Biogeosciences Discuss., 9, 16239–16301, 2012
www.biogeosciences-discuss.net/9/16239/2012/
doi:10.5194/bgd-9-16239-2012

Biogeosciences
Discussions

Soil respiration compartments on an aging managed heathland: can model selection procedures contribute to our understanding of ecosystem processes?

G. R. Kopittke[1], E. E. van Loon[2], A. Tietema[1], and D. Asscheman[1]

[1]Earth Surface Science Research Group, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands
[2]Computational Geo-Ecology Research Group, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands

Received: 15 October 2012 – Accepted: 29 October 2012 – Published: 15 November 2012

Correspondence to: E. E. van Loon (e.e.vanloon@uva.nl); G. R. Kopittke (g.r.kopittke@uva.nl)

Published by Copernicus Publications on behalf of the European Geosciences Union.

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

Abstract

Soil respiration studies are increasingly undertaken with the aim of quantifying C fluxes and predicting changes for the future. The interpretation of field data into annual C loss predictions requires the use of modeling tools which generally include model variables related to the underlying drivers of soil respiration, such as soil temperature, soil moisture and plant activity. Very few studies have reported using model selection procedures in which structurally different models are calibrated, then validated on separate observation datasets and the outcomes critically compared. This study utilized thorough model selection procedures to determine soil heterotrophic (microbial) and autotrophic (root) respiration for a heathland chronosequence. The model validation process identified that none of the six measured plant variables explained any data variation when included in models with soil temperature, which contradicts many current studies. The best predictive model used a generalized linear mixed effect model format with soil temperature as the only variable. There were no heterotrophic respiration differences between the community ages. In contrast, autotrophic respiration was significantly greater on the youngest vegetation (55 % of total soil respiration in summer) and decreased as the plants aged (oldest vegetation: 37 % of total soil respiration in summer). Total annual soil C loss from the youngest and oldest communities was estimated to be 650 and 435 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ respectively. Heathlands are cultural landscapes which are managed through cyclical cutting, burning or grazing practices. Understanding the C fluxes from these ecosystems provides information on the optimal management cycle-time to maximize C uptake and minimize C output. Inclusion of the predicted soil fluxes into a preliminary ecosystem C balance suggested that the youngest vegetation is a C sink while the oldest vegetation is a C source, indicating that shorter management cycles could reduce C emissions.

1 Introduction

Soil respiration represents an important source of CO_2 in the biosphere as it is the second largest flux in the carbon cycle and contributes 20–40 % of atmospheric annual C input (Raich and Schlesinger, 1992; Schlesinger and Andrews, 2000). Soil respired CO_2 originates from a number of partitioned belowground sources. These different components of total soil respiration (R_S) can be broadly categorized into autotrophic respiration (R_A: the activity of roots and rhizosphere organisms) and heterotrophic respiration (R_H: bacteria and fungi decomposition of organic matter and soil faunal activity in the organic and mineral horizons) (Hanson et al., 2000). There has been increasing research attention directed towards quantifying C losses from these compartments, both at a local ecosystem scale and at a global scale, with the aim of quantifying C balances and predicting C flux changes for the future.

These changes to soil C fluxes have been linked to anthropogenically induced changes, such as the IPCC predicted climate change (IPCC, 2007), where increased soil warming has resulted in increased C efflux rates (e.g. Davidson and Janssens, 2006; Rustad et al., 2001; Schindlbacher et al., 2012), and prolonged drought periods resulted in reduced C efflux rates (e.g. Selsted et al., 2012; Sowerby et al., 2008, Suseela et al., 2012). Changes in C fluxes can also be associated with anthropogenic land management regimes, such as the selected land use (e.g. grazing; Peichl et al., 2012), any subsequent land use change (Perez-Quezada et al., 2012); soil disturbances (Novara et al., 2012) and cyclical vegetation management practices like heathland burning or plantation forest harvesting (Clark et al., 2004; Clay et al., 2010). The changes observed in CO_2 efflux in all of these studies were associated with the changes to the underlying drivers of R_S activity.

The major drivers of R_S activity in an ecosystem include abiotic factors, such as temperature and soil moisture and include biotic factors, such as gross primary productivity (Bahn et al., 2010a; Davidson and Janssens, 2006; Trumbore, 2006). These factors can interact with each other or can independently affect soil respiration from each of the compartments (Davidson et al., 2006). The R_H is proportionate to the decomposition of soil carbon by microbial communities, which use recently produced organic matter as an energy source (Ryan and Law, 2005; Trumbore, 2006). In contrast, CO_2 lost from autotrophic activity is tied to the assimilation of organic compounds supplied by plant metabolism with a part of this carbon rapidly released from the soil (Horwath et al., 1994; Metcalfe et al., 2011; Ryan and Law, 2005). Thus, the fraction of R_S derived from live roots is independent of soil C pools, and live root contributions to respiration must be understood before measurements of R_S can be used to infer rates of long term soil C storage (Hanson et al., 2000). Live root respiration is typically quantified either by using an isotopic approach, such as repeated pulse labeling, continuous labeling, natural abundance (following change of land use/species), by vegetation removal techniques, such as tree girdling, or by using one of the root exclusion methods, such as root removal, trenching and gap analysis (Chemidlin Prévost-Bouré et al., 2009; Díaz-Pinés et al., 2010; Gomez-Casanovas et al., 2012; Graham et al., 2012; Hanson et al., 2000; Jassal and Black, 2006).

Once field data has been collected, the interpretation of the R_S, R_A and R_H data has generally been undertaken through a comparative analysis and discussion of the original observations. Many studies then additionally processed their observations using modeling tools. As organic matter decomposition is temperature dependent, most soil respiration models related the efflux of CO_2 from soils to temperature in an exponential function (Davidson and Janssens, 2006; Sierra et al., 2011). Organic matter decomposition and plant activity are also affected by moisture availability and therefore many models also included some scalar of soil water content or precipitation (Davidson et al., 2006; Raich and Schlesinger, 1992). Increasingly, measures of plant activity, such as plant metabolism or litter production, have also been included within the soil respiration models to link the aboveground processes with the belowground processes that occur within ecosystems (Bahn et al., 2010b; Metcalfe et al., 2011; Ryan and Law, 2005). The degree to which soil respiration models were process-based or were more empirical was often dependent on both the spatio-temporal scale at which the models were to be applied and the available environmental data (Keenan et al., 2012).

Most studies that used modeling tools investigated the sensitivity of R_S to temperature within their studied treatments (e.g. Sowerby et al., 2008; Suseela et al., 2012; Webster et al., 2009; Xiang and Freeman, 2009). However, a much fewer number of studies used the modeling tools to predict a continuous CO_2 efflux time series for either the length of the study period or for a projection into the future, to allow the annual C loss from R_S (or R_H and R_A) to be estimated. Where modeling was used to generate predictions (rather than to generalize the results of an experiment or survey), most studies assessed their selected model using measures of fit for the calibration-data (e.g. Kutsch et al., 2010; Selsted et al., 2012), but many fewer studies evaluated the models through a (cross-)validation procedure on separate observation data sets (Caquet et al., 2012; Webster et al., 2009). Furthermore, relatively few studies considered the evaluation of structurally different models and a complete variable selection procedure (Chen et al., 2011; Webster et al., 2009). Recently, several review studies have discussed progress in the modeling of soil respiration and proposed better model-data integration with more rigorous and critical procedures to test respiration models (Keenan et al., 2012; Vargas et al., 2011). Interestingly, soil respiration trials or surveys measurements have often been collected repeatedly in time (i.e. longitudinal) and clustered in space but this method has generally not been discussed within the context of soil respiration models. This type of data should ideally be analyzed by hierarchical (multi-level) model framework. However, only a few soil respiration studies adopt a multi-level modeling approach (Bernhardt et al., 2006), whereas multi-level modeling is commonplace in many other areas of ecology and the environmental sciences (Qian et al., 2010). In this study, we aimed to follow these guidelines to implement good modeling practices and build predictive models for total, autotrophic and heterotrophic soil respiration for a managed heathland site. The ultimate goal of this research was to evaluate soil respiration fluxes for the heathland at different vegetation development phases, which would allow for future calculation of a C balance.

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

Heathlands are cultural landscapes in which cyclical management practices, such as cutting, burning or grazing are undertaken (Webb, 1998). It is known that the structure of the dominant heathland plant (*Calluna vulgaris*) changes with increasing plant age, from a "net biomass gain" phase up until 15 yr of age, to a "net biomass loss" phase after this time (Gimingham, 1985). Where stands were all of similar age, it was hypothesized that the younger vegetation ages would have the highest plant activity, resulting in greater allocation of carbon to the roots and therefore a greater R_A (and subsequently greater R_S) than on the older communities. Community age was not expected to influence R_H as there was no significant difference in the quantity of microbial energy source (carbon stock) between the vegetation ages (Kopittke et al., 2012). Therefore, in the modeling process, it was hypothesized that soil temperature and soil moisture would be significant variables for the R_H model, while it was hypothesized that soil temperature, soil moisture and a measure of plant activity would contribute significantly to the R_S models for all three ages.

2 Materials and methods

2.1 Study site

The investigation was undertaken at a dry heathland, located approximately 25 m a.s.l. at Oldebroek, the Netherlands. The dominant vascular species at the site is *Calluna vulgaris* (L.) Hull which grows to a maximum height of 75 cm and provides approximately 95 % of the groundcover, with some *Deschampsia flexuosa* and *Molinia caerulea*. The dominant non-vascular species is *Hypnum cupressiforme* Hedw. with two ecological phenotypes, one growing under Calluna protection and the other adapted to more light between Calluna plants.

The trial was established within a 50 m × 50 m area, at the convergence of three Calluna communities of different ages. Each community age was considered to be a treatment. Replication of these treatments was not possible due to the inherent nature of the site. Therefore, a quasi-experimental design was used, in which groups were selected upon which the variables were tested but where randomization and replication processes were not possible (Campbell and Stanley, 1966).

Heathlands are mostly cultural landscapes that have been formed by human activities, where organic matter is regularly exported from the heathlands to improve arable lands by methods such as grazing, burning, mowing or sod removal (Diemont and Heil, 1984). This vegetation removal cycle had not occurred at the study site for a period of time and the growth rings of the Calluna stems combined with site information were used to establish the ages of the areas. The oldest heathland area (the Old community) was determined to be approximately 28 yr of age at the conclusion of the investigation, while the vegetation on the south-eastern third of the research site was approximately 19 yr of age (the Middle community). The southern portion of the site was last cut in the year 2000 as part of the creation of a fire break and was 12 yr old (the Young community) at the conclusion of the study.

The site is relatively flat in the west and rises in the east and north-east onto a gentle slope with a south-western aspect. The soil is a nutrient-poor, well drained, acid sandy haplic podzol. The soil has an organic horizon which ranged between 1.4 and 8 cm thick, with the mean thickness of 3.9 cm ± 0.04 (Kopittke et al., 2012b). The carbon stock of the soil (organic layer and to 25 cm depth of mineral soil) was $8.01 \pm 0.6\,\mathrm{kg\,m^{-2}}$ on the Young community, $7.61 \pm 0.5\,\mathrm{kg\,m^{-2}}$ on the Middle community and $6.18 \pm 0.4\,\mathrm{kg\,m^{-2}}$ on the Old community and were not significantly different to each other (Kopittke et al., 2012b). Further information about the site location, species composition and climate is provided in Table 1.

2.2 Experimental design

To measure soil respiration and calibrate soil respiration models, eight experimental plots (60 cm × 60 cm) were established within each heathland age in April 2011 ($n = 24$). Four of these plots were used to measure heterotrophic respiration on each community age (henceforth called “Trenched” plots; $n = 12$) and the other four were used to measure total respiration on each community age ("Untrenched" plots; $n = 12$). In this study, the terminology "total soil respiration" and "heterotrophic soil respiration" refers to the observed field data from the Untrenched plots and Trenched plots, respectively. The terminology "R_S", "R_H" and "R_A" refers to the modeled total soil respiration, modeled heterotrophic soil respiration and modeled autotrophic respiration compartments, respectively.

The plots were placed in pairs (one Trenched in combination with one Untrenched plot) that were 1.5 m apart, but the exact location of the individual plot as well as the location of the pairs were randomly allocated within each vegetation age (Fig. 1). In May 2011, the aboveground biomass was harvested from the four Trenched plots within each age group and a narrow trench was excavated to 50 cm depth around the 60 × 60 cm plot area. This depth extended below the main rooting zone, but was above the water table and did not encounter any impermeable layers, all of which may have affected CO_2 concentration productions at depths (Jassal and Black, 2006). A nylon mesh (Plastok Associated Ltd, Birkenhead, Wirral, UK) of 41 µm was placed in the trench to prevent the new roots growing into the plots during the experiment. The soil horizons were backfilled in the order of removal to keep soil disturbance to a minimum. Any subsequent vegetation regrowth was periodically removed but the remains left in the plot on the soil surface. The remaining four Untrenched plots in each vegetation age were not disturbed and were used as a control treatment.

For the purposes of soil respiration model validation, an additional four plots ("Trenched Validation" plots) in each heathland age group were trenched using the described method ($n = 12$) and data collected for the purposes of validating the derived R_H model. A further nine untrenched plots ("Untrenched Validation" plots) were established in the Old vegetation and the collected data was used for validation of the derived R_S model.

2.3 Site meteorological and treatment soil conditions

Site meteorological conditions were recorded on an hourly basis (Decagon Devices Inc.; DC, USA). Air temperature and relative humidity measurements were obtained from 20 cm above ground surface at a central location on the site. Rainfall was measured using a Vaisala tipping bucket rain gauge (Vaisala; Vantaa, Finland) connected to a Decagon datalogger.

Treatment soil conditions were recorded on an hourly basis (Decagon Devices Inc.; DC, USA). Soil moisture ($m^3\,m^{-3}$) and soil temperature (°C) measurements were obtained from 4–7 cm below ground surface in two Trenched plots, two Untrenched plots, and two Trenched-Validation plots in each heathland age group (5TM Sensor, Decagon Devices Inc., DC, USA). The same measurements were obtained from the three Untrenched-Validation plots on the Old community. In total, 21 soil probes were installed, with six being in the Young community, six in the Middle community and nine in the Old community.

2.4 Soil respiration measurements

Respiration collars of 10 cm diameter and 6 cm height were inserted approximately one centimeter into the soil surface in each plot, maintaining a buffer zone of 10 cm from the plot boundary. In the Untrenched plots, moss was removed from inside these collars, to ensure that only soil respiration was measured. Moss was not present on the Trenched plots as it had been removed during trenching activities. Soil respiration measurements were obtained using a Portable Gas Exchange and Fluorescence System (LI-6400XT; LICOR Biosciences, Lincoln, NE USA) in combination with a soil CO_2 flux chamber (LI-6400-09; LICOR Biosciences) which fitted onto the collars.

Soil respiration measurements using this methodology commenced in May 2011, three days after trenching occurred, and continued until August 2012. A total of 29 measurement events occurred post-trenching on the three ages of vegetation. A common effect of the trenching methodology is a flush of CO_2 within the first weeks or months after trenching which originates from decomposing roots (Hanson et al., 2000). To minimize this effect of root decomposition, the first four months of CO_2 efflux measurements were excluded from the study and only observations after 21 September 2011 are included in the analyses. In addition, to determine if there had been significant root biomass loss from the Trenched plots (i.e. decomposition) during the study period, the root biomass in the Trenched and the Untrenched plots was assessed one year after trenching activities. There were 19 soil respiration measurement events from September 2011 until August 2012.

Soil respiration measurements using the above methodology were also obtained from the Trenched Validation plots to validate the R_H model and from the Untrenched Validation plots to validate the Old vegetation R_S model.

Total soil respiration over a 24 h period was investigated on three occasions on the Old community in 2000 as part of an ongoing heathland study. These measurement events were spread over a one year period (in May, July and November) and each event included eight separate soil respiration observations in a 24 h period. These soil respiration rates were determined with a different methodology, in which measurements were obtained from three permanent collars of 24 cm diameter that had been previously inserted at 5–10 cm depth in the soil with a 13 cm edge above the soil surface. Measurements were obtained by placing a gas tight lid on the collar and gas samples were taken using a vacuumized blood tube (10 cm^3 volume) at 15, 30, 60 and 120 min intervals to determine CO_2 accumulation rates within the chamber (Sowerby et al., 2008). Gas samples were analyzed for CO_2 concentration using gas chromatography (GC). A calibration of the two methods (that is, the GC method and the Portable Gas Exchange and Fluorescence System method) was undertaken in 2003 at this site and it was concluded that the methods produced comparable results (Sowerby et al., 2008).

2.5 Photosynthesis measurements

The gross photosynthetic rate provided a measure of photosynthetic activity for the three heathland ages. The gross photosynthetic rate (P_G) was calculated as the Net

Ecosystem Exchange (NEE) rate of CO_2 flux minus the Ecosystem Respiration (ER) rate of CO_2 flux ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$). This photosynthetic rate has a negative sign. A loess smoother curve was applied to the photosynthesis data to obtain daily estimates of plant activity.

The CO_2 fluxes of the vegetation were measured with the same LI-6400 infrared gas analyzer as used for the soil respiration measurements (LI-COR, Lincoln, NE, USA) but in this case attached to a 288 L ultra-violet light transparent Perspex chamber (60 cm × 60 cm × 80 cm) using the method described in (Larsen et al., 2007). The chamber was installed with a fan as well as a soil temperature probe (LI-6400-09 temperature probe) and a PAR sensor (LI-COR quantum sensor).

Three permanent sampling locations were selected in each vegetation age. A metal base frame (60 cm × 60 cm) was permanently installed using small, narrow sandbags to provide a seal between the frame and the soil surface and fixed with metal pins. Measurement of CO_2 fluxes commenced immediately prior to the Perspex chamber being placed on the frame so as to capture the point at which the chamber was sealed and NEE occurred entirely within the chamber. The LICOR measurement program ran for 180 s however, the results obtained while the chamber was being fitted were later discarded so that only data obtained from the sealed chamber (approximately 150 s) were utilized for calculation of NEE rates. After the NEE measurements, the chamber was vented and measurements of the ER rate were obtained by covering the chamber with a fitted blackout-cloth, in which the outer layer was white and the inner lining was black, to minimize any heating effect within the darkened chamber.

In most cases, NEE 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. Therefore a linear regression did not provide a good fit for all measurements. To overcome this problem, the HMR procedure was used (Pedersen et al., 2010). This procedure was developed for soil-atmosphere trace-gas flux estimation with static chambers and tests the fit of both log-linear and linear regression models to the NEE or ER data at each measurement. If linear regression provided the best fit, the flux value was determined by the slope of the regression line. If non-linear regression gave the best fit, the flux was determined by the slope at $t = 0$ s. The HMR procedure has been implemented in an R-package (Pedersen 2011) and this implementation was used in our study. The NEE and ER measurements were only used to calculate P_G and are reported here only as a possible explanatory variable of plant activity within the R_S models. They are evaluated in more detail in another publication.

2.6 Plant and microbial biomass

The biomass harvested from the Trenched plots in April 2011 was separated into Calluna and moss layers. These components were oven dried at 70 °C and the dry weight recorded ($n = 12$).

Microbial biomass and root biomass were sampled in May 2012, approximately one year after trenching activities. Soil sampling was undertaken using a soil corer of 5 cm diameter and intact soil samples were obtained from the organic horizon and 0–5 cm mineral soil. Three cores were obtained and were bulked by soil horizon from each Trenched plot ($n = 12$) and Untrenched plot ($n = 12$). The soils were kept refrigerated during preparation. All the soil was sieved and roots were separated, washed, oven dried at 70 °C and the root dry weight calculated for the organic and the mineral horizon.

In the organic horizon, each sample was divided into three subsamples of each 10 g. One part was analyzed for water content by drying at 70 °C and bulk density was then calculated. Samples were ground and the carbon concentrations were analyzed on a CNS analyzer (Vario EL Analyzer, Elementar). Another subsample was fumigated with the chloroform-fumigation method and extracted for 1 h in 50 ml 0.1 M K_2SO_4 (Jonasson et al., 1996). The third soil fraction was extracted for 1 h without prior fumigation for initial content of carbon and nutrients. The extractions were frozen until shortly before analysis. Upon defrosting, analysis of total organic C (TOC) was undertaken on a Shimadzu TOC 5000 Analyzer. Microbial C was estimated as the difference between the concentration of TOC in the fumigated and unfumigated extract.

An extractability constant of $K_{EC} = 0.45$ was used for microbial C (Jensen et al., 2003). Microbial C (mg) of the organic horizon is reported per gram of substrate C.

2.7 Data analysis

The data analysis workflow approach is described in the following sections and is summarized in Fig. 2. Initially, the observational data was analyzed to determine if there were statistically significant differences between community ages (an age effect) or between Trenched and Untrenched plots (a methodological effect). This indicated how the datasets should be grouped in the later modeling phase; for example, if there was no soil respiration difference between Trenched plots on the three community ages and there was no hypothesized environmental reason as to why there should be a R_H difference, then the three age datasets were grouped for the modeling phase.

Once the observation data had been statistically analyzed, a number of plausible model formats and explanatory variables were chosen for calibration and validation. The explanatory variables were chosen around the major drivers of R_S and R_H: abiotic factors, such as temperature and soil moisture, and biotic factors, such as gross primary productivity (Bahn et al., 2010a; Davidson and Janssens, 2006; Trumbore, 2006). A number of biotic factors were considered for inclusion as explanatory variables but the final decision was based on the observation data available, the outcome of the statistical analysis, the variables used in other studies and the outcome of a preliminary fitting of the models.

Preliminary model fitting indicated that no model could account for the extreme values recorded on 21 March 2012. In addition, the misfit on this day dominated the overall performance criterion. These extreme values are most likely associate with the death of fine roots and microbial populations, followed by the rapid recovery of microbial populations which all lead to short term fluxes of CO_2 from the soil (Matzner and Borken, 2008; Sulkava and Huhta, 2003). Although these CO_2 releases occur, there is strong evidence that these events have little effect on soil C losses at an annual time scale (Matzner and Borken, 2008), therefore it was decided to omit this specific extreme event in the modeling process. This allowed the model to be calibrated and validated more accurately on the observations in which non-extreme processes are believed to be dominant.

The models were calibrated and validated, using the procedures described in the following sections. Based on these results, a model was selected and soil respiration rates were predicted for each compartment. These values were used to estimate annual C losses for each respiration compartment for each community.

2.7.1 Observational data analysis

The effect of vegetation age on the observed vegetation biomass was investigated by a linear model ANOVA. If a treatment effect was identified, then a pairwise *t* tests (using the Bonferroni correction factor) was undertaken whereby an effect is considered as significant if its associated *p*-value is smaller than 0.05. The effect of vegetation age on soil respiration and on photosynthetic activity was investigated using a linear mixed effects model (Pinheiro and Bates, 2000). Where the response variable in the linear mixed effects model was the CO_2 efflux measurement (a repeated measurement per location), the vegetation ages formed the fixed effects and the measurement locations formed the random effects.

Where mean results are referenced, the standard errors of the mean (SEM) are provided in both text and graphics. For all statistical analyses, the R statistical computing program was used (R Development Core Team 2008).

2.7.2 Soil moisture model

A zero-dimensional finite difference soil moisture model (i.e. a “bucket model”), with a daily time resolution and rainfall plus air temperature as model inputs, was constructed and calibrated on the observed soil moisture data (see Appendix A for further details). The soil moisture information in this study is used as a potential explanatory variable for respiration. A soil moisture model, rather than observed soil moisture, was used for two reasons. Firstly, a dynamic model is an appropriate method to integrate the soil moisture values per sensor to an average soil moisture value per treatment and this integration is necessary because not all plots were equipped with a soil moisture sensor. Secondly, it overcomes problems of missing data, such as when a respiration model is used at other sites for predictive purposes, the soil moisture data is usually not available, whereas daily rainfall and temperature are commonly present.

2.7.3 Soil respiration model calibration and validation

A model comparison framework was used to assess the total soil respiration (R_S) models and heterotrophic respiration (R_H) models (Burnham and Anderson, 2002). A number of plausible models were calibrated and only the models with significant parameter values were retained. These models were ranked according to the root mean squared error for the calibration data ($\mathrm{RMSE_C}$) and the models with low $\mathrm{RMSE_C}$ were considered suitable for further validation and discussion.

Validation of the suitable models was done with soil respiration data obtained from the validation plots. The models were fitted and validated to data in accordance with Table 2. This table shows that for R_S and R_H validation was conducted on different observation data over the same time period as the calibration period (Validation Type I). In addition, a second validation of the R_S models was conducted for a different time period (Validation Type II) using the different observation data. However, this validation of R_S models was only conducted within the Old vegetation. For each of the validation data sets, a root mean squared error ($\mathrm{RMSE_V}$) has also been calculated. The RMSE is specified in Eq. (1).

$$\mathrm{RMSE} = \sqrt{\frac{\sum\limits_{i=1}^{n}\left(\hat{R}_i - R_i\right)^2}{n}} \tag{1}$$

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

where $\hat{R}_i$ is the predicted respiration at time i, R_i is the observed respiration at time i and n is total number the number of observations. The general equation is identical when applied to calibration or validation data, as well as for R_S and R_H.

The group of plausible models were built-up as follows. First, an existing empirical soil respiration model was selected from a study undertaken on a comparable *Calluna vulgaris* heathland located in Denmark (Selsted et al., 2012). This model (henceforth denoted as the Selsted model) is used in this study as a null model for both R_S and R_H. It is a non-linear model with three explanatory variables (temperature, soil moisture and biomass) and four parameters that need to be calibrated (further details follow below). Not only the full model with three explanatory variables was calibrated and validated, but also the more parsimonious variants with two variables (temperature and soil moisture or temperature and biomass) and with one variable (temperature).

Next, a linear mixed-effects model (LMM) with the same variables as the Selsted model was calibrated and validated. The mixed-effects structure is required to deal with the repeated measurements on individual locations. Furthermore, a generalized mixed effects model (GLMM) with a Poisson error and a log link function (again with the same variables) was calibrated and validated. In a next step, the soil moisture and biomass variables were transformed into quadratic variables and the LMM and GLMM models using these variables were also calibrated and validated (these models are denoted by LMM2 and GLMM2). These quadratic forms of the models were successfully applied in the study by Khomik et al. (2009).

Following the approach by Selsted et al. (2012), soil moisture as well as biomass were scaled to represent relative soil moisture and relative biomass. Equations (2) and (3), respectively, provide the details of these transformed variables.

$$M = \frac{\theta}{\theta_\mathrm{fc}} \tag{2}$$

where M is the relative soil moisture content (a fraction between approximately 0.1 and 1), θ is the volumetric soil moisture content (in this study output from a dynamic soil moisture model, Sect. 2.7.2), θ_{fc} is the soil moisture content at field capacity. An estimate for θ_{fc} was available per treatment from the soil moisture model (Sect. 2.7.2).

$$B = \frac{\text{Biomass}}{\text{Max Biomass}} \tag{3}$$

where B is the relative biomass (a fraction between approximately 0.3 and 1), "Biomass" is the aboveground Calluna biomass in $\mathrm{g\,m^{-2}}$ for a given observation plot and "Max Biomass" for the plot with the greatest quantity of aboveground biomass. Moss was also harvested from the plots, however only the Calluna biomass was used in this calculation as the Calluna root systems were expected to contribute to R_A but the moss layer lacks a rooting system and would not contribute to R_A. For the model developed by Selsted et al. (2012), peak biomass was estimated using non-destructive techniques. In the current study, the biomass initially harvested from the Trenched plots within each nested replicate was used as an estimate of aboveground biomass for the Untrenched plots in the same nested replicate.

However, as harvested biomass does not give a dynamic measure of plant activity throughout the year and the changes of seasons, a measure of photosynthetic activity (Sect. 2.5) was included in the model testing process as an alternative variable for Calluna biomass. A value for relative photosynthetic activity was calculated as follows.

$$P = \frac{P_G}{\text{Maximum } P_G} \tag{4}$$

where P_G is the gross photosynthesis measured per plot in $\mathrm{\mu mol\,CO_2\,m^{-2}\,s^{-1}}$, and Maximum P_G is the maximum CO_2 consumption rate measured during the study, as described in Sect. 2.5.

In the first modeling cycle, the soil temperature at 5 cm depth (T_{soil}) was used, as it is a common component of soil respiration models. However, in a second modeling cycle, air temperature (T_{air}) was also tested as a substitute for soil temperature, as it is often a more commonly recorded variable across ecosystems. The equations for the

Selsted, LMM, LMM2, GLMM and GLMM2 models using the T, M, B and P variables (see Eqs. 2–4) as predictor variables are shown in Table 3.

In addition to the variables detailed above, a number of other variables were tested in an early explorative phase that occurred prior to the formal model identification process. This other variables included Photosynthetically Active Radiation (PAR) values used as a substitute for the T_{soil} or P variables, the microbial biomass as a substitute for the B variable and the root biomass as a substitute for the B variable in both R_{S} and R_{H} models. In that explorative phase, it was found that the RMSE_{C} and RMSE_{V} values for the models involving these variables were higher or close to those variables shown in Table 3. Therefore, the results of these alternative variable combinations were not tested further.

2.7.4 Soil respiration model selection and generation of predictions

The final models for R_{S} and R_{H} were selected using the following rationale. Firstly, the calibrated models in which all coefficients were significant were identified and retained for further consideration. Hereby, the parameter reasonableness for basal respiration rate (R_0), temperature (k) and photosynthetic activity (c) were also used as a criterium: the only models acceptable were where parameter values of $R_0 < 0.5$ (for the Selsted and GLMM formats), $a > 0$ and $c > 0$ (GLMMformats) or $a < 0$ and $c < 0$ (LMM formats). For the R_{H} models, a complete set of validation data for each vegetation age was available. Therefore, the subset of R_{H} models with significant parameter values were further assessed by their RMSE_{V1} values, and those with the lowest values were considered most suitable.

In the R_{S} models, the validation data and therefore, the RMSE_{V1} and RMSE_{V2}'s, were only available for the Old community. Consequently, the RMSE_{C} provided a better measure of model performance across each age of vegetation. Hence, the R_{S} models with significant parameter values and the lowest RMSE_{C} were selected while the values for RMSE_{V1} and RMSE_{V2} were of secondary importance (these should lie in the lower to middle-range of all RMSE values).

Following the selection of the model, R_S and R_H were predicted for the length of the study period using a single hourly soil temperature dataset from the Untrenched treatment.

3 Results

3.1 Vegetation characteristics

Destructive vegetation sampling indicated that mean Calluna aboveground biomass was lowest on the Young community and greatest on the Middle community. This difference was just above the 0.05 significance level after the Bonferroni correction ($p = 0.059$; Fig. 3a). The biomass of the moss layer was almost double on the Young community ($0.43 \pm 0.09\,\mathrm{kg\,m^{-2}}$) than the moss biomass on either the Middle community ($0.27 \pm 0.04\,\mathrm{kg\,m^{-2}}$) or Old community ($0.26 \pm 0.04\,\mathrm{kg\,m^{-2}}$; results not shown).

Photosynthesis, as a measure of plant activity throughout the year, was greatest in the summer months and least in the winter months (Fig. 3b). In winter months, there was no significant difference between mean photosynthesis on the Young ($-2.1 \pm 0.7\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$), Middle ($-1.0 \pm 0.3\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) or Old ($-1.8 \pm 0.5\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) communities. However, in summer months there was significantly greater photosynthesis on the Young community ($-16.0 \pm 1.4\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) than on either the Middle community ($-5.7 \pm 1.5\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$) or the Old community ($-5.2 \pm 1.0\,\mu\mathrm{mol\,CO_2\,m^{-2}\,s^{-1}}$). The Old community was significantly different to the Middle community in summer ($p = 0.049$) but there were no other seasonal differences between the mean photosynthetic rates of the Middle and Old communities during the study period.

3.2 Soil respiration

In every season of the year, total soil respiration was significantly greater on the Young community than on the Old community (winter $p = 0.034$, spring $p = 0.0144$, summer $p = 0.007$, autumn $p = 0.006$). The greatest mean total soil respiration was recorded in summer months on all three communities, ranging from a mean of $2.8 \pm 0.2\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$ on the Young community to $2.1 \pm 1.9\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$ on the Old community (Fig. 4a). The differences between the communities were greatest in spring with total soil respiration on the Young community ($1.9 \pm 0.2\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) exceeding respiration on the Middle community by a factor of 1.6 and exceeding the Old community by a factor of 1.7.

There was no effect of community age in any season for heterotrophic soil respiration on the Trenched plots (Fig. 4b). Therefore, the heterotrophic data was not split into age treatments for further analyses, but was treated as a single dataset. Mean heterotrophic soil respiration was least in winter months ($0.4 \pm 0.05\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) and greatest in summer months ($1.7 \pm 0.09\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$).

A peak was observed in both total soil respiration and heterotrophic soil respiration on 21 March 2012. The elevated respiration results were observed on both Trenched and Untrenched plots and, although the CO_2 flux was variable between measurement locations, the largest fluxes were generally observed on the Young community. The maximum respiration observed on this day for the Trenched plots was $10.28\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$ (Young community) and for the Untrenched plots was $5.11\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$ (also Young community).

The diurnal variation of total soil respiration was determined in 2000 on the Old community (Fig. 5). The greatest variation in rates occurred in July, with the lowest mean total soil respiration occurring at 04:00 ($1.0\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) and increasing until 15:00 ($1.6\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$). The least diurnal variation was observed in November and means ranged between 0.6 and $0.4\,\mu\text{mol}\,\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$.

3.3 Treatment effect

Soil temperature at 5 cm below ground surface was significantly different between the Trenched plots and the Untrenched plots over the study period (Fig. 6a). The mean soil temperature in winter was significantly lower on the Trenched plots (3.8 ± 0.03 °C) than on the Untrenched plots (4.8 ± 0.03 °C). However, the reverse occurred in summer, where mean soil temperature was significantly greater on the Trenched plots (16.9 ± 0.03 °C) than on the Untrenched plot (15.5 ± 0.02 °C). Mean air temperature at 20 cm above ground surface 3.0 ± 0.03 °C in winter and 15.7 ± 0.11 °C in summer. Soil moisture was significantly different between the Trenched and Untrenched plots with lower soil moisture values observed on the Trenched plots than the Untrenched plots in non-rainfall periods (Fig. 6b).

Microbial C was not significantly different between the Trenched plots and the Untrenched plots in the organic horizons of the in either the Young ($p = 0.21$), Middle ($p = 0.49$) or in the Old ($p = 0.93$) vegetation (Fig. 7). On Untrenched plots, the organic horizon microbial C was significantly greater in the Young vegetation than in the Middle ($p = 0.006$) or the Old ($p < 0.001$) vegetation but there was no significant difference between the Middle and the Old vegetation ($p = 0.22$).

Root biomass (summed for organic horizon and 0–5 cm mineral horizon) was not significantly different between the Trenched and Untrenched plots in either the Young ($p = 0.42$), Middle ($p = 0.76$) or in the Old ($p = 0.18$) vegetation (Fig. 7). Additionally, the root biomass in the Untrenched plots was not significantly affected by the vegetation age ($p = 0.95$). There was however, a significantly greater root biomass in the organic horizon than in the 0–5 cm mineral horizon for all vegetation ages ($p < 0.02$; data not shown).

3.4 Calibration of the model for total soil respiration (R_S)

All model predictions of soil respiration generally followed the seasonal soil temperature patterns, where the lowest respiration was recorded in winter (in February). However, not all models predicted the highest respiration equally, with some models predicting peak values in June, while others predicted peak values in August.

3.4.1 Selsted equation models

The step-wise addition of the Selsted equation components to the Untrenched datasets for the Young, Middle and Old communities produced models with absolute RMSE_C values ranging from 0.30 to 0.66 (Fig. 8, left panel). When soil temperature (T_soil) was assigned as the T variable within the models (similar to Selsted et al., 2012), the RMSE's were generally lower than when air temperature was used (T_air). Within the soil temperature subset, there were only two combinations of variables which resulted in all parameters being significantly different from zero. The first was when T_soil was the only explanatory variable used and it was significant for the Young, Middle and Old datasets (Fig. 8). The second was the combination of $T_\text{soil} + P$ in the Middle dataset, but once this model was screened for parameter reasonableness (as defined in Sect. 2.7.4), it was excluded from further consideration.

Substituting air temperature for the T variable did not produce a better model, as indicated by the higher mean RMSE_C values produced. However, there were also two combinations of variables which resulted in models where all parameters were significant; when T_air was the only variable (for Young, Middle and Old datasets), and when $T_\text{air} + P$ were used in combination (Young and Middle datasets). Of these, only the T_air and P combination for the Middle model returned reasonable parameter values.

The model did not converge when the explanatory variables T_soil and M were used with the Old vegetation datasets, for T_soil, M and B with the Old vegetation dataset and for T_air, M and B with the Middle and Old vegetation datasets.

3.4.2 Linear mixed effects models

Step-wise application of variables into the LMM and LMM2 model formats resulted in absolute RMSE_C values that ranged between 0.30 and 0.58 (Fig. 8). Application of the explanatory variable T_{soil} resulted in models with lower mean $RMSE_C$ values (0.35 to 0.40) than the inclusion of T_{air} (0.37 to 0.54).

When the LMM format was used with the three variables $T+M+P$, the model consistently over-predicted soil respiration for both the Young and the Old communities. There were no LMM models in which T_{air} was a significant explanatory variable. There were three combinations of explanatory variables in which parameters were significant. These were when T_{soil} was applied alone (on the Middle dataset), and $T_{soil}+M$ (Old dataset) or $T_{soil}+P$ (Old dataset).

Within the LMM2 format, the inclusion of the three variables $T+M+B$ resulted in under-prediction of soil respiration in summer months and in the coldest winter months. Of the remainder variable combinations, there were three combinations that resulted in all parameters being significantly different to zero: $T_{soil}+M$ (Old dataset), $T_{air}+M$ (Old model) and $T_{air}+P$ (Young and Middle datasets). The parameters in all of these models were considered reasonable.

3.4.3 Generalized linear mixed models

The GLMM and GLMM2 model formats resulted in absolute $RMSE_C$ values that ranged between 0.19 and 0.38 (Fig. 8, left panel). The use of the explanatory variable T_{soil} resulted in models with lower mean $RMSE_C$ values (0.20 to 0.25) than the inclusion of T_{air} (0.25 to 0.38). When T (both for T_{soil} and T_{air}) was the only variable used, the model parameters were significant for all three Young, Middle and Old dataset. When all three variables $T+M+P$ were used in combination in the GLMM format, the model over-predicted soil efflux for both the Young and the Old communities. This did not occur with the GLMM2 format.

Within the GLMM2 model format, there were six variable combinations in which all parameters were considered to be significant. Four of these used T_{soil} in combination with B (Young dataset), with P (Middle dataset), with M (Middle dataset) and with both $M+P$ (Middle dataset). All of these models had parameter variables that were considered reasonable.

The GLMM models in which all parameters were considered significant were similar to those of the GLMM2, although $T_{soil} + M$ and $T_{soil} + P$ were also significant for the Old dataset when the GLMM format was used (Fig. 8, left panel). Additionally, the T_{air} combination with P resulted in significant parameters in all three Young, Middle and Old models. The parameters in all of these models were considered reasonable.

3.5 Calibration of the model for heterotrophic soil respiration (R_H)

3.5.1 Selsted equation models

The Selsted equation resulted in absolute $RMSE_C$ values that ranged from 0.30 to 0.43 and were lower on the heterotrophic models in which T_{soil} was used as the T variable (Fig. 8, right panel). When T (either T_{soil} and T_{air}) was the single variable or when T_{air} was used in combination with M, all model parameters were significant. All parameters were considered to be reasonable for these combinations.

3.5.2 Linear mixed effects model

Application of the LMM or LMM2 format to the heterotrophic soil respiration data resulted in $RMSE_C$ values that ranged between 0.30 to 0.39 (Fig. 8). No model in which T was used singly was this parameter significant, but when M was included with T (both T_{soil} and T_{air}) in the model, the parameters were all then significant.

3.5.3 Generalized mixed effects model

The GLMM and GLMM2 formats resulted in model $RMSE_C$ values of between 0.27 and 0.36 (Fig. 8, right panel). The T variables (both T_{soil} and T_{air}) were significant when applied singly and also when applied in combination with M, with the exception of the GLMM2 for $T_{soil} + M$. All parameters were considered to be reasonable for these combinations.

3.6 Model validation

The calibrated models were used on the validation data for period one (September 2011–August 2012) and period two (November 2012–August 2011, see Table 2). The resulting RMSE validation values (RMSE_{V1} and RMSE_{V2}) were then compared to the RMSE calibration values (RMSE_{C}). The R_{S} models which had both the lowest RMSE_{C} and the lowest RMSE_{V} values used the GLMM format with T_{soil} as a single variable ($\text{RMSE}_{\text{C}} = 0.23$, $\text{RMSE}_{\text{V1}} = 0.51$ and $\text{RMSE}_{\text{V2}} = 0.57$), with $T_{\text{soil}} + P$ ($\text{RMSE}_{\text{C}} = 0.23$, $\text{RMSE}_{\text{V1}} = 0.51$ and $\text{RMSE}_{\text{V2}} = 0.48$) and with $T_{\text{air}} + P$ ($\text{RMSE}_{\text{C}} = 0.27$, $\text{RMSE}_{\text{V1}} = 0.57$ and $\text{RMSE}_{\text{V2}} = 0.52$). Of these, the GLMM T_{soil} model and the GLMM $T_{\text{air}} + P$ model were the only ones were all parameters were significant for all vegetation ages.

The R_{S} models which performed the worst in the validation phase also used the GLMM format and included the T variable (both T_{soil} and T_{air}) in combination with $M + P$ (e.g. $T_{\text{soil}} + M + P$ results were $\text{RMSE}_{\text{C}} = 0.20$, $\text{RMSE}_{\text{V1}} = 2.85$ and $\text{RMSE}_{\text{V2}} = 3.54$), so these models were clearly over-parameterized.

Generally, the average ratio of RMSE_{V1}: RMSE_{C} in the R_{S} models was 1.8 and the ratio of RMSE_{V2} : RMSE_{C} was 1.6. The ranges for RMSE_{V1} (approx. 0.5 to 0.75) and RMSE_{V2} (approx. 0.45 to 0.65) were comparable, with the same four of the fifty-seven R_{S} models (LMM and GLMM, using T, M and P, for both air and soil temperature) leading to very high values for RMSE_{V1} as well as for RMSE_{V2}. For the R_{S} models, there was no correlation between RMSE_{C} and RMSE_{V1} nor between RMSE_{C} and RMSE_{V2} (omitting the 4 extreme values for RMSE_{V}). It should be noted that the validation was done only for the old vegetation and the relation between RMSE_{C} and RMSE_{V1} or RMSE_{V2} could be stronger for the other ages.

The R_{H} models produced relatively low RMSE_{V} values for all combinations and formats (< 0.49).The R_{H} models which produced the lowest RMSE_{V} values were the GLMM format with $T_{\text{soil}} + M$ ($\text{RMSE}_{\text{C}} = 0.27$ and $\text{RMSE}_{\text{V1}} = 0.37$), the GLMM format with T_{soil} alone ($\text{RMSE}_{\text{C}} = 0.28$ and $\text{RMSE}_{\text{V1}} = 0.39$), and the LMM format with $T_{\text{soil}} + M$ ($\text{RMSE}_{\text{C}} = 0.30$ and $\text{RMSE}_{\text{V1}} = 0.38$). Generally, the ratio of RMSE_{V1} : RMSE_{C} in the

R_H models was, on average, 1.26. There was a strong correlation between RMSE_C and RMSE_{V1} (Pearson correlation coef. of 0.88).

3.7 Model selection

Following the rationale described in the methodology to select the best predictive models, the GLMM model using only T_{soil} and the model using $T_{soil} + M$ were chosen to predict R_H. The performance of the two models was so similar, that the simplest model (using only T_{soil} as predictor) was selected to be used for further predictions.

For the R_S models, the best predictive models were the GLMM models, using only T_{soil} or using $T_{soil} + P$. As with the R_H models, the differences between these two models (with respect to RMSE_C, RMSE_{V1} and RMSE_{V2}) were so small that the most attractive R_S model choice was the one in which the structure coincided with the R_H model, that is, using only T_{soil}. The GLMM T_{soil} parameterized models were then used to predict soil respiration over the length of the study period (Table 4 and Fig. 9).

3.8 Autotrophic soil respiration

Autotrophic soil respiration was determined by subtracting the model predicted heterotrophic soil respiration results from the total soil respiration results in each vegetation community ($R_S - R_H = R_A$; Fig. 10). The R_A component was approximately zero on the Middle and Old communities in winter. The greatest R_A was predicted to occur on the Young community in the summer months, with a maximum in July when approximately 55 % of soil respiration was attributable to autotrophic sources. In this same time period, approximately 45 % and 37 % of soil respiration on the Middle and Old communities, respectively, was attributable to autotrophic sources.

3.9 Annual carbon loss estimates

Based on model predictions, annual carbon loss from R_S was estimated at 650 $\text{g C m}^{-2}\,\text{yr}^{-1}$ for the Young community and 435 $\text{g C m}^{-2}\,\text{yr}^{-1}$ for the Old community

(Fig. 11). The annual losses from R_A and R_H compartments were approximately equal in the Young vegetation, but it was estimated that there was greater C loss from R_H than from R_A sources in both the Middle and the Old communities. The C loss from soil compartments was plotted against community age, using a "time for space" chronosequence approach to approximate changes in C loss over a 30 yr period. Year zero represents the bare soil which would be expected following a vegetation cutting cycle. In this case, all soil respiration would be expected to be from the R_H compartment, as there are no plant roots respiring and the lack of vegetation cover would result in more variable soil temperatures, as observed in the bare Trenching plots. Therefore, C loss in year zero was predicted using the more variable Trenched soil temperatures ($350\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$). Soil temperatures were less variable under plant cover and so the Untrenched temperatures were used in the model to predict annual R_H C loss ($322\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) where plant cover was present.

4 Discussion

Carbon loss from soil respiration was greatest on the Young community and root-associated respiration contributed approximately equally to the annual C sum as was contributed by microbial respiration. As the community age increased, the annual C loss from soil respiration decreased and this change was driven by the decreasing contribution of root respiration.

The following sections have been grouped around discussion of the soil respiration, of the trenching effects, the modeling process and finally a discussion of the annual model predictions.

4.1 Soil respiration

In general, the greatest soil respiration (both total and heterotrophic) occurred in summer. This corresponded with the warmest mean air temperatures, warmest mean soil temperatures and greatest plant activity (photosynthesis). The lowest soil respiration was in winter, which likewise corresponded with the coldest mean air temperatures, coldest mean soil temperatures and least plant activity.

The similarity in heterotrophic respiration rates on the three communities was consistent with the original hypothesis that CO_2 efflux would not be different between vegetation ages. The CO_2 effluxes observed from microbial decomposition are determined by the quantity and quality of available substrate, the soil temperature and other conditions that control decomposer activity (Kirschbaum, 2006). On the three ages of vegetation, there was no difference between the quantity of available substrate, that is, the soil C stocks in the organic layer to 10 cm depth (Kopittke et al., 2012b). There were also no soil temperature or soil moisture pattern differences between the Trenched plots on the three community ages. However, the quality of the organic matter and recently deposited litter (prior to trenching) was not known. The proportion of lignin in the litter could be expected to increase with increasing community age, as woody stem growth increases with increasing plant age (Gimingham, 1985). Increasing the lignified material in organic matter results in slower decomposition rates (Filley et al., 2008; Kalbitz et al., 2003). However, as no differences in respiration were observed, it is possible that the rapid decomposition of the labile organic matter masked any underlying differences (if indeed present) in the more recalcitrant pools.

This ecosystem is subject to high bulk N deposition rates (10.7 to 37.4 $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ 1998–2012; Kopittke et al., 2012a) which can have direct and indirect effects on decomposition rates. Elevated N deposition decreases the decomposition rates of recalcitrant organic matter, while also increasing the decomposition rates of easily degradable organic material (Fog, 1988). Indirectly, leaf chemistry and litter quality can change under elevated N deposition, thus leading to an accelerated decomposition rate (Kozovits et al., 2007; Nierop and Verstraten, 2003). Root respiration rates have also been observed to increase under elevated N deposition (Burton et al., 2012). However, all plots were subjected to similar N deposition rates and so this is not expected to result in respiration differences in the community ages.

The difference in total soil respiration between the community ages was not associated with heterotrophic respiration and therefore, were associated with the root-associated respiration. The greater total soil respiration on the Young community indicated that the Calluna plant roots were more actively respiring than on the Middle or Old communities. These higher rates corresponded to the higher photosynthetic rates observed on the Young community. This supported the hypothesis that the youngest plants had the highest plant activity, resulting in greater allocation of carbon to the roots. Interestingly, these increased photosynthetic rates originated from a much lower Calluna biomass, and are likely to be associated with a greater leaf area index on the Young community, which was in a "net biomass gain" phase of growth, than the Middle and Old communities, which were in a "net biomass loss" phases of growth (Gimingham, 1985).

However, Calluna biomass was not the only contributor to photosynthetic activity. Mosses also contributed to photosynthesis, with almost double the moss biomass on the Young community than on the Middle or Old communities. Although moss did not contribute directly to R_A, as it lacks a root system, this mismatch in aboveground and belowground rates is likely to have introduced additional bias when including photosynthesis as a variable in the R_S models. This study did not quantify the separate contributions of moss and Calluna to the overall photosynthetic rates. However, based on the ratio of moss biomasses and the ratio of photosynthetic rates, it can be estimated that the younger Calluna plants were still more photosynthetically active than the Old community. The contribution of the moss to ecosystem functions other than photosynthesis should not be overlooked either, as moss has been shown in this study and in others to moderate soil temperature throughout the year and influence soil moisture in between rainfall events (Startsev et al., 2007).

The peak respiration values recorded in March 2012 corresponded to the first warm period in which air temperatures exceeded 15 °C, following from a severe frost (–20 °C) in February 2012. These extreme values were most likely associated with the death of fine roots and microbial populations, followed by the rapid recovery of microbial populations which lead to short term fluxes of CO_2 from the soil (Matzner and Borken, 2008; Sulkava and Huhta, 2003). In addition, Calluna litter fall measurements on the Old vegetation have shown peak fall rates occur in January and February and old flowers are the dominant litter type (unpublished data from the adjacent long term trial). This unlignified litter is likely to provide a rapidly decomposable energy source for microbial populations and may have contributed to the CO_2 efflux peak that was observed in spring.

The observed total soil respiration rates were comparable to other Calluna heathland communities, such as in Brandbjerg, Denmark (Selsted et al., 2012). The mean summer total soil respiration rates in Brandbjerg ranged between 1.2 and 2.9 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ (2008 and 2006, respectively) and this was within the same range observed at Oldebroek in the summer of 2012 (Young: 2.78 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$, Middle: 2.36 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ and Old: 2.12 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$).

In a soil respiration study undertaken on a hydric Calluna heathlands in the Northern Pennines England, the total soil respiration rate observed in September 2006 (1.8 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$: Calluna age unknown) was within the same range as observed on the Oldebroek Old community in autumn 2011 (Heinemeyer et al., 2011). The diurnal respiration pattern of this English heathland closely followed the daytime peak in soil temperature, which was similar to the Oldebroek results. Interestingly, this trend was not observed on a similarly studied forest or grassland, where peak respiration occurred during the night time (Heinemeyer et al., 2011).

Total soil respiration of other heathlands far exceeded the observations recorded at the Oldebroek study site. In the mesic heathland at Mols in Denmark, mean summer total soil respiration rates were 16 $\mu mol\,CO_2\,m^{-2}\,s^{-1}$ in 2003 (Sowerby et al., 2008), which was approximately 5.8 times the mean summer respiration observed on the Young community at Oldebroek in 2012. This large difference is most likely associated with the age of the vegetation and possibly differences in vegetation composition rather than soil differences. The soil type at Mols was similar, but the heathland experienced a heather beetle attack in 1999, which mainly resulted in Deschampsia regrowth and regrowth of only very few young Calluna plants (four years old). Similarly, total soil respiration on a hydric Calluna heathland at Clocaenog in Wales was also consistently greater in every season than the Young community, even when the peak values of 5.6 µmol CO_2 m^{-2} s^{-1} (Young community) and 7.6 µmol CO_2 m^{-2} s^{-1} (Clocaenog) were compared (Emmett et al., 2004).

4.2 Trenching effect

The soil temperature difference observed between Trenched and Untrenched plots is likely to be a function of the Calluna plants providing shade and the thick moss layer providing insulation at the soil surface. These two factors are hypothesized to have regulated soil temperature in the Untrenched plots but not in the Trenched plots where the aboveground vegetation had been removed. Temperature determines the rate of organic matter decomposition and CO_2 production (Kirschbaum, 2006). Therefore, the Trenched plots (producing autotrophic respiration) and Untrenched plots (producing total soil respiration) were exposed to different temperature regimes. In principle, R_A is the difference between the R_S and R_H, however, under these differing temperature conditions, the observed results cannot be directly used to calculate autotrophic respiration. This temperature difference confirmed the necessity of using soil respiration models to predict both total soil respiration and autotrophic respiration for the same temperature range.

Soil moisture patterns were also observed to differ between the Trenched and Untrenched plots, where the Trenched plots were drier than the Untrenched plots in non-rainfall periods. This is contrary to other studies in which trenching was observed to result in higher soil moisture than the control plots (Hanson et al., 2000). It is hypothesized that vegetation removal led to a loss of shade cover and this resulted in the organic layer and litter layer being exposed to greater evaporation rates. This hypothesis is supported by visual observations of a drier and cracked organic layer on the Trenched plots. The respiration models being tested incorporated a soil moisture parameter so that any moisture effect could be assessed.

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

The advantages and disadvantages of the trenching trial have previously been documented in review discussions (Hanson et al., 2000; Ryan and Law, 2005) and field based studies (Díaz-Pinés et al., 2010; Jassal and Black, 2006) but it is worth mentioning a few points in this discussion. The ability to measure soil respiration compartments under field conditions rather than laboratory conditions is advantageous for assessment of respiration responses to current environmental conditions and trenching trials can provide satisfactory estimations of field based R_A rates, as long as the error is corrected for during data analysis (Díaz-Pinés et al., 2010). The soil temperature and soil moisture effects were corrected for through application of a model, which generates predictions on a standardized soil temperature and soil moisture time series.

4.3 Model evaluation

All models followed generally the same pattern in the prediction of minimum effluxes in the winter, maximum effluxes in the summer and the highest autotrophic respiration for the Young community (see Fig. 9, showing only the results for GLMM). However, the specific fit to the observations (as summarized by RMSE) was quite different between the different models (see Fig. 8).

The RMSE values for all models using soil temperature were consistently lower than those using air temperature. Additionally, the GLMM models lead to lower RMSE values and a lower spread in RMSE between the different vegetation ages than the other models (the RMSE values for the LMM and Selsted models were comparable). These results indicated that the complex parameterization of soil moisture and biomass effects in the Selsted model were not suitable for our site. This difference in model fitness may be due to the differences between the Brandbjerg heathland site in Denmark (for which the Selsted model was developed) and our site. The Brandbjerg site had a much greater percentage of grass (*Deschampsia flexuosa*, c. 70 % cover and *Calluna vulgaris*, c. 30 % cover) with the Calluna approximately 4 to 6 yr old for the first year of soil respiration measurements (Mikkelsen et al., 2008; Selsted et al., 2012). Additionally, although the soil type was similar between Brandbjerg and Oldebroek, there were climatic differences with mean annual temperature of 2 degrees cooler and approximately 400 mm lower average annual rainfall at the Danish site. In a future research it would be interesting to pool the two data sets and re-evaluate the models to see whether a model can be identified that is adequate for both sites.

In consideration of the R_H models, the RMSE values were similar and well correlated between the calibration and validation phases. Therefore, these models were considered stable and it can be assumed that the model predictive uncertainty was mainly due to parametric uncertainty.

In contrast, the R_S models showed no relation between the calibration and validation RMSE values. Based on our current data set, we have no conclusive explanation for this phenomenon. However, by assuming that the validation data was representative for all vegetation ages, the most plausible explanation for the lack of correlation between RMSE_C and RMSE_V (as well as between $\mathrm{RMSE}_\mathrm{V1}$ and $\mathrm{RMSE}_\mathrm{V2}$) was that an important covarying variable is lacking in the models that were parameterized so far. Hence, the model predictive uncertainty is larger than what is expected on the theoretical prediction error by a single best model.

From the variables assessed and available for inclusion in our model selection process, the best fit of the observed data was provided by a model using soil temperature alone. The application of only a temperature function to model soil respiration data has previously been questioned since, as already discussed, other factors such as soil moisture limitation of microbial processes and the C allocation via plant roots are all reported to influence soil respiration rates (Davidson et al., 2006; Rustad et al., 2000). Therefore, the original hypothesis had proposed that the most appropriate R_H and R_S models would include soil temperature and soil moisture variable, with the R_S model also including a measure of plant activity to explain variance in soil respiration. However, our results indicated that soil moisture and plant activity (Calluna biomass, photosynthetic rate, microbial biomass and root biomass) were not significant variables for our site.

Soil moisture has been shown to impact microbial respiration (and therefore R_H) only at extremely low water contents when desiccation stress becomes important for microbial substrate supply (Davidson et al., 2006). In the case of root respiration (and therefore R_A), the exact effect of low soil moisture on Calluna plants and belowground C allocation is not known. Calluna plants appear to be resilient to water stress and heathlands can withstand quite severe summer droughts, if annual rainfall is high enough to compensate for the drought (Loidi et al., 2010). Additionally, the Oldebroek heathland is established on a free-draining, sandy soil that has a relatively low stored soil moisture in the mineral soil. The majority of the Calluna roots were identified within the nutrient-rich, organic layer of the soil and this is also where the largest proportion of the soil moisture is stored (see Table 1). However, continuous soil moisture measurements in the organic layer are very difficult due to instrumentation constraints (Schaap et al., 1997). Because of this, it is likely that a large proportion of the soil respiration response to reductions in soil moisture occurred in the organic horizon, and this was not able to be quantified with the current technology. Although the effect of soil moisture stress on heathland R_A was not able to be determined in this study, future investigations will assess the long term effect of repeated drought on the soil respiration compartments.

Plant activity measures from other published soil respiration models that could be considered as alternative model variables have included using relative PAR with soil temperature and soil moisture (Caquet et al., 2012). In our study, PAR was included in the initial model screening process as a single predictor variable and as a predictor variable together with temperature. However, neither of these models resulted in a better fit than soil temperature alone and therefore, PAR was not included in further model testing.

Alternatively, another plant variable which has been considered in other respiration models is the rate of litter decomposition (Kutsch and Kappen, 1997; Kutsch et al., 2010). However, it is unclear from these studies whether the addition of litter decomposition to the soil temperature and moisture model resulted in a better model fit, as the parameter significance was not reported. Soil temperature has been found to generally have a good relationship with organic matter decomposition rates (Davidson and Janssens, 2006) and therefore it is hypothesized that a litter decomposition variable would not explain significantly more variability than already explained by soil temperature. Other plant litter variables, such as litter fall rates, are also often included in dynamic models as they provide an important feedback into the carbon cycle and substrate available for decomposition (Keenan et al., 2012).

Root maintenance (as a function of root nitrogen concentrations) and root growth have also been included in soil respiration models (Chen et al., 2011). In study in Tennessee USA, this model with root variables was able to describe more of the biological dynamics than the other models tested although it was still not capable of capturing all the data variation across the different study treatments (Chen et al., 2011). Root dynamics provide a direct measure of root activity and, if it had been measured at the Oldebroek site, may have explained more variance that the photosynthetic rates.

It is worth considering that soil temperature is likely to be also related to seasonal plant activity and may simply be the overwhelming driver of soil respiration in this system. A similar finding was reported by (Bahn et al., 2010a) where differences in R_S between different sites were largely determined by plant productivity. However, since both the R_S and productivity fluxes increased with temperature, it was concluded that the soil temperature (T_soil) typically sufficed to explain most of the seasonal variation of R_S in ecosystems that did not experience extended periods of drought (Janssens et al., 2001; Reichstein et al., 2003).

A further layer of complexity to the discussion is that model results may be influenced by a suboptimal measurement integration volume or integration time, as well as the alignment in space and time of different measurements. Problems of this kind (generally discussed as “scale problems”) are common in the natural sciences and are an important source of model error, thus are considered as the most important challenge in ecology (Blöschl and Sivapalan, 1995; Wiens, 1989). An example of a data alignment problem in our study is the collection of soil respiration measurements on different days than the photosynthesis measurements, which required intermediate data processing for photosynthesis (viz. Fig. 3). Also, soil temperature was measured at a depth (5 cm), whereas the soil respiration was an integral measurement over a soil column (e.g. Reichstein and Beer, 2008). There may also be a lag time present within the data, where plant growth on one day does not immediately correspond to root respiration (Gomez-Casanovas et al., 2012; Kuzyakov and Gavrichkova, 2010), which our non-continuous data would not have been able to detect. These trial design aspects may have resulted in small data mismatches that contributed to the non-correlation of R_S, RMSE$_C$ and RMSE$_V$ values. It is possible that the model calibration and validation results would have also improved if the resolution and alignment of the data had improved.

Some of these mismatches were able to be assessed using the available data. Continuous soil respiration measurements were not undertaken on all three vegetation communities, however 24 h observations obtained on three occasions during one year (but not included in the modeling process) could be compared with the model predictions. The diurnal variations were measured in 2000. At that time, the Old community was approximately 16 yr old and most comparable to the Middle community in 2012. Comparison days were chosen based on similarities between the soil temperatures in the prediction dataset and in the 24 h observation datasets. These comparisons showed that a similar daily range of R_S was predicted by the GLMM T_{soil} model as was observed in the 24 h dataset. For example, the diurnal range observed on the 24 May 2000 was 1.0–1.4 μmol CO_2 m^{-2} s^{-1} and the diurnal range predicted for the 19 May 2012, in which similar soil temperatures were recorded, was 1.1–1.6 μmol CO_2 m^{-2} s^{-1}. Therefore, the total sums of C loss for the total soil respiration are considered to provide a good approximation of the diurnal variation.

The heterotrophic soil respiration could not be assessed for diurnal variation as there were no 24 h measurements undertaken on the Trenched plots, but given the temperature relationship already observed on the R_S model, it is likely that a similar goodness of fit would be observed on the R_H model.

By using a model selection process, we have been able to reduce some of the uncertainty associated with the predictions of annual C loss. However, we have also found that the current variables are not adequate to model all the variation observed in the R_S (and therefore R_A) data. This finding supports te discussion presented by Subke and Bahn (2010) on the ability to use the immeasurable to predict the unknown.

In nature, many interactions can occur and when our field trials don't test these interactions, it is not possible to incorporate them into long-term model predictions. Therefore, it is necessary to develop field trials which incorporate this increased complexity, as suggested by Dieleman et al. (2012). However, if early consideration isn't given to the models that we later want to fit to the data (and the data required to rigorously test the models), then increasing the complexity of field experiments will not necessarily provide us with better predictions of these interactions. Therefore, attention should be given to the trial layout, variable selection, measurement intensity and model selection process prior to the start of a trial to determine if they will provide the appropriate data for model predictions. Consideration also needs to be given to the cost associated with obtaining the appropriate measurements, in terms of collection frequency, method accuracy and overall outcomes of the project. In some cases, it may be that using a proxy such as soil temperature (or even air temperature for rough estimations) with the soil respiration observations is a suitable substitute in models in the absence of suitable and significant variables.

4.4 Annual C loss and links to global change

Our model interpolations identified an annual C loss from R_S (Young: 649 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$; Old: 434 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$) that was at the lower end of the range identified on the Danish heathland ecosystem of 672–719 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Selsted et al., 2012). To place this within a broader European context, the heathland soil respiration is within the same range as temperate forest ecosystems, which have been reported between 430 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Belgium) and 859 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ (Germany) (Bahn et al., 2010a; Khomik et al., 2009; Raich and Schlesinger, 1992). In contrast, the heathland is at the lower end of the scale for annual C loss in comparison to temperate grasslands, which ranged between 729 g C m^{-2} yr^{-1} (Germany) and 1988 g C m^{-2} yr^{-1} (Switzerland) (Bahn et al., 2010a).

The study also identified a change in soil respiration with an increasing age of heathlands. The R_A compartment provided the largest change over time, from a complete absence on bare soil to a maximum at the 12 yr and then decreasing up to the maximum studied age of 28 yr. A similar relationship between soil respiration and vegetation age has been previously found for forest stands, where the younger stands had significantly higher respiration rates than the more mature sites (Saiz et al., 2006; Wang et al., 2011).

Within the last 50 yr, the cutting, burning and grazing cycles on heathlands have not occurred as frequently or as regularly as during the intensive agricultural periods of past centuries (Webb, 1998). Management of heathlands is required to maintain these cultural landscapes and in past times this management occurred on a 3–4 yr cycle (Webb, 1998). Currently, this cycle length has extended or is non-existent (Diemont and Heil, 1984; Wessel et al., 2004). From the perspective of optimizing C uptake and minimizing C output, having an understanding the C dynamics of these ecosystems allows us to determine the optimum time to cut the vegetation, thus contributing to global C emission mitigation measures. Based on a preliminary assessment of other fluxes within the system (data to be reported at a later stage), it is hypothesized that the younger vegetation will be a C sink and the older vegetation will be a C source, indicating management of these cultural landscapes should occur on relatively shorter cycle lengths if C emission mitigation is of concern.

Appendix A

Details of the soil moisture model

The soil moisture model used in this study is a zero-dimensional finite difference model using a daily time resolution of rainfall data and air temperature data as model inputs.

It was constructed and calibrated on approximately one year of observed soil moisture, rainfall and temperature data for 12 individual soil moisture sensors. The model comprises the following equations:

$$\mathrm{Drain}_t = \max\left(0; \mathrm{Smoist}_{t-1} - \mathrm{depth}\cdot\mathrm{fc}\right)\cdot\mathrm{df} \tag{A1}$$

$$\mathrm{AvSmoist}_t = \max\left(0; \mathrm{Smoist}_{t-1} - \mathrm{depth}\cdot\mathrm{wp}\right) \tag{A2}$$

$$\mathrm{ET}_t = \min\left(\mathrm{Temp}_t\cdot\mathrm{tf}; \mathrm{AvSmoist}_t\right)\cdot\mathrm{ef} \tag{A3}$$

$$\mathrm{EfRain}_t = \mathrm{Rain}_t\cdot\left(\frac{\mathrm{Smoist}_t}{(\mathrm{depth}\cdot\mathrm{poros})}\right)^{\mathrm{rf}} \tag{A4}$$

$$\mathrm{Smoist}_t = \min\left(\mathrm{depth}\cdot\mathrm{poros}; \mathrm{Smoist}_{t-1} + \mathrm{EfRain}_t\right) + \mathrm{Drain}_t - \mathrm{ET}_t \tag{A5}$$

In the equations, t refers to a day. Equation (A1) calculates drainage (Drain_t, in $\mathrm{mm\,day^{-1}}$) as a linear reservoir with soil moisture (Smoist_{t-1}, in mm) above a threshold ($\mathrm{depth}\cdot\mathrm{fc}$) as the driving force. Drain_t refers to the drainage of soil moisture from the soil layer under consideration (i.e. the top of the mineral soil down to depth mm); Smoist_{t-1} refers to the soil moisture in the soil layer under consideration, and depth, fc (field capacity, as a fraction of the soil volume) and df (drainage fraction) are model parameters. The depth parameter is set to 100 mm, while the values for fc and df were identified by model calibration.

Equation (A2) calculates the soil moisture available for evapotranspiration ($\mathrm{AvSmoist}_t$, in mm) and the parameter wp (as a fraction of the soil volume) represents the wilting point below which only a negligible rate of evapotranspiration occurred. The value for wp was found by model calibration.

Evapotranspiration (ET_t) is calculated in Eq. (A3). Evapotranspiration is a modeled linear reservoir with either the air temperature or the available soil moisture as the driving force, depending of which factor is limiting. The parameter tf is set to $1\,\mathrm{mm\,°C^{-1}}$, and the value for the parameter ef was identified by model calibration.

The effective rain, i.e. the rainfall which enters the soil layer under consideration (EfRain_t, in mm), is calculated in Eq. (A4). EfRain_t is proportional to a soil saturation factor which contains two parameters: soil porosity (poros) and a rainfall factor (rf). The porosity is calculated by taking the maximum observed soil moisture content over the measurement period, while the rainfall factor is calculated by model calibration.

In Eq. (A5), an update of the soil moisture is calculated by a balance equation, whereby it is assumed that any rainfall which cannot be stored in the soil layer under consideration is lost as surface runoff.

The water balance model thus contains eight parameters, three of which have fixed values (depth = 100 mm, $\mathrm{poros} = \max_{\mathrm{all}\ t}\left(\mathrm{Smoist}_t/\mathrm{depth}\right)$, and $\mathrm{tf} = 1\,\mathrm{mm}\,{}^{\circ}\mathrm{C}^{-1}$, and five of which were found via calibration (df, ef, fc, rf and wp). Calibration was undertaken by minimizing the root mean squared error between observed and predicted soil moisture, using the optimization routine by Byrd et al. (1995), as implemented in the standard R function “optim”.

Acknowledgements. The present study was carried out and funded by European Commission under the FP7-Research Infrastructures Programme (Grant Agreement no. 227628) as a part of the Integrated Network on Climate Research Activities on Shrubland Ecosystems (INCREASE) project. The authors would like to thank the trench diggers Karsten Kalbitz, Joke Westerveld, Andrea Carboni, Richard van Heck and Jennifer Schollee. The authors would also like to thank Sharon Mason, Louise Andresen, Elsa Sorgedrager, Jessica Noun and Laura Fernández Fraile for their contributions to this paper, the University of Amsterdam (Universiteit van Amsterdam) for making this research possible and the Royal Netherlands Army (Koninklijke Landmacht) for access to the field site.

References

Bahn, M., Reichstein, M., Davidson, E. A., Grünzweig, J., Jung, M., Carbone, M. S., Epron, D., Misson, L., Nouvellon, Y., Roupsard, O., Savage, K., Trumbore, S. E., Gimeno, C., Curiel Yuste, J., Tang, J., Vargas, R., and Janssens, I. A.: Soil respiration at mean annual temperature predicts annual total across vegetation types and biomes, Biogeosciences, 7, 2147–2157, doi:10.5194/bg-7-2147-2010, 2010a.

Bahn, M., Janssens, I. A., Reichstein, M., Smith, P., and Trumbore, S. E.: Soil respiration across scales: towards an integration of patterns and processes, New Phytol., 186, 292–296, doi:10.1111/j.1469-8137.2010.03237.x, 2010.

Bernhardt, E. S., Barber, J. J., Pippen, J. S., Taneva, L., Andrews, J. A., and Schlesinger, W. H.: Long-term effects of free air CO_2 enrichment (FACE) on soil respiration, Biogeochemistry, 77, 91–116, 2006.

Blöschl, G. and Sivapalan, M.: Scale issues in hydrological modelling: a review, Hydrol. Process., 9, 251–290, 1995.

Burnham, K. P. and Anderson, D. R.: Model Selection and Multi-Model Inference: a Practical Information-Theoretic Approach, Springer-Verlag, New York, 2002.

Burton, A. J., Jarvey, J. C., Jarvi, M. P., Zak, D. R., and Pregitzer, K. S.: Chronic N deposition alters root respiration-tissue N relationship in northern hardwood forests, Glob. Change Biol., 18, 258–266, 2012.

Byrd, R., Lu, P., Nocedal, J., and Zhu, C: A limited memory algorithm for bound constrained optimization, Siam J. Sci. Comput., 16, 1190–1208, 1995.

Campbell, D. T. and Stanley, J. C.: Experimental and Quasi-Experimental Designs for Research, Rand McNally, Chicago, Illinois, 1966.

Caquet, B., De Grandcourt, A., Thongo M'bou, A., Epron, D., Kinana, A., Saint André, L., and Nouvellon, Y.: Soil carbon balance in a tropical grassland: Estimation of soil respiration and its partitioning using a semi-empirical model, Agr. Forest Meteorol., 158–159, 71–79, 2012.

Chemidlin Prévost-Bouré, N., Ngao, J., Berveiller, D., Bonal, D., Damesin, C., Dufrêne, E., Lata, J., Le Dantec, V., Longdoz, B., Ponton, S., Soudani, K., and Epron, D.: Root exclusion through trenching does not affect the isotopic composition of soil CO_2 efflux, Plant Soil, 319, 1–13, 2009.

Chen, X., Post, W., Norby, R., and Classen, A.: Modeling soil respiration and variations in source components using a multi-factor global climate change experiment, Clim. Change, 107, 459–480, 2011.

Clark, K. L., Gholz, H. L., and Castro, M. S.: Carbon Dynamics along a chronosequence of slash pine plantations in North Florida, Ecol. Appl., 14, 1154–1171, 2004.

Clay, G. D., Worrall, F., and Rose, R.: Carbon budgets of an upland blanket bog managed by prescribed fire, J. Geophys. Res., 115, G04037, doi:10.1029/2010JG001331, 2010.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, 2006.

Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems: moving beyond Q10, Glob. Change Biol., 12, 154–164, 2006.

Díaz-Pinés, E., Schindlbacher, A., Pfeffer, M., Jandl, R., Zechmeister-Boltenstern, S., and Rubio, A.: Root trenching: a useful tool to estimate autotrophic soil respiration? A case study in an Austrian mountain forest, Eur. J. For. Res., 129, 101–109, 2010.

Dieleman, W. I. J., Vicca, S., Dijkstra, F. A., Hagedorn, F., Hovenden, M. J., Larsen, K. S., Morgan, J. A., Volder, A., Beier, C., Dukes, J. S., King, J., Leuzinger, S., Linder, S., Luo, Y., Oren, R., De Angelis, P., Tingey, D., Hoosbeek, M. R., and Janssens, I. A.: Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature, Glob. Change Biol., 18, 2681–2693, 2012.

Diemont, W. H. and Heil, G. W.: Some long-term observations on cyclical and seral processes in Dutch heathlands, Biol. Conserv., 30, 283–290, 1984.

Emmett, B. A., Beier, C., Estiarte, M., Tietema, A., Kristensen, H. L., Williams, D., Peñuelas, J., Schmidt, I., and Sowerby, A.: The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient, Ecosystems, 7, 625–637, 2004.

Filley, T. R., Boutton, T. W., Liao, J. D., Jastrow, J. D. and Gamblin, D. E.: Chemical changes to nonaggregated particulate soil organic matter following grassland-to-woodland transition in a subtropical savanna, J. Geophys. Res., 113, G03009, doi:10.1029/2007JG000564, 2008.

Fog, K.: The effect of added nitrogen on the rate of decomposition of organic matter, Biol. Rev., 63, 433–462, 1988.

Gimingham, C. H.: Age-related interactions between *Calluna vulgaris* and phytophagous insects, Oikos, 44, 12–16, 1985.

Gomez-Casanovas, N., Matamala, R., Cook, D. R., and Gonzalez-Meler, M. A.: Net ecosystem exchange modifies the relationship between the autotrophic and heterotrophic components of soil respiration with abiotic factors in prairie grasslands, Glob. Change Biol., 18, 2532–2545, 2012.

Graham, S. L., Millard, P., Hunt, J. E., Rogers, G. N. D., and Whitehead, D.: Roots affect the response of heterotrophic soil respiration to temperature in tussock grass microcosms, Ann. Bot., 110, 253–258, doi:10.1093/aob/mcs073, 2012.

Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A.: Separating root and soil microbial contributions to soil respiration:x a review of methods and observations, Biogeochemistry, 48, 115–146, 2000.

Heinemeyer, A., Di Bene, C., Lloyd, A. R., Tortorella, D., Baxter, R., Huntley, B., Gelsomino, A., and Ineson, P.: Soil respiration: implications of the plant-soil continuum and respiration chamber collar-insertion depth on measurement and modelling of soil CO, Eur. J. Soil Sci., 62, 82–94, 2011.

Horwath, W. R., Pregitzer, K. S., and Paul, E. A.: ^{14}C allocation in tree–soil systems, Tree Physiol., 14, 1163–1176, 1994.

IPCC: Climate Change: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, Glob. Change Biol., 7, 269–278, 2001.

Jassal, R. S. and Black, T. A.: Estimating heterotrophic and autotrophic soil respiration using small-area trenched plot technique: theory and practice, Agr. Forest Meteorol., 140, 193–202, 2006.

Jensen, K. D., Beier, C., Michelsen, A., and Emmett, B. A.: Effects of experimental drought on microbial processes in two temperate heathlands at contrasting water conditions, Appl. Soil Ecol., 24, 165–176, 2003.

Jonasson, S., Michelsen, A., Schmidt, I. K., Nielsen, E. V., and Callaghan, T. V.: Microbial Biomass C, N and P in two Arctic soils and responses to addition of npk fertilizer and sugar: implications for plant nutrient uptake, Oecologia, 106, 507–515, 1996.

Kalbitz, K., Schmerwitz, J., Schwesig, D., and Matzner, E.: Biodegradation of soil-derived dissolved organic matter as related to its properties, Geoderma, 113, 273–291, 2003.

Keenan, T. F., Davidson, E., Moffat, A. M., Munger, W., and Richardson, A. D.: Using model-data fusion to interpret past trends, and quantify uncertainties in future projections, of terrestrial ecosystem carbon cycling, Glob. Change Biol., 18, 2555–2569, 2012.

Khomik, M., Arain, M. A., Liaw, K.-L., and McCaughey, J. H.: Debut of a flexible model for simulating soil respiration-soil temperature relationship: Gamma model, J. Geophys. Res., 114, G03004, doi:10.1029/2008JG000851, 2009.

Kirschbaum, M. U. F.: The temperature dependence of organic-matter decomposition – still a topic of debate, Soil Biol. Biochem., 38, 2510–2518, 2006.

Kopittke, G. R., Tietema, A., and Verstraten, J. M.: Soil acidification occurs under ambient conditions but is retarded by repeated drought: Results of a field-scale climate manipulation experiment, Sci. Total Environ., 439, 332–342, doi:10.1016/j.scitotenv.2012.09.044, 2012a.

Kopittke, G. R., Tietema, A., van Loon, E. E., and Kalbitz, K.: "The age of managed heathland communities: implications for carbon storage?" Plant & Soil, PLSO-D-12-00650R1, accepted, 2012b.

Kozovits, A. R., Bustamante, M. M. C., Garofalo, C. R., Bucci, S., Franco, A. C., Goldstein, G., and Meinzer, F. C.: Nutrient resorption and patterns of litter production and decomposition in a neotropical Savanna, Funct. Ecol., 21, 1034–1043, 2007.

Kutsch, W. L. and Kappen, L.: Aspects of carbon and nitrogen cycling in soils of the Bornhöved lake district, II: Modelling the influence of temperature increase on soil respiration and organic carbon content in arable soils under different managements, Biogeochemistry, 39, 207–224, 1997.

Kutsch, W., Persson, T., Schrumpf, M., Moyano, F., Mund, M., Andersson, S., and Schulze, E.: Heterotrophic soil respiration and soil carbon dynamics in the deciduous Hainich forest obtained by three approaches, Biogeochemistry, 100, 167–183, 2010.

Kuzyakov, Y. and Gavrichkova, O.: REVIEW: time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls, Glob. Change Biol., 16, 3386–3406, 2010.

Larsen, K. S., Ibrom, A., Beier, C., Jonasson, S., and Michelsen, A.: Ecosystem respiration depends strongly on photosynthesis in a temperate health, Biogeochemistry, 85, 201–213, 2007.

Loidi, J., Biurrun, I., Campos, J. A., Garciá-Mijangos, I. and Herrera, M.: A biogeographical analysis of the European Atlantic lowland heathlands, J. Veg. Sci., 21, 832–842, 2010.

Matzner, E. and Borken, W.: Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review, Eur. J. Soil Sci., 59, 274–284, 2008.

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

Metcalfe, D. B., Fisher, R. A., and Wardle, D. A.: Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change, Biogeosciences, 8, 2047–2061, doi:10.5194/bg-8-2047-2011, 2011.

Mikkelsen, T. N., Beier, C., Jonasson, S., Holmstrup, M., Schmidt, I. K., Ambus, P., Pilegaard, K., Michelsen, A., Albert, K., Andresen, L. C., Arndal, M. F., Bruun, N., Christensen, S., Danbæk, S., Gundersen, P., Jørgensen, P., Linden, L. G., Kongstad, J., Maraldo, K., and Priemé, A.: Experimental design of multifactor climate change experiments with elevated CO_2, warming and drought: the CLIMAITE project, Funct. Ecol., 22, 185–195, 2008.

Nierop, K. G. J. and Verstraten, J. M.: Organic matter formation in sandy subsurface horizons of Dutch coastal dunes in relation to soil acidification, Org. Geochem., 34, 499–513, 2003.

Novara, A., Armstrong, A., Gristina, L., Semple, K. T., and Quinton, J. N.: Effects of soil compaction, rain exposure and their interaction on soil carbon dioxide emission, Earth Surf. Process. Landforms, 37, 994–999, 2012.

Pedersen, A. R.: HMR: Flux estimation with static chamber data, R package version 0.3.1, R Foundation for Statistical Computing, Vienna, Austria, 2011.

Pedersen, A. R., Petersen, S. O., and Schelde, K.: A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers, Eur. J. Soil Sci., 61, 888–902, 2010.

Peichl, M., Carton, O., and Kiely, G.: Management and climate effects on carbon dioxide and energy exchanges in a maritime grassland, Agric. Ecosyst. Environ., 158, 132–146, 2012.

Perez-Quezada, J. F., Bown, H. E., Fuentes, J. P., Alfaro, F. A. and Franck, N.: Effects of afforestation on soil respiration in an arid shrubland in Chile, J. Arid Environ., 83, 45–53, 2012.

Pinheiro, J. C. and Bates, D. M.: Mixed-Effects Models in S and S-Plus, Springer, New York, 2000.

Qian, S. S., Cuffney, T. F., Alameddine, I., McMahon, G., and Reckhow, K. H.: On the application of multilevel modeling in environmental and ecological studies, Ecology, 91, 355–361, 2010.

R Development Core Team: R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria, 2008.

Raich, J. W. and Schlesinger, W. H.: The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, Tellus B, 44, 81–99, 1992.

Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y. F., Grunzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J. M., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M. and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, Global Biogeochemical Cycles, 17, 1104–1119, doi:10.1029/2003GB002035, 2003.

Reichstein, M. and Beer, C.: Soil respiration across scales: the importance of a model-data integration framework for data interpretation, J. Plant Nutr. Soil Sc., 171, 344–354, 2008.

Rustad, L. E., Campbell, J. L., Marion, G. M., Norby, R. J., Mitchell, M. J., Hartley, A. E., Cornelissen, J. H. C., Gurevitch, J., and GCTE-NEWS: A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming, Oecologia, 126, 543–562, 2001.

Rustad, L. E., Huntington, T. G., and Boone, R. D.: Controls on soil respiration: implications for climate change, Biogeochemistry, 48, 1–6, 2000.

Ryan, M. G. and Law, B. E.: Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73, 3–27, 2005.

Saiz, G., Byrne, K. A., Butterbach-Bahl, K., Kiese, R., Blujdea, V., and Farrell, E. P.: Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in Central Ireland, Glob. Change Biol., 12, 1007–1020, 2006.

Schaap, M. G., de Lange, L., and Heimovaara, T. J.: TDR calibration of organic forest floor media, Soil Technol., 11, 205–217, 1997.

Schindlbacher, A., Wunderlich, S., Borken, W., Kitzler, B., Zechmeister-Boltenstern, S., and Jandl, R.: Soil respiration under climate change: prolonged summer drought offsets soil warming effects, Global Change Biol., 18, 2270–2279, doi:10.1111/j.1365-2486.2012.02696.x, 2012.

Schlesinger, W. H. and Andrews, J. A.: Soil respiration and the global carbon cycle, Biogeochemistry, 48, 7–20, 2000.

Selsted, M. B., van der Linden, L., Ibrom, A., Michelsen, A., Larsen, K. S., Pedersen, J. K., Mikkelsen, T. N., Pilegaard, K., Beier, C., and Ambus, P.: Soil respiration is stimulated by elevated CO_2 and reduced by summer drought: three years of measurements in a multifactor ecosystem manipulation experiment in a temperate heathland (CLIMAITE), Glob. Change Biol., 18, 1216–1230, 2012.

Sierra, C. A., Harmon, M. E., Thomann, E., Perakis, S. S., and Loescher, H. W.: Amplification and dampening of soil respiration by changes in temperature variability, Biogeosciences, 8, 951–961, doi:10.5194/bg-8-951-2011, 2011.

Sowerby, A., Emmett, B. A., Tietema, A., and Beier, C.: Contrasting effects of repeated summer drought on soil carbon efflux in hydric and mesic heathland soils, Glob. Change Biol., 14, 2388–2404, 2008.

Startsev, N. A., Lieffers, V. J., and McNabb, D. H.: Effects of feathermoss removal, thinning and fertilization on lodgepole pine growth, soil microclimate and stand nitrogen dynamics, For. Ecol. Manage., 240, 79–86, 2007.

Subke, J. and Bahn, M.: On the "temperature sensitivity" of soil respiration: can we use the immeasurable to predict the unknown?, Soil Biol. Biochem., 42, 1653–1656, 2010.

Sulkava, P. and Huhta, V.: Effects of hard frost and freeze-thaw cycles on decomposer communities and N mineralisation in boreal forest soil, Appl. Soil Ecol., 22, 225–239, 2003.

Suseela, V., Conant, R. T., Wallenstein, M. D., and Dukes, J. S.: Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment, Glob. Change Biol., 18, 336–348, 2012.

Trumbore, S.: Carbon respired by terrestrial ecosystems – recent progress and challenges, Glob. Change Biol., 12, 141–153, 2006.

Vargas, R., Carbone, M., Reichstein, M., and Baldocchi, D.: Frontiers and challenges in soil respiration research: from measurements to model-data integration, Biogeochemistry, 102, 1–13, 2011.

Wang, B., Jiang, Y., Wei, X., Zhao, G., Guo, H., and Bai, X.: Effects of forest type, stand age, and altitude on soil respiration in subtropical forests of China, Scand. J. For. Res., 26, 40–47, 2011.

Webb, N. R.: The traditional management of European heathlands, J. Appl. Ecol., 35, 987–990, 1998.

Webster, K. L., Creed, I. F., Skowronski, M. D., and Kaheil, Y. H.: Comparison of the performance of statistical models that predict soil respiration from forests, Soil Sci. Soc. Am. J., 73, 1157–1167, 2009.

Wessel, W. W., Tietema, A., Beier, C., Emmett, B. A., Peñuelas, J., and Riis–Nielsen, T.: A qualitative ecosystem assessment for different shrublands in Western Europe under impact of climate change, Ecosystems, 7, 662–671, 2004.

Wiens, J. A.: Spatial scaling in ecology, Funct. Ecol., 3, 385–397, 1989.

Xiang, W. and Freeman, C.: Annual variation of temperature sensitivity of soil organic carbon decomposition in North peatlands: implications for thermal responses of carbon cycling to global warming, Environ. Geol., 58, 499–508, 2009.

Table 1. Description of the Oldebroek Trial Location.

Location	ASK Oldebroek, Oldebroekse heide, Province of Gelderland, The Netherlands						
Co-ordinates	52°24′ N 5°55′ E						
Elevation	25 m a.s.l.						
Slope	2 %						
Climate	Temperate, humid.						
Rainfall	1018 mm						
Air Temperature	Average for January: 2.0 °C; July: 17.8 °C; Annual: 10.1 °C						
Plant Species	*Calluna vulgaris, Molinia caerulea, Deschampsia flexuosa, Pinus sylvestris, Betula pendula, Empertrum nigrum, Juniperus communis, Hypnum cupressiforme* Hedw, *Hypnum jutlandicum* Holmen et Warncke, *Dicranum scoparium* Hedw.						
Soil	Haplic Podzol with mormoder humus form						
Parent Material	Coversand, fluvioglacial deposits						
Soil Chemistry[a]	Organic Horizons		Mineral Horizons				
Name	L+F	H	Ae	Bs	1BC	2BC	C
Depth (cm)	+8.0 to +1.4	+1.4 to 0	0 to 5.5	5.5 to 13	13 to 21	21 to 27	> 27
pH	3.7	3.9	3.9	4.0	4.5	4.4	4.9
EC (µS cm^{-1})	197.9	92.0	88.7	73.2	32.3	46.3	30.8
NO$_3$ (µmol kg^{-1})	646.6	216.2	20.2	62.4	22.1	47.6	13.1
PO$_4$ (µmol kg^{-1})	1589	126	4.6	1.4	0.1	0.1	0.1
C/N ration	40.4	17.7	27.7	18.0	16.7	18.5	11.7
Soil Moisture[b] %	104.8	47.1	15.7	14.9	6.3	6.3	6.3

[a] Water extraction of 1 : 5 for organic horizons and 1 : 1 for mineral horizons.

[b] Obtained following a rainfall event and reported as a percentage (g per g dry weight soil).

Table 2. Description of the data used for model calibration and validation.

Modelling Stage	Total Soil Respiration Models (R_S)	Heterotrophic Respiration Models (R_H)
Calibration	Data: Untrenched plots Dates: Sep 2011–Aug 2012	Data: Trenched plots Dates: Sep 2011–Aug 2012
Validation (Type I)	Data: Untrenched Validation plots Dates: Sep 2011–Aug 2012	Data: Trenched Validation plots Dates: Sep 2011–Aug 2012
Validation (Type II)	Data: Untrenched Validation plots Dates: Nov 2010–Aug 2011	–

BGD
9, 16239–16301, 2012

Soil respiration compartments on an aging managed heathland

G. R. Kopittke et al.

Table 3. The Models to estimate R_S and R_H in µmol CO$_2$ m^{-2} s^{-1}. The explanatory variables are T (models using air temperature at 20 cm above ground surface and soil temperature at 5 cm below ground surface are evaluated) and M, B, P as defined in Eqs. (2)–(4). The model parameters are R_0, k, a, b and c and the units vary per model. R_0 is always in µmol CO$_2$ m^{-2} s^{-1}. Parameter k is in °C^{-1} for Selsted, GLMM and GLMM2 models, and in µmol CO$_2$ m^{-2} s^{-1} °C^{-1} for LMM and LMM2. The parameters a, b and c are dimensionless for Selsted, GLMM and GLMM2 models and are in µmol CO$_2$ m^{-2} s^{-1} for the LMM and LMM2 models.

Model Type	Variables	Equations fo R_S Model	Equations for R_H Model
Selsted	T	R_0e^{kT}	R_0e^{kT}
	TM	$R_0e^{kT}(1-e^{a-b(1-M)^{-2}})$	$R_0e^{kT}(1-e^{a-b(1-M)^{-2}})$
	TB	$R_0e^{kT}(B+c)$	–
	TP	$R_0e^{kT}(P+c)$	–
	TMB	$R_0e^{kT}(1-e^{a-b(1-M)^{-2}})(B+c)$	–
	TMP	$R_0e^{kT}(1-e^{a-b(1-M)^{-2}})(P+c)$	–
LMM	T	R_0+kT	R_0+kT
	TM	$R_0+kT+aM$	$R_0+kT+aM$
	TB	$R_0+kT+cB$	–
	TP	$R_0+kT+cP$	–
	TMB	$R_0+kT+aM+cB$	–
	TMP	$R_0+kT+aM+cP$	–
LMM2[b]	TM	$R_0+kT+a(M-1)^2$	$R_0+kT+a(M-1)^2$
	TB	$R_0+kT+c(B-1)^2$	–
	TP	$R_0+kT+c(P-1)^2$	–
	TMB	$R_0+kT+a(M-1)^2+c(B-1)^2$	–
	TMP	$R_0+kT+a(M-1)^2+c(P-1)^2$	–

Table 3. Continued.

Model Type	Variables	Equations fo R_S Model	Equations for R_H Model
GLMM[a]	T	$R_0 e^{kT}$ (identical to Selsted – T)	$R_0 e^{kT}$
	TM	$R_0 e^{kT} e^{aM}$	$R_0 e^{kT} e^{aM}$
	TB	$R_0 e^{kT} e^{cB}$	–
	TP	$R_0 e^{kT} e^{cP}$	–
	TMB	$R_0 e^{kT} e^{aM} e^{cB}$	–
	TMP	$R_0 e^{kT} e^{aM} e^{cP}$	–
GLMM2[b]	TM	$R_0 e^{kT} e^{a(M-1)^2}$	$R_0 e^{kT} e^{a(M-1)^2}$
	TB	$R_0 e^{kT} e^{c(B-1)^2}$	–
	TP	$R_0 e^{kT} e^{c(P-1)^2}$	–
	TMB	$R_0 e^{kT} e^{a(M-1)^2} e^{c(B-1)^2}$	–
	TMP	$R_0 e^{kT} e^{a(M-1)^2} e^{c(P-1)^2}$	–

[a] The equation for the GLMM-T model is identical to the Selsted-T equation. The GLMM-T model is still included as a separate model due to a different treatment of model residuals and different optimality criteria in the calibration of the Selsted and the GLMM models, which results in different optimal parameters for the two models.

[b] The equations and the optimal parameters for the LMM-T and GLMM-T models are identical to those of respectively LMM2-T and GLMM-T. Therefor LMM2-T and GLMM2-T are not included in the table.

Table 4. Optimal parameter values of R_S and R_H models for the Young, Middle and Old communities (GLMM T_{soil} Model), with 95 % confidence intervals for the parameters in brackets. All models have the form R_0e^{kT}. See text and Table 3 for parameter explanations.

Model	Young	Middle	Old
R_S	R_0 = 0.45 (0.35–0.56) k = 0.115 (0.103–0.128)	R_0 = 0.23 (0.19–0.29) k = 0.138 (0.128–0.149)	R_0 = 0.25 (0.21–0.32) k = 0.128 (0.113–0.142)
R_H		R_0 = 0.27 (0.23–0.31) k = 0.100 (0.093–0.108)	

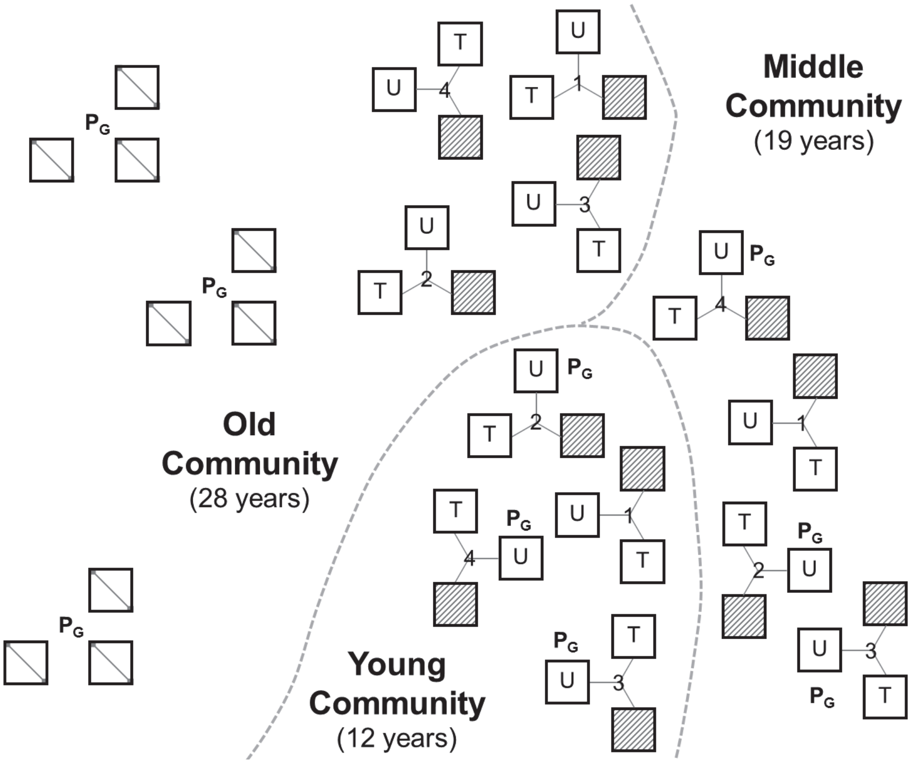

Fig. 1. The experimental layout showing the nested design of the Untrenched plots (“U”), Trenched plots (“T”) and the Trenched Validation plots (▨) in the Young, Middle and Old vegetation communities (not to scale). The Untrenched Validation plots (⧅) are shown in the Old community. Gross photosynthesis measurement locations are shown with a “P_G”. The boundaries of the three communities are represented by a dotted grey line.

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

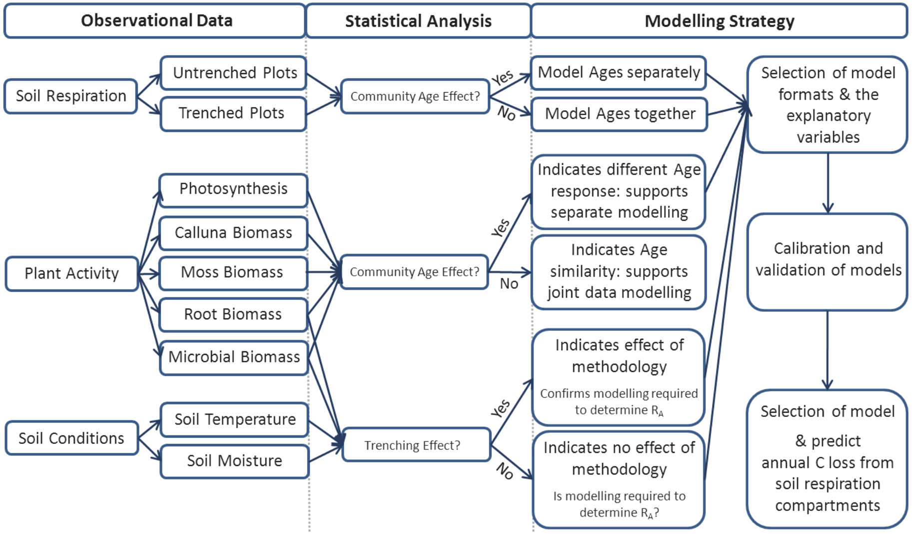

Fig. 2. Schematic Representation of the Data Analysis Workflow.

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

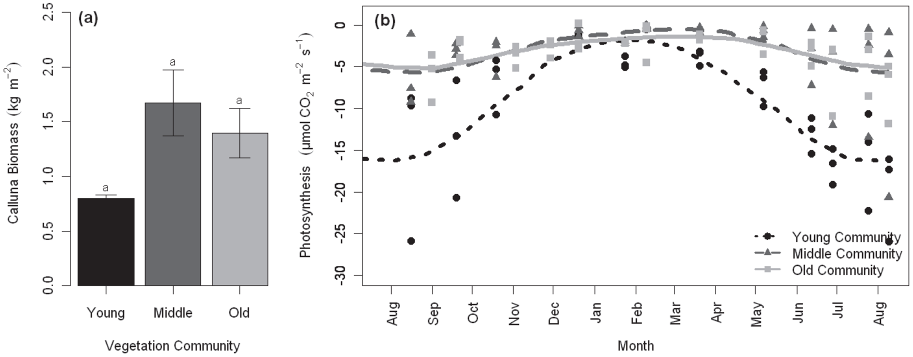

Fig. 3. Measures of Plant Activity for the Young, Middle and Old communities, showing **(a)** Calluna Biomass (kg m^{-2}) obtained in April 2011 during trenching activities ($n = 12$); and **(b)** C uptake by Photosynthesis (µmol CO$_2$ m^{-2} s^{-1}) obtained between August 2011 and August 2012 ($n = 9$) with observations represented by symbols and the mean curves (loess curves) represented by lines.

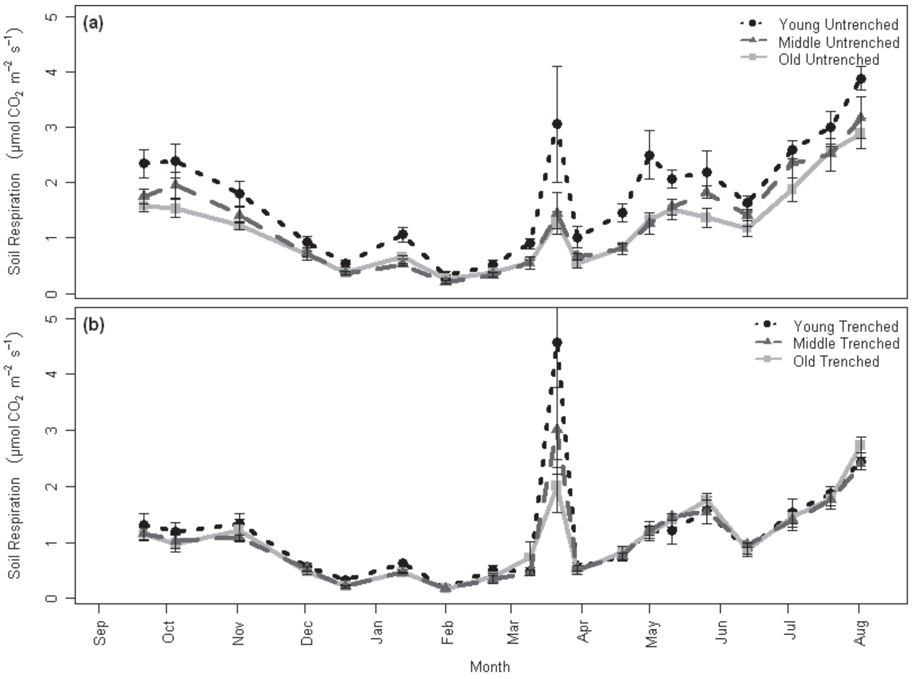

Fig. 4. Soil Respiration (μmol CO_2 m^{-2} s^{-1}) on three ages of vegetation for the **(a)** total soil compartment as represented by the Untrenched plots; and **(b)** heterotrophic soil compartment, as represented by the Trenched plots from September 2011 until August 2012 ($n = 4$ per age per sampling event). For plot **(b)**, the Young community SEM bar in March 2012 extends outside the graphical boundaries to 6.79 μmol CO_2 m^{-2} s^{-1}.

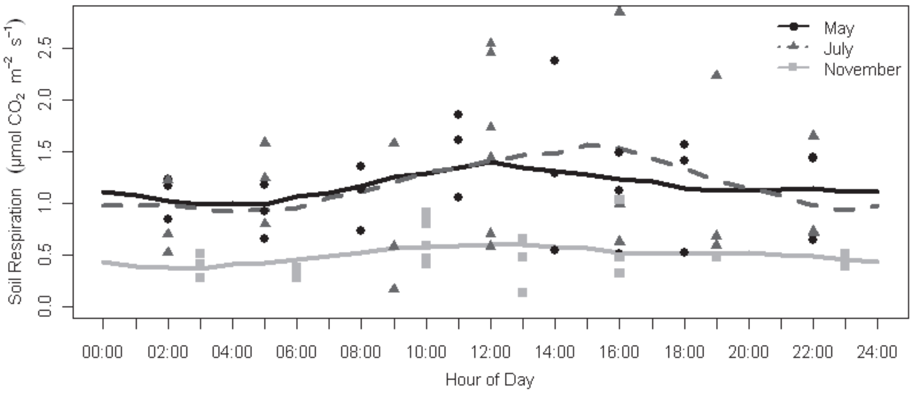

Fig. 5. Diurnal variation in total soil respiration (μmol $CO_2\,m^{-2}\,s^{-1}$) in May, July and November 2000 for the Old community. In each of the three measurement events, eight observations were obtained in a 24 h period (*n* = 3) and are represented by symbols with the mean curves (loess curves) represented by lines.

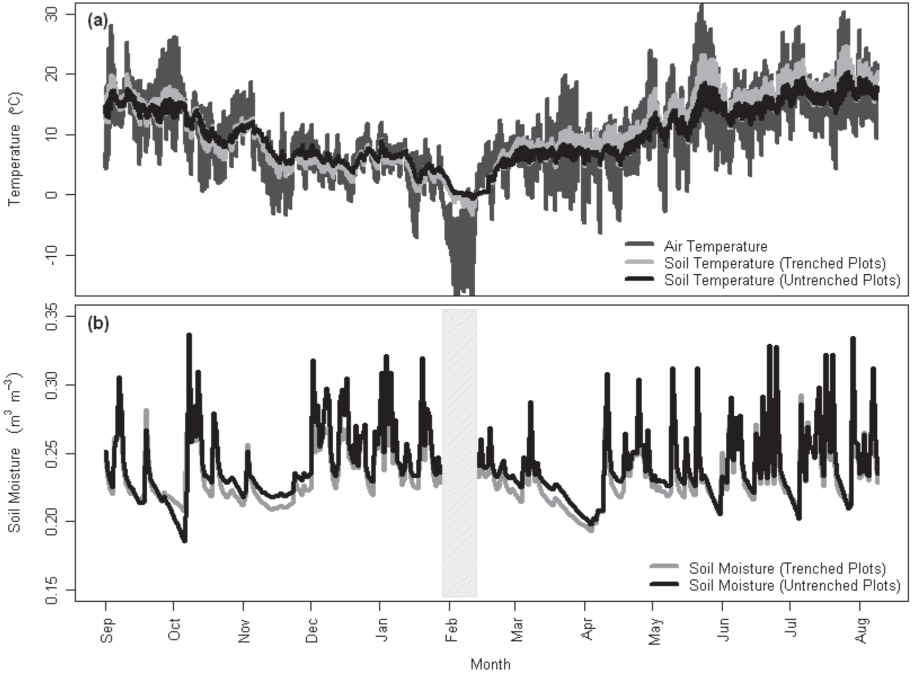

Fig. 6. Environmental parameters for September 2011–August 2012, showing **(a)** hourly temperatures (°C) of the air at 20 cm above ground surface and of the soil at 5 cm below ground surface; and **(b)** mean daily soil moisture (m^3 m^{-3}) at 5 cm below ground surface for the Trenched Plots and the Untrenched Plots. Periods of frozen soil moisture are indicated by shading (■).

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

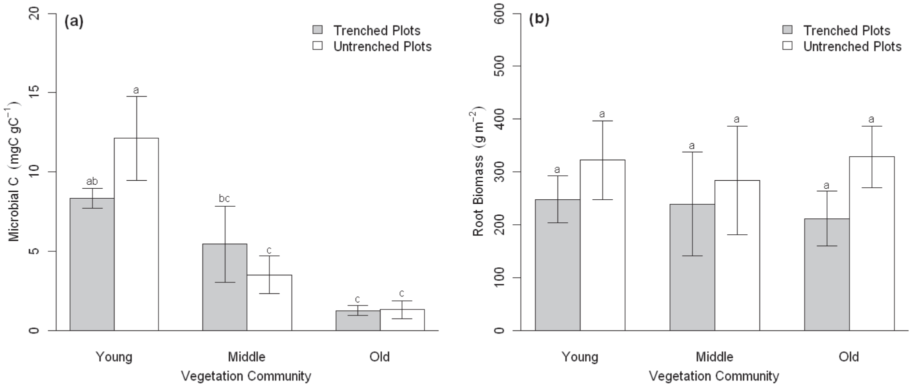

Fig. 7. A comparison of the Trenched plots (n = 12) and Untrenched plots (n = 12) for **(a)** microbial C biomass (mg C (g C)$^{-1}$) in the organic horizon and **(b)** root biomass (g m^{-2}) in the summed (organic + 0–5 cm mineral) horizons shown for the three ages of heathland vegetation.

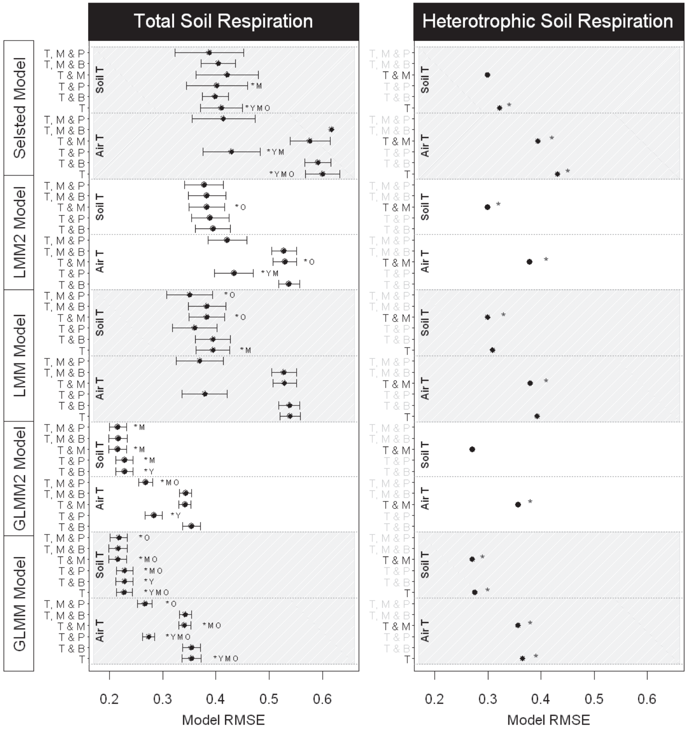

Fig. 8. Comparison of $RMSE_C$ values for models of **(a)** total soil respiration data (Untrenched plots) and **(b)** heterotrophic soil respiration data (Trenched plots). The models tested are listed on the left side of the figure. The explanatory variables within each model are listed on the y-axis and are abbreviated as: T = temperature (soil or air °C as indicated), M = soil moisture, B = relative biomass, P = relative photosynthesis. The "*" indicates that all model parameters were significant for one of either "Y" (Young), "M"(Middle) or "O" (Old) vegetation community models. The SEM bars on the total soil respiration means were calculated from the $RMSE_C$'s of the three community ages. SEM bars could not be calculated for the heterotrophic models.

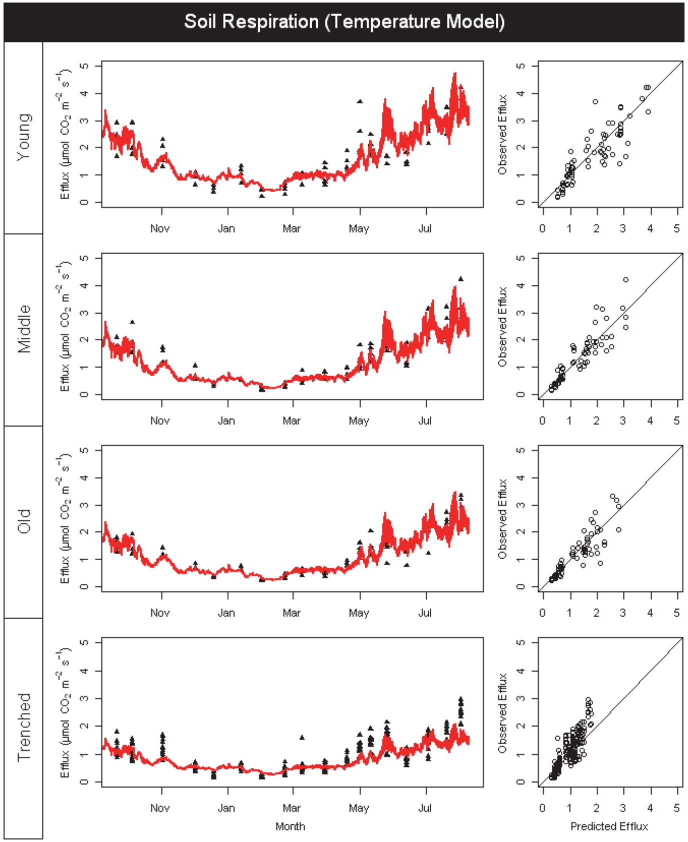

Fig. 9. Predicted and observed soil respiration on the Young, Middle and Old community "Untrenched" plots (total soil respiration: µmol CO$_2$ m^{-2} s^{-1}) and the "Trenched" plots (heterotrophic soil respiration: µmol CO$_2$ m^{-2} s^{-1}) calculated with the GLMM T_{soil} model. The observed values from 21 March 2012 are excluded from these plots.

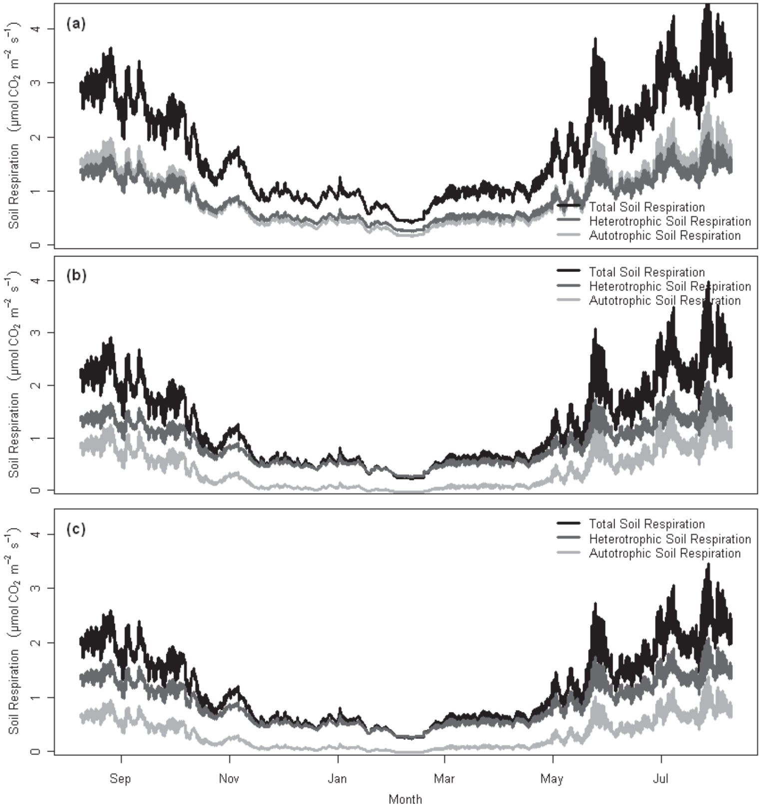

Fig. 10. Predictions of the components of soil respiration for **(a)** Young community, **(b)** Middle community and **(c)** Old community calculated using the GLMM T_{soil} model.

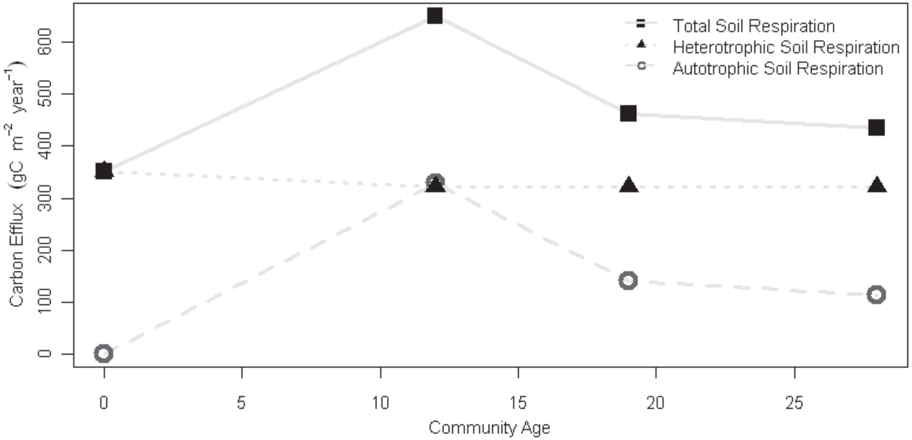

Fig. 11. Estimated annual C loss from total soil respiration (R_S), heterotrophic soil respiration (R_H) and autotrophic soil respiration (R_A) as predicted by the GLMM T_{soil} model. Year 0 is represented by respiration from bare soil, Year 12 by the Young community, Year 19 by the Middle community and Year 28 by the Old community.