 2005, respectively. During the second year, when all fluxes were modelled through the entire year, R_{photo} accounted for 24% of the annual R_E and 20% of annual P_g. With annual P_g during the second year of 1774 ± 11 g C m^{-2} $year^{-1}$, the ecosystem was an estimated sink of 112 ± 19 g C m^{-2} $year^{-1}$ using the classic R_E model (data not shown) compared to 293 ± 12 g C m^{-2} $year^{-1}$ if using the modified R_E model.

Discussion

Application and effects of the modified R_E model

Our modified model of ecosystem respiration introduces R_{photo} as an estimate of the part of ecosystem respiration, which is tightly coupled to the photosynthetic rate. R_{photo} includes the direct effect of the instant rate of photosynthesis on plant respiration as well as the indirect effects of photosynthetically supplied C to the mycorrhizal fungi and rhizosphere organisms. Consequently, our method does not separate the autotrophic and heterotrophic respiration, which is attempted in many studies on ecosystem respiration partitioning. However, our non-intrusive modelling approach indicates several important traits of the ecosystem carbon cycling, partitioning and seasonality.

First, our results indicate that the ecosystem respiration was greatly affected by the instant carbon sequestration of the plants. This interpretation is supported by recent reports of links between photosynthesis and respiration from a variety of forests (Hogberg et al. 2001; Irvine et al. 2005; Knohl et al. 2005), an oak-grass savanna (Tang et al. 2005), and grassland ecosystems (Craine et al. 1999). Second, we could only find marginal effects of drought on respiration, although drought effects have been reported to modify respiration, e.g., in Mediterranean ecosystems (Reichstein et al. 2002). Third, the modified R_E model provided a direct estimate of the fraction of photosynthesis being respired instantly, which was unexpectedly large at about 5% of the instant P_g rate at 0°C and increasing to ca. 35% of the instant P_g rate at 20°C during both years.

Due to inclusion of the photosynthetic rate in the temperature response of R_E, the temperature sensitivity of ecosystem respiration was considerably decreased from an annual Q_{10} of up to 3.9 by the classic model to only 2.5 using the modified model,

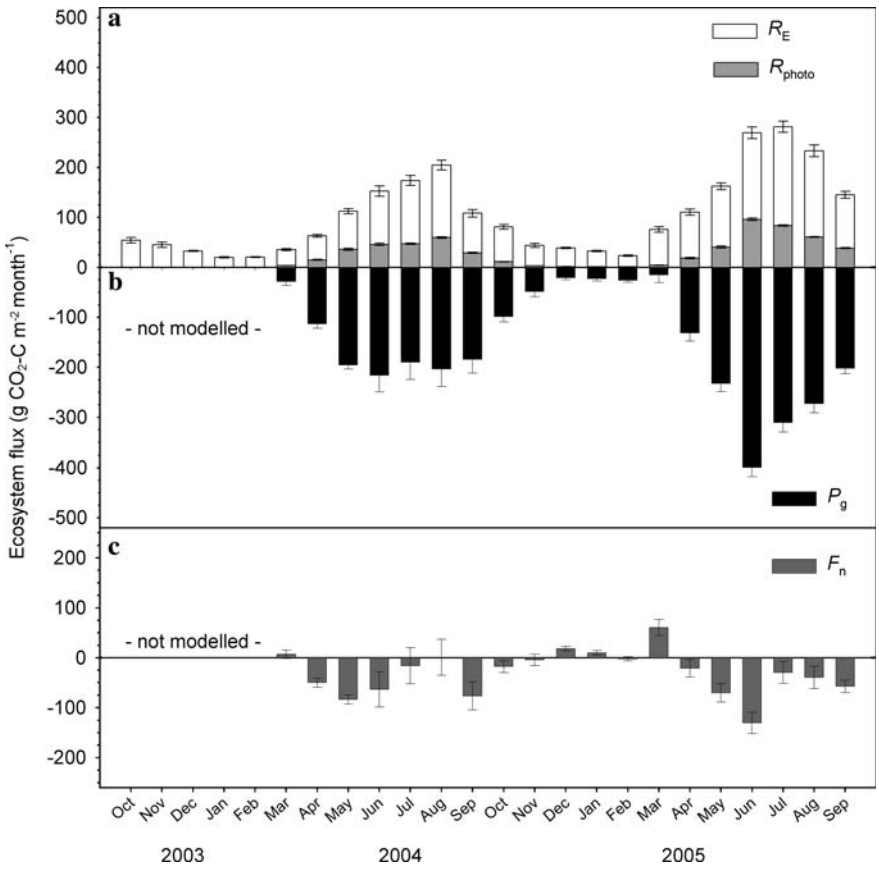

Fig. 8 Estimated monthly ecosystem respiration (**a**) as total respiration (R_E) using the modified R_E model (see text, Eq. 4d) and the part, which is coupled to the photosynthetic rate (R_{photo}), (**b**) estimated ecosystem gross photosynthesis (P_g), and (**c**) net exchange of carbon (F_n). Data are means ± SE, $n = 6$. Because of lack of data prior to 24 February 2004, monthly rates of P_g, R_{photo} and F_n could only be modelled from March 2004. For the same reason, R_E until March 2004 was modelled using the classic first-order exponential equation (see text, Eq. 3)

corresponding to about the upper limit for physiologically realistic Q_{10} values proposed by Davidson et al. (2006). They argue that if observed Q_{10} values exceed 2.5, processes other than temperature fluctuations are likely to influence the respiration rates. This important effect of our modified R_E model exemplifies how a high model fit of a classic model can be misleading (Trumbore 2006). For instance, during the first year of our study, the classic model yielded a high R^2 of 0.91, which was only slightly improved by the modified model ($R^2 = 0.93$). However, the significant decrease of the temperature sensitivity by the modified model strongly suggests that the photosynthesis was an important driver of respiration, but that the effect was hidden in the classic model because the P_g rates co-varied with temperature. Similarly, other potentially important factors, e.g., phenology, substrate supply or soil water content, may co-vary with temperature (Trumbore 2006; Davidson et al. 2006) and mask the true drivers of the respiration. Our approach indicates that the possible unaccounted effects may be revealed by our simple modification of the model. For instance, a similar approach revealed that the supply of dissolved organic carbon and nitrogen to the soil microbes played a dominant role controlling the ecosystem respiration in a subarctic heath during spring-thaw (Larsen et al. 2007).

Unravelling of the seasonal patterns and controls of autotrophic and heterotrophic respiration is important for understanding ecosystem functioning as well as for assessing possible impacts of future climate changes. Still, studies focusing on the seasonal relationship between these two components are lacking. Our modified R_E model provided the opportunity to estimate ecosystem respiration without photosynthesis, because the model can easily distinguish between R_{base} and R_{photo}. The model indicated a strong seasonal pattern of the photosynthesis-related respiration being of minor importance from October to February while contributing considerably with of up to 38% of total respiration during the growing season.

The model fit improvement of the modified R_E model compared to the classic model was higher during the second year in the absence of grazing (R^2 = 0.79 and 0.65, respectively) than during the first year (R^2 = 0.93 and 0.91, respectively) when the area was still grazed by cattle. However, the estimates of λ were similar in both years. Still, the doubling of plant height over the second growing season suggests that photosynthesis became a more important factor for ecosystem respiration relative to temperature during the second year. As a consequence, the peak season respiration related to the photosynthesis was slightly higher during the second (38% of R_E) than during the first year (34%).

Seasonality of carbon fluxes

The flux rates of ecosystem respiration were high, usually reaching between 5 μmol and 10 μmol CO_2 m^{-2} s^{-1} during the growing season, peaking at 12.2 ± 1 μmol CO_2 m^{-2} s^{-1} in June 2005. In comparison, peak rates from plots at the nearby CLIMOOR site without *C. vulgaris*, and with less than half of standing plant biomass of that in our plots, were 6.3 ± 0.3 μmol CO_2 m^{-2} s^{-1} (Tesgaard 2006). Soil respiration rates, i.e., excluding above-ground respiration, of up to about 7.5 μmol CO_2 m^{-2} s^{-1} has been reported from a Calluna heath in Wales, UK (Emmett et al. 2004). In North-American grassland ecosystems R_E rates peak at 9 μmol to 10 μmol CO_2 m^{-2} s^{-1} (Xu and Baldocchi 2004; Flanagan and Johnson 2005) with annual ecosystem respiratory carbon loss of e.g., 735 g to 758 g C m^{-2} $year^{-1}$ (Xu and Baldocchi 2004). Our annual estimate of 1481 ± 11 g C m^{-2} $year^{-1}$ is about twice as high and even slightly higher than the annual ecosystem respiration of various temperate European forest ecosystems, estimated on average to 1100 ± 260 g C m^{-2} $year^{-1}$ (Janssens et al. 2001). However, several factors are likely to explain the high rates in our study. First, the *C. vulgaris* was most probably re-established after an outbreak of the heather beetle (*Lochmaea suturalis*) in the area in 1998. Being about six years old, the shrubs were entering the building phase of their life cycle (Gimingham 1960), and the rapidly increased plant biomass in the absence of grazing during the second year indicates that growth respiration was considerable. Second, respiration rates were not suppressed by water stress at any time.

These factors may also explain why the annual P_g was high and comparable to the highest estimates from temperate forest ecosystems. Another indication for high plant productivity is the relatively high leaf area index (LAI) of *C. vulgaris* estimated to 5.3 ± 0.4 m^2 m^{-2} at another Danish heath site (Sørensen, unpublished data), which is only slightly less than reported LAI of, e.g., evergreen forests (Ibrom et al. 2006), but higher than peak values in a broadleaved forest ecosystem (Pilegaard et al. 2001).

An alternative reason for the relatively large gross CO_2 fluxes of R_E and P_g, if compared to, e.g., the estimates for forests (Janssens et al. 2001), may be methodological. The estimates for forest are all based on the eddy correlation technique where daytime R_E have been extrapolated from night time fluxes, overlooking any particular enhancement of daytime R_E that is not related to temperature. If a similar relationship between photosynthesis and respiration exists for forest ecosystems as seen in the current study, the respiration based on night time measurements only would correspond to R_{base} in our study, indicating that R_E and P_g are underestimated with eddy correlation technique by about 20% annually judging from our results. However, unlike in our study, a time lag between carbon sequestration and increased ecosystem respiration rates on a diurnal (Tang et al. 2005) as well as seasonal (Hogberg et al. 2001) basis has been reported for forest ecosystems, indicating a different pattern of the photosynthesis–respiration interaction. Clearly, more research on this interaction is urgent in order to increase the confidence of carbon flux estimates.

The high net fluxes coincide with the observed increase in plant height. The net carbon gain of 293 ± 11 g C m^{-2} $year^{-1}$ during the second year represents a biomass gain of approximately 580 ± 22 g dry mass m^{-2} $year^{-1}$ assuming a carbon content of dry biomass of 50%. This corresponds to a net increase of about 34% of the total above- and below-ground biomass. The large P_g during all seasons of the year and the high net carbon gain during the second year of the study demonstrate that heath ecosystems may act as large carbon sinks when *C. vulgaris* is in its peak growth phase. Second, although the photosynthetic rates during winter were low compared to peak growing season rates, they had a considerable effect on the net carbon exchange by practically always cancelling out the respiratory

carbon loss. The carbon exchange during the cold season of the year is therefore at least as important for the resulting carbon balance as during the growing season, when both ecosystem respiration and photosynthesis are much higher. *C. vulgaris* has previously been suggested to be dormant from October to February based on the cessation of growth (Miller 1979), irregular stomata opening and accumulation of sugar in the leaves (Miller 1979; Kwolek and Woolhouse 1981). Recently, however, both *C. vulgaris* and *D. flexuosa* have been shown to absorb considerable amounts of nitrogen during the cold season (Andresen and Michelsen 2005; Larsen et al. unpublished data). Although mosses and graminoids may have contributed to the observed photosynthesis during the cold season, the dominance of *C. vulgaris*, the fact that is evergreen, and that mid day flux rates were considerable, indicate that it was photosynthetically active throughout the year.

Conclusion

The exchange rates of carbon in the investigated heath ecosystem were high and of similar magnitude as for productive forest ecosystems. Our results showed that the carbon sink strength of heather-dominated ecosystems may be considerable when *C. vulgaris* is in the building phase of its life cycle. By incorporating a simple relationship between the instant photosynthesis rate and ecosystem respiration into a classic, first-order exponential equation related to temperature, we showed that ecosystem respiration was significantly affected by the carbon uptake of the vegetation. We estimated that annually 24% of ecosystem respiration was tightly coupled to the photosynthetic rate. In addition, the modified model resulted in a lower and more realistic temperature sensitivity of respiration and provided an opportunity to explore seasonal patterns in the relationship between ecosystem respiration and photosynthesis. Our study indicates that the traditional method of extrapolating daytime respiration from night time flux measurements will underestimate daytime ecosystem respiration for ecosystems, where respiration is coupled to photosynthesis. Where photosynthesis is extrapolated as the difference between daytime net carbon flux and respiration rates based on night time measurements, i.e., the eddy co-variance method, photosynthesis may also be underestimated. We suggest that our easily applied and non-intrusive approach is tested in future modelling of ecosystem respiration in other ecosystems to test its general applicability.

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