



Title	Soil respiration partitioning in afforested temperate peatlands
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Publication date	2018-09-12
Publication information	Jovani-Sancho, A. Jonay, Thomas Cummins, and Kenneth A. Byrne. "Soil Respiration Partitioning in Afforested Temperate Peatlands." Springer Nature America, Inc, September 12, 2018. https://doi.org/10.1007/s10533-018-0496-0 .
Publisher	Springer Nature America, Inc
Item record/more information	http://hdl.handle.net/10197/10136
Publisher's statement	This is a post-peer-review, pre-copyedit version of an article published in Biogeochemistry. The final authenticated version is available online at: http://dx.doi.org/10.1007/s10533-018-0496-0
Publisher's version (DOI)	10.1007/s10533-018-0496-0

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Soil respiration partitioning in afforested temperate peatlands

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Abstract

Understanding and quantifying soil respiration and its component fluxes are necessary to model global carbon cycling in a changing climate as small changes in soil CO₂ fluxes could have important implications for future climatic conditions. A soil respiration partitioning study was conducted in eight afforested peatland sites in south-west Ireland. Using trenched points, annual soil CO₂ emissions, and the contributions of autotrophic and heterotrophic respiration as components of total soil respiration, were estimated. Nonlinear regression models were evaluated to determine the best predictive soil respiration model for each component flux, using soil temperature and water table level as explanatory variables. Temporal variation in soil CO₂ efflux was driven by soil temperature at 10 cm depth, with all treatment points also affected by water table level fluctuations. The effect of water table level on soil respiration was best accounted for by incorporating a water level Gaussian function into the soil-temperature–soil-respiration model. Mean autotrophic respiration was 44% of mean total soil respiration, varying between 1100–2049 g CO₂ m⁻² year⁻¹. Heterotrophic respiration was divided between peat respiration and litter respiration, which accounted for 35 and 21% of total soil respiration, respectively. While peat respiration varied between 774–1492 g CO₂ m⁻² year⁻¹, litter respiration varied between 514–1013 g CO₂ m⁻² year⁻¹. Although the extrapolation of these results to other sites should be done with caution, the empirical models developed for the entire dataset in this study are a useful tool to predict and simulate CO₂ emissions in afforested peatland in temperate climates.

Key words: *autotrophic respiration, heterotrophic respiration, litter decomposition, soil CO₂ efflux, Sitka spruce, lodgepole pine, blanket peat.*

Introduction

Forest ecosystems contain approximately 80% of all terrestrial aboveground organic carbon (C) and around 40% of all belowground terrestrial C (Dixon et al. 1994). These ecosystems have great importance in global C cycling and they can act as sinks or sources of carbon dioxide (CO₂) depending on the balance between photosynthesis and ecosystem respiration (Hargreaves et al. 2003; Houghton 2005; Saiz et al. 2006a). Ecosystem respiration can be partitioned into aboveground plant respiration and belowground respiration (soil respiration) (Janssens et al. 2001). Depending on the vegetation type and on the season, soil respiration can represent between 45 and 95% of total ecosystem respiration (Davidson et al. 2006; Janssens et al. 2001; Law et al. 1999; Yuste et al. 2005) and it is the main pathway for soil C returning from ecosystems to the atmosphere (Raich and Schlesinger 1992; Ryan and Law 2005).

Soil respiration is a biological process mostly originating in the surface organic horizons, which sustain most of the nutrient cycling and biological activity in soils (Kutsch et al. 2001). Furthermore, about 90% of total soil respiration (R_{TOT}) originates within the top 30 cm of soil (Goffin et al. 2014; Wiaux et al. 2015). This flux originates from root respiration (R_A), which includes all rhizospheric activity, and heterotrophic respiration, which includes decomposition of newly deposited litter (R_L) and oxidation of older and more recalcitrant soil organic matter (R_P) (Mäkiranta et al. 2008). In afforested peatlands ecosystems, R_{TOT} and its component fluxes have been shown to be mainly regulated by soil temperature (T) (Byrne and Farrell 2005; Mäkiranta et al. 2008; Minkkinen et al. 2007; Ojanen et al. 2010). Water level (WL) regulates the volume of oxic peat where aerobic respiration occurs, and thus plant productivity (Chivers et al. 2009; Tuittila et al. 2004). Despite this, only a few studies have been able to include WL as a significant variable in empirical models simulating soil respiration

across different peatland ecosystems (Laine et al. 2007; Mäkiranta et al. 2009; Renou-Wilson et al. 2014; Tuittila et al. 2004). The dependence of soil respiration on soil T and moisture content in mineral soils has been investigated recently by using multiple nonlinear analysis and statistics (Jovani-Sancho et al. 2017a; Lellei-Kovács et al. 2016). However, unlike in mineral soils, the various WL response functions that have been proposed in peatlands ecosystems, including linear (Mäkiranta et al. 2008), sigmoidal (Tuittila et al. 2004) and Gaussian type equations (Jovani-Sancho et al. 2017b; Mäkiranta et al. 2009) have not been compared. Moreover, there is a lack of consensus between studies regarding not only the optimum WL for soil respiration but also how increasing or decreasing WL may limit or increase soil CO₂ emissions in peatlands ecosystems. In addition, soil respiration component fluxes may have different sensitivities to soil T and moisture changes (Boone et al. 1998; Mäkiranta et al. 2008; Wei et al. 2010). Therefore, accurate partitioning of R_{TOT} into R_A , R_L and R_P is necessary to understand the response of soil respiration to environmental changes (Hanson et al. 2000; Lee et al. 2003; Mäkiranta et al. 2008) and to constrain the C budget of forest ecosystems.

In a boreal peatland forest experiment, Mäkiranta et al. (2008) measured R_P on points that had been trenched to a depth of 30 cm and where the aboveground litter had been removed. Litter decomposition was estimated by subtracting R_P rates from soil CO₂ effluxes measured in similar trenched points with the litter left intact. They finally estimated R_A by subtracting R_P values from emissions in control points where the roots were left intact but the aboveground litter was removed. Although the trenching approach is one of the most commonly used methods to separate R_A from R_{TOT} (Bond-Lamberty et al. 2011; Hanson et al. 2000), other partitioning methods (e.g. C isotopic techniques and component integration) exist. It is well known that trenching methods

cause some disturbance effects in the soil and that they may overestimate lead to overestimation of R_H because decomposition of fine roots in the trenched points gives an extra source of CO_2 emissions (Díaz-Pinés et al. 2010). However, all partitioning methods have some disadvantages and previous research has not found significant differences between different methods for partitioning soil respiration (Kuzyakov 2006).

Several studies have been conducted to assess soil respiration and its component fluxes on forest mineral soils in temperate climates (Díaz-Pinés et al. 2010; Drake et al. 2012; Saiz et al. 2006a). However, partitioning of soil respiration in afforested peatland in temperate climates has received little attention. The proportion of each soil respiration component contributing to R_{TOT} is still unclear as, to date, no data have been published. In pursuance of this, the objectives of this study were to: (i) study the effect of soil T and WL on soil respiration; (ii) compare the suitability of different multiple nonlinear models and determine the best predictive soil respiration model; (iii) quantify the contribution of the soil respiration components to R_{TOT} , and; (iv) estimate their annual CO_2 emissions, in afforested organic soils on temperate climate. It was hypothesized, that (a) the inclusion of a WL Gaussian function in the soil respiration model would improve the model performance; (b) the effect of WL on soil respiration was dependent on soil T, and; (c) pooled data from all sites could be used to develop a model to scale up soil respiration in afforested peatlands to regional level under similar climatic and environmental conditions.

Material and Methods

Study sites

This research was conducted in southern Ireland on the Mullaghareirk Mountains. The climate is temperate maritime, with mild mean annual air temperatures ($10^\circ C$) and mean

annual rainfall (1,350 mm), with nearly 200 days with 1 mm or more rainfall and potential evapotranspiration of about 500 mm (Collins and Cummins 1996), leading to persistently wet soils. The study sites were seven plantations of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and one of lodgepole pine (*Pinus contorta* Dougl.) (Table 1), all established in poorly drained Dystric Histosols (IUSS Working Group WRB 2015). They were located within a radius of 12 km. The youngest site (SS₁₈) was a second rotation plantation 18 years old and the oldest site (SS₄₄) was 44 years old. All sites had closed canopy and the older sites were mature and ready for harvesting. The youngest site (SS₁₈) was unthinned but all the other sites had undergone one systematic thinning (one row of trees removed in every five rows). Sites SS₁₈, SS₂₄ and LP₂₃ were mounded. The ground preparation included the digging of surface drains every 10–11 m and mounds at approximately 1.9 × 1.9 m spacing. The other sites were either single or double mouldboard ploughed at about 2.1 m intervals. The latter sites were wetter, and deeper drains (up to 1 m deep) were dug at approximately 7 m intervals. No further works had been conducted at any of the sites since tree planting. Ground vegetation in all sites consisted of diverse mosses (*Hylocomium splendens*, *Pleurozium schreberi* and *Polytrichum* sp.) and forest lichens. In addition, bilberry (*Vaccinium myrtillus*) grew at LP₂₃. The youngest site had natural regeneration of Sitka spruce growing between the planted trees. Trees were planted in all sites on top of the cultivation features, whether excavated mounds or plough ridges.

Site installations

The eight sites were established during January and February 2014. At each site two temperature probes, inserted horizontally at 10 cm soil depth, were used to record soil T at 10 minutes intervals and then averaged for hourly and daily values (TG-4520 & PB-

5002; Gemini Data Loggers UK Ltd., UK). Long-term precipitation and air temperature data were obtained from Mount Russell climatological station (Met Éireann, Data licensed under a Creative Commons Attribution-ShareAlike 4.0 International licence).

For soil gas efflux measurements, seven subsites were established at each site. Three subsites were established on the flat and undisturbed ground, two on the furrows, and two on the tree-planting lines (Figure 1a). Subsites were separated from each other by at least 3 m and located within an area of 20×20 m. Each subsite consisted of three treatment points: (i) an undisturbed point, representing R_{TOT} ; (ii) a trenched point with a root-cutting collar inserted through the intact litter and the peat layers, representing peat and litter respiration (R_{PL}) and; (iii) a trenched point like in R_{PL} but with the aboveground litter removed, representing R_P ; as represented in Figure 1b. There were 168 sample points in total (3 respiration partitions $\times 7$ subsites $\times 8$ sites). The undisturbed point had a surface collar not inserted into the ground, used to mark the exact location for soil respiration measurements. Each trenched point consisted of a rigid PCV cylinder with 15.4 cm internal diameter and 32 cm long driven vertically 30 cm into the soil and functioning as collars to initially cut roots, prevent root ingrowth, and provide a soil-surface contact for the measurement device. Removable aluminium nets of 1 mm mesh size were laid over the collar openings to prevent soil disturbances by animals and to prevent the further accumulation of fresh litter within each collar between measurements. Mosses and tree seedlings growing inside the collars were removed at the beginning of the measurements and when necessary throughout the study period. At each subsite, one dipwell, consisting of a perforated pipe (Figure 1b), was installed to 100 cm depth for WL measurements.

Soil CO₂ efflux measurements and soil respiration partitioning

Soil CO₂ efflux was measured weekly or fortnightly from June 2014 until mid-February 2016 using a portable infrared gas analyser attached to a closed chamber of 2755 cm³ (EGM-4 and modified SRC-1; PP Systems Ltd., UK). The total volume of the chamber including the collar's head-space volume was 2755 cm³. For a full description of the chamber and the method see Jovani-Sancho et al. (2017b). This study demonstrated that in these ecosystems, a trenching depth of 30 cm is sufficient to exclude the entire R_A efflux by severing all fine roots inside the collar. R_A and R_L were estimated as follows:

$$R_A = R_{TOT} - R_{PL} \quad (1)$$

$$R_L = R_{PL} - R_P \quad (2)$$

During soil respiration measurements, soil temperature (T) was measured at 0–10 cm soil depth (including the litter layer) and in triplicate next to each collar (HD-2307.0 & TP-473 P.O; Delta OHM S.r.L., UK). At each subsite, WL was measured at the same time. Water table level was measured from the ground surface (± 1 cm) using an electric contact meter (KLL-Mini; SEBA Hydrometrie GmbH & Co. KG, Germany).

Soil sampling and analysis

During summer 2015, litter and peat samples were collected at all eight sites, in each case only from undisturbed, flat microtopographic positions. At each site, four sampling points were selected along a transect of the study zone, at about 2 m spacing. At each sampling point, forest litter (L and F layers combined) was collected using a circular frame 15.4 cm inner diameter. With the full thickness of forest-derived litter layer sampled, a peat core, 7.0 × 7.5 × 30 cm was collected, using a modification of the volumetric peat sampler proposed by Jeglum et al. (1991). The peat extraction produced

minimum compaction and each core was then divided into three 10 cm long sections. Samples were placed in zipper plastic bags and stored at 4°C. Within one day, soil pH was measured by mixing 10 g of peat with 25 ml of distilled water. Moisture and ash content were determined according to the EN 14774-3:2009 and EN 14775:2009 standards, respectively. Soil bulk density (BD) was calculated for every 10 cm depth interval by dividing the dry mass (at 70°C) by the volume of fresh samples, based on the dimensions of the corer. Oven-dry samples were ground in a rotor mill to pass through a 2 mm sieve. Two bulked samples from each soil depth interval were used to assess soil organic C (SOC) and Nitrogen (N) content in an elemental analyser (according to EN 15104:2011 standard). Soil C stocks (SCS) were then calculated for each depth interval and for the soil profile to 30 cm depth. Soil C stocks for the L–F layers were calculated using their site-specific C content and the total dry mass collected within the quadrat.

Data analysis and modelling

Daily WL gaps between measurement days were filled by linear interpolation. Occasionally, logged soil T values were missing due to malfunctioning of the equipment. Gaps were filled based on soil T data from the nearest site. In addition, gaps in soil T occurred in all sites for September 21–24, 2014 and July 07–22, 2015. Missing soil T data were derived by site-specific correlations between soil T at Mount Russell weather station and soil T at each site.

Mean values of all variables at each site (mean of seven subsites) were calculated for each day. Thereafter, several simple and multiple nonlinear regressions were used to study the relationship between the soil respiration components, soil T and WL. The

relationship between soil CO₂ efflux and soil T was tested by an exponential function with two parameters Eq. 3,

$$y = a_i(\exp)^{b_i T} \quad (3)$$

where y is the measured soil CO₂ efflux rate, T is the measured soil temperature at 10 cm depth and a_i and b_i are fitted parameters greater than 0 obtained by nonlinear regression analysis.

Multiple models that had been previously used to study the relationship between soil CO₂ efflux and WL in peatlands were tested for each site: a linear relationship Eq. 4 (Mäkiranta et al. 2008), a sigmoidal relationship Eq. 5 (Tuittila et al. 2004), and a Gaussian form equation Eq. 6 (Jovani-Sancho et al. 2017b). These are:

$$y = y_i + a_i WL \quad (4)$$

$$y = \left[\frac{a_i}{1 + \exp\left(\frac{WL - b_i}{c_i}\right)} \right] \quad (5)$$

$$y = a_i \exp\left[-0.5 \left(\frac{WL - b_i}{c_i}\right)^2\right] \quad (6)$$

where y is the measured soil CO₂ efflux rate, WL is the measured water table level, y_i is a parameter derived by linear regression, a_i , b_i and c_i are specific-fitted parameters determined using least squares nonlinear regression for each of the equations tested. Multiplicative and additive paired combinations of Eq. 3 with Eq. 4, Eq. 5 and Eq. 6 were tested to develop site-specific empirical models. In addition, daily pooled data from all sites were used to develop models for the entire dataset for each soil respiration component.

Model accuracy and performance were evaluated according to different statistics and criteria. Firstly, the model parameters had to be statistically significant ($p < 0.05$). Then, the standard error of the estimates had to be as low as possible. Third, the coefficient of the determination had to be as high as possible. When two or more models were statistically indistinguishable, the best fit model was evaluated by the Akaike's Information Criterion (AIC_c) with a bias-adjustment for finite samples (Eq. 7) (Burnham and Anderson 2004; Jovani-Sancho et al. 2017a; Lellei-Kovács et al. 2016). Also, the statistical performance for modelled effluxes was evaluated by residual analysis of observed versus modelled respiration values and by calculating the mean bias (Eq. 8). Finally the model efficiency (MEF) was tested using Eq. 9 (Elsgaard et al. 2012; Soares et al. 1995). These are described as follow,

$$AIC_c = n \times \ln \frac{RSS}{n} + 2 \times K + \frac{2 \times K \times (K + 1)}{(n - K - 1)} \quad (7)$$

$$Mean\ bias = \frac{1}{n} \sum_i^n (Efflux_{Mod_i} - Efflux_{Obs_i}) \quad (8)$$

$$MEF = 1 - \frac{\sum_i^n (Efflux_{Obs_i} - Efflux_{Mod_i})^2}{\sum_i^n (Efflux_{Obs_i} - Efflux_{Mean})^2} \quad (9)$$

where n is the total number of observations, RSS is the residual sum of squares, K is the number of parameters in the model, $Efflux_{Mod_i}$ is the modelled soil respiration efflux, $Efflux_{Obs_i}$ is the measured soil respiration efflux, and $Efflux_{Mean}$ is the mean of the observed soil respiration effluxes. The model with the minimum AIC_c may be interpreted as the model which best fits the relationship of CO_2 efflux with soil temperature and WL. The MEF statistic gives the relative performance of the model,

where negative values indicate poor performance, 1 indicates an “almost perfect” fit and 0 means that the model is not better than using the mean of the measured effluxes.

Based on the above, best site-specific models were used to simulate soil CO₂ effluxes. Annual R_{TOT}, R_{PL} and R_P were estimated by summing up daily simulated values over two 12-months periods (Year 1: February 22, 2014 to February 21, 2015; Year 2: February 22, 2015 to February 21, 2016). Daily R_A and R_L values were estimated using Eqs. 1 and 2, respectively. To cross-validate the models developed for the entire dataset, these models were also used to simulate daily fluxes for each individual site, year and soil-respiration component. Annual soil CO₂ values simulated with site-specific models and with the models for the entire dataset were compared to assess the validity of the models. These models were intended to scale up soil respiration in afforested peatlands at regional and national level under similar climatic and environmental conditions.

Statistics and uncertainty

Soil T and WL values were tested for normality and homogeneity of variance using the Kolmogorov–Smirnov and Lavene’s tests. Parametric and non-parametric tests were used to examine differences between sites. This was necessary because the study variables were not normally distributed at all the sites. Firstly, a one way ANOVA test followed by a Bonferroni post-hoc test were performed for both soil T and WL. After that, the non-parametric Kruskal–Wallis and Mann–Whitney U tests were also conducted for WL values. Parametric and non-parametric tests produced similar results. Differences in soil CO₂ efflux between subsite-types within each site and between sites were also studied with non-parametric tests only.

All raw data were processed with EXCEL 2010; statistical analyses were performed using SPSS 22.0 (IBM Corp., Armonk, NY, USA) and all regression analyses and graphs were conducted using SigmaPlot 12.0 (Systat Software Inc. USA). All the statistical tests were carried out at the $P = 0.05$ significance level.

Results

Environmental factors

Daily mean air temperature throughout the study period ranged between -0.2 and 20.9°C (measured at Mount Russell climatological station, ~ 35 km east of the study sites). Mean air temperature was 10.2°C . Monthly soil T was normally distributed in all sites. The one way ANOVA and the Bonferroni post-hoc tests did not show any significant difference between sites. Mean soil T across all sites was 8.7°C and mean daily values varied between 2.7 – 15.8°C . Pairwise comparison did not show any statistical difference between the two years. While maximum mean daily soil T recorded during the second year was around 2°C lower than during the first year, minimum soil T was very similar between the two years. Both air and soil T followed the same seasonal pattern, increasing towards the summer months and decreasing gradually into the winter months (Figure 2ab).

As is typical of maritime temperate climate, winter months were wetter than summer months. Moreover, rainfall occurred in every month and it presented a small seasonal trend with a distinct summer effect of evapotranspiration in year 1 leading to deeper WL. The driest (26 mm) and the wettest (372 mm) months throughout the study period were September 2014 and December 2015, respectively (Figure 2c). Annual rainfall for the first and second study years was 1,313 and 1,871 mm, respectively.

Water table level had a temporal variation related to precipitation, increasing after rainfall events and decreasing during lower-rainfall periods (Figure 2c). Mean site-specific WL (measured from the soil surface) varied between 24.6–50.1 cm and 29.6–48.0 cm during the first and second year, respectively. Site-specific mean WL was on average 10% deeper in the first year than in the second year. Minimum and maximum daily WL were 10.6 and 95.9 cm and they were measured at sites SS₂₇ and LP₂₃, respectively. Mean monthly WL was normally distributed in all sites except in SS₂₇ and SS₂₈. The One way ANOVA and the Bonferroni tests concluded that mean monthly WL in LP₂₃ was significantly deeper than in the other sites (Figure S1a). The results of the Kruskal-Wallis and the pairwise comparisons with the Mann-Whitney U tests agreed with the former conclusion but also that mean monthly WL in SS₂₇ was significantly shallower than in all the other sites. Water table level differed between subsite-types. In all sites, mean WL measured in the different subsite-types increased in the following order: furrow, flat, and ridge microtopographies (Figure S1b).

Soil analysis

In all sites, except in SS₃₈, SOC increased with depth. Consistent with this, ash content decreased with each depth increment in all sites except SS₃₈ where it increased with depth. Nitrogen content, C/N ratios and pH increased or decreased with depth depending on the site without any clear pattern. Bulk density and SCS decreased with depth in half of the sites, and increased with depth in the other half. Mean SOC and peat N content for the top 30 cm of soil ranged between 47.5–56.5% and 1.7–3.2%, respectively (Table 2). Mean BD (to a depth of 30 cm) and ash content varied between 0.10–0.24 g cm⁻³ and 2.4–17.1%, respectively, with site SS₃₈ a clear outlier in both cases. For the same peat profile, C/N ratios and pH ranged between 16.9–33.2 and 3.43–4.54, respectively. While SCS to 30 cm soil depth (including the forest floor) measured

at SS₃₈ was 449.9 t C ha⁻¹ it varied between 204.4 and 288.4 t C ha⁻¹ among the other sites.

Soil respiration partitioning

Mean measured hourly (\pm SE) R_{TOT} ranged between 0.33 ± 0.02 and 0.48 ± 0.03 g CO₂ m⁻² h⁻¹. In addition, mean measured hourly (\pm SE) R_P varied between 0.10 ± 0.01 and 0.19 ± 0.03 g CO₂ m⁻² h⁻¹. On the other hand, estimated mean hourly R_A (\pm SE) varied between 0.15 ± 0.01 and 0.24 ± 0.02 g CO₂ m⁻² h⁻¹. Mean estimated hourly R_L varied between 0.06 ± 0.01 and 0.12 ± 0.01 g CO₂ m⁻² h⁻¹ (Figure 3). In all sites, the highest soil respiration rates were measured during the summer months. Conversely, minimum effluxes were measured during the winter months. Heavy rainfall events (Figure 2) produced a sudden decrease in WL, with associated decreased soil respiration rates at all sites (Figure 4).

Site-specific hourly emissions were not normally distributed for any of the soil respiration components. The non-parametric Kruskal-Wallis test showed statistical differences among sites. Pairwise comparisons with the Mann-Whitney test indicated that mean hourly R_{TOT} was significantly lower at sites SS₄₃, SS₄₄ and LP₂₃ than at the other sites (Figure 3). In addition, mean hourly R_P from SS₄₃ was significantly lower than in all the other sites. Mean hourly R_A was highest at site SS₂₈ and lowest at LP₂₃. By contrast mean hourly R_L was highest at SS₁₈ and minimum at SS₄₄.

Modelling soil respiration

In all sites, R_{TOT} , R_{PL} and R_P were strongly dependent on soil T and this relationship was described by an exponential function (Eq. 3). Within each site, soil T alone explained 51–88%, 51–92% and 52–82% of the temporal variation in R_{TOT} , R_{PL} and R_P respectively (Table S1). To study the relationship between the soil respiration

components and WL, Eq. 2, 3 and 4 were added separately to the temperature model. Among the multiple nonlinear equations producing models with statistically significant parameters and after comparing them with the AICc statistic, the incorporation of the WL Gaussian function resulted in better models in all sites except in LP₂₃ (Table 3). The addition of a WL linear equation to the R_P model best fulfilled the model selection criteria at LP₂₃. Additive combinations of Eq. 3 & 6 were best in some sites, while multiplicative combinations of the same equations were best in others (Table S1). Combined models accounted for 56–91%, 68–95% and 66–88% of the variation in the R_{TOT}, R_{PL} and R_P models, respectively. The residual analysis did not show any specific pattern (Figure S2). Modelled values were highly correlated with the observed effluxes and ME varied between 0.55–0.96. The mean bias between modelled and observed R_P effluxes were slightly positive (i.e. observed R_P > modelled R_P) suggesting that these models underestimate R_P effluxes, particularly at higher R_P. Site-specific mean bias values for R_{TOT} and R_{PL} were neutral.

Pooled data from all sites were fed into a single nonlinear model following the same approach. A multiplicative combined model of Eq. 3 & 6 (Table 4) resulted in the best model combination to simulate R_{TOT}, R_{PL} and R_P emissions. These models satisfied all the model selection criteria and they also fit the data well (P value < 0.001). Residuals were evenly distributed and did not show any specific pattern (Figure 5). The mean bias between modelled and observed was almost zero and the ME varied between 0.60 and 0.63. Moreover, they performed similarly to the site-specific models (Figure 6). Nevertheless, these models tended to underestimate higher measured CO₂ effluxes at all treatment points (Figure 5b, d & f).

Annual soil respiration

Soil respiration followed a clear seasonal pattern in all sites and was closely related to the soil temperature trend. All component fluxes followed the same seasonal variation. Soil CO₂ effluxes increased exponentially during the summer months and they decreased towards the winter months (Figure 4). Mean annual R_{TOT} at the study sites varied between 2669 and 4057 g CO₂ m⁻² year⁻¹. On the other hand, mean annual R_A varied between 1110 and 2049 g CO₂ m⁻² year⁻¹. Mean annual R_P and R_L varied from 774 to 1492 and from 514 to 1013 g CO₂ m⁻² year⁻¹, respectively (Table 5). The contribution of the different component fluxes to R_{TOT} differed among sites and also between years. Annual estimated R_P and R_L during the second year were on average 8 and 13% lower than during the first year. Mean annual R_{TOT} was also 12% lower in the second than in the first one. By contrast, annual estimated R_A was approximately 13% higher in the second year.

Discussion

Seasonal trend and temporal variation of in soil respiration

Among all sites and all treatment points, soil T was the main factor controlling soil CO₂ efflux (Table S1). Soil respiration followed a clear seasonal trend and it was regulated by the temporal variation of soil T. This observed strong correlation is reported in numerous former studies (Buchmann 2000; Byrne and Kiely 2006; Mäkiranta et al. 2009; Saiz et al. 2006b). The effect of WL on soil respiration was also significant but weaker than soil T. Water table level determines the volume of aerated peat and therefore it regulates the soil CO₂ efflux production rate. Tuittila et al. (2004) found that WL controlled soil respiration in two different ways. On one hand, the authors found that soil CO₂ increased with increasing WL as this increases the volume of oxic peat.

Thereafter, WL reaches a depth at which soil CO₂ production is maximum. On the other hand, the same authors found that soil CO₂ decreased for WL values less than 30 cm as the lack of water became a limiting factor for peat decomposition. Although the same effect has been found in this study, the optimum WL for soil CO₂ production differed between sites and also between treatment points. Treatment-specific pooled data showed that soil CO₂ efflux was maximum when WL was on average 55 cm — for the R_{TOT} treatment —, 66 cm — for the R_{PL} treatment — and 63 cm — for the R_P treatment — (Figure 5). These results are in agreement with Mäkiranta et al. (2009) who, in a similar experiment in Finland, found an optimum WL for R_P of 61 cm.

Soil respiration was affected concurrently by soil T and WL. In this study, it was found that depending on the site, either an additive or a multiplicative approach was the best model that satisfied all the model selection criteria (Table S1). However, when pooled data was used together to develop equations for the entire dataset, the multiplicative combined model resulted in the best model to simulate soil respiration. This result supports the hypothesis that the effect of WL on soil respiration is dependent on soil T in all treatment points as reported by Tuittila et al. (2004) and Mäkiranta et al. (2009). Although it is clear that soil temperature and WL are the main variables controlling soil CO₂ efflux in afforested peatland, the disparity in the equations used to model soil CO₂ efflux found in the literature (Mäkiranta et al. 2009; Mäkiranta et al. 2008; Tuittila et al. 2004), and the way that they are used in combined models (additive and multiplicative combinations), confirm that there is a need for continued research to improve our understanding of carbon efflux from drained peatland forests.

Total soil respiration

In this study, momentary R_{TOT} fluxes ranged from 0.08–1.20 g CO₂ m⁻² h⁻¹ among all Sitka spruce sites and between 0.03–0.88 g CO₂ m⁻² h⁻¹ at the lodgepole pine site. In a 31-year-old Sitka spruce site growing on a low-humic gley soil in Ireland, Saiz et al. (2006b) reported R_{TOT} values between 0.06 and 0.49 g CO₂ m⁻² h⁻¹. Similarly, Zerva and Mencuccini (2005) reported R_{TOT} emissions between 0.05 and 0.63 g CO₂ m⁻² h⁻¹ from a 4-year-old Sitka spruce site growing on a peaty gley soil in the UK. While minimum soil respiration values recorded in this study match those of these other experiments, maximum R_{TOT} differ greatly from them. Substrate availability is a key factor in soil respiration (Ryan and Law 2005). Organic C in litter, top soil and roots (the most readily decomposable carbon in soils) can significantly influence soil respiration (Zhou et al. 2013) as these soil C stocks provide an excellent substrate for soil heterotrophs (Wang et al. 2006). Although the reason for the discrepancy in R_{TOT} emissions is not clear, the higher soil C content of the afforested peatland sites compared to the low-humic gley and peaty gley Sitka spruce sites could explain the higher momentary R_{TOT} emissions. In addition, differences in age, spatial location, fine root biomass, forest productivity and specific soil temperature, soil moisture and WL conditions presented during the years when the experiments were conducted could have influenced the momentary R_{TOT} emissions (Buchmann 2000; Davidson et al. 2006; Janssens et al. 2001; Lecki and Creed 2016).

Previously estimated mean annual R_{TOT} values reported for afforested peatlands in Ireland are 953 g CO₂ m⁻² year⁻¹ for a mature Sitka spruce and 367–513 g CO₂ m⁻² year⁻¹ for a lodgepole pine chronosequence (four sites of different ages) (Byrne and Farrell 2005). By contrast, mean annual R_{TOT} values estimated in this study are 3563 and 2669 g CO₂ m⁻² year⁻¹ for the Sitka spruce chronosequence and for the lodgepole

pine site respectively, that is, larger by several times. Byrne and Farrell (2005) used the soda-lime method to estimate these annual fluxes. This method may have underestimated these fluxes (Janssens et al. 2001; Wei et al. 2010), potentially explaining the discrepancy in the annual R_{TOT} values. Total soil respiration reported for lodgepole pine site in a raised peat-bog in central Scotland is $1650 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ (Yamulki et al. 2013). More recent R_{TOT} values simulated for afforested peatlands (average value of six sites of different ages and tree species) in boreal climates are $2530 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ (Mäkiranta et al. 2008). These two studies used a similar method (infrared gas analyser attached to soil respiration chamber) to measure soil CO_2 efflux in their sites and therefore, with comparable results. The spatial variation in R_{TOT} values may be explained by differences in the mean annual temperatures registered in the Finnish and Irish sites respectively (4.0 vs. 10.2°C), differences in previous land use and management (agricultural fields vs. heather-dominated blanket peat) and root biomass (Schwendenmann and Macinnis-Ng 2016).

Heterotrophic respiration

In this study, simulated annual heterotrophic respiration was $1926 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$. This is approximately 60% greater than previously reported annual heterotrophic respiration in a Sitka spruce chronosequence on wet mineral gley in central Ireland (Saiz et al. 2006a). However, this annual value is about 37% lower than heterotrophic respiration reported for a 19-years old Sitka spruce plantation on an industrial cutaway peatland in the Irish midlands (i.e. $2641 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$) (Wilson and Farrell 2007). The peat type at the industrial cutaway experiment was a woody fen/*Phragmites* overlying a sub-peat mineral soil consisting of glacial till and clay. Therefore, the higher annual values reported by Wilson and Farrell (2007) may be due to the higher pH and nutrient content of the residual peat compared to the blanket peat of the present study.

On one hand, mean annual R_P was $1196 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ which is somewhat lower than annual R_P reported for a hemiboreal forestry-drained peatland in central Estonia (i.e. $1379 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$) (Minkkinen et al. 2007) but higher than values reported by Mäkiranta et al. (2008) for afforested organic soil croplands in Finland $1080 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$. On the other hand, mean annual R_L was $730 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$. Although R_L is greatly influenced by the litter type and the environmental conditions (Laiho et al. 2008), the mean R_L value in this study is slightly higher than previous values reported by Mäkiranta et al. (2008) (i.e. $430 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$) for afforested organic soil croplands in Finland. The high SCS of the accumulated in the L/ F layers ($25.6\text{--}54.3 \text{ t C ha}^{-1}$) would explain the high soil CO_2 emissions attributed to R_L (Table 2). In this study, mean R_P and R_L represented 34.7 and 21.2% of R_{TOT} , respectively. No other soil respiration partitioning studies in afforested peatland in temperate climates are known to have been conducted so far. However, the results presented here are similar to those reported by Mäkiranta et al. (2008) for boreal afforested organic soil croplands ($R_P=41\%$; $R_L=17\%$).

Autotrophic respiration

Autotrophic respiration was estimated as the difference between R_{TOT} and R_{PL} . In this study, simulated mean annual R_A was 1586 and $1100 \text{ g CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ for the spruce chronosequence and the pine sites respectively. The greater R_A efflux in the Sitka spruce could explain the higher productivity of this species over the lodgepole pine. Farrell and Boyle (1990) reported yield classes of $10.6 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ for lodgepole pine and of $13.3 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ for Sitka spruce growing on low-level blanket peat in western Ireland. The annual R_A estimates presented in this study are at the higher end of previously reported values. This suggests that, in temperate climates, root activity in afforested peatland may be relatively high. Moreover, this would also be supported by

the fact that roots were actively respiring throughout the year, though less during the winter months.

Autotrophic respiration can vary between 10–90% of R_{TOT} and it depends on the plant community, the season and the amount of fine roots (Hanson et al. 2000; Heinemeyer et al. 2007; Saiz et al. 2006a). In this study, R_A represented 44.5 and 41.3% of R_{TOT} in the Sitka spruce sites (mean of the seven sites) and the lodgepole pine site, respectively. This is slightly lower than mean R_A contributions reported by Saiz et al. (2006a) for another Sitka spruce chronosequence in Ireland in mineral soils (i.e. 55.6%) but higher than R_A contributions reported by Mäkiranta et al. (2008) for afforested peatlands in Finland (i.e. 41%).

Errors and assumptions

The main assumption of trenching experiments is that trenching collars completely terminate the R_A component by severing all roots within the collar (Lee et al. 2003; Mäkiranta et al. 2008). Jovani-Sancho et al. (2017b) demonstrated that an insertion depth of 30 cm, as used in this study, was able to suppress all rhizospheric activity in the trenched area, supporting this assumption. Notwithstanding this, Uchida et al. (1998) found that excised roots may still respire for some time after trenching. This was also acknowledged by Lee et al. (2003) and Mäkiranta et al. (2008) in other trenching experiments. In this study, soil respiration measurements started between four and six months after trenching, so it is assumed that the respiration from excised roots was completely terminated when the first measurements started.

It has been previously reported that soil CO_2 emissions significantly increase after trenching as a consequence of soil disturbance and injured roots (Lee et al. 2003; Uchida et al. 1998). In a similar experimental setup, Jovani-Sancho et al. (2017b)

showed that soil CO₂ emissions from trenched points exceeded those from non-trenched points during the first two months after trenching and decreased significantly thereafter. Therefore, it is assumed that the same effect occurred in this trenching experiment.

Although some studies have estimated that the effect of fine root decomposition on soil respiration was minor some time after trenching (Lee et al. 2003; Mäkiranta et al. 2008), it is possible that this effect could have led to underestimation of R_A and overestimation of R_P and R_L emissions (Hanson et al. 2000). Bond-Lamberty et al. (2004) estimated that R_A was underestimated by 5–10% due to root decay in trenched points in a boreal black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) chronosequence. In a similar manner, Díaz-Pinés et al. (2010) demonstrated that decomposition of roots after trenching may lead to an overestimation of R_H effluxes. The authors concluded that over a period of two years, R_A increased from 26 to 44% of R_{TOT} between the first and the second growing season in a mountain forest in Austria. Nevertheless, roots from coniferous trees contain high concentrations of lignin and recalcitrant organic carbon and it has been found that their decay rate is slow (Silver and Miya 2001).

By contrast, root and litter exclusion may have underestimated heterotrophic respiration due to the suppression of fresh decomposable substrate inputs from tree litterfall and root turnover (Heinemeyer et al. 2012). Hartley et al. (2007) found that the availability of labile C for decomposition is a limiting factor for heterotrophic respiration. Root exudates are an important source of substrate for soil respiration and continuous microbial decomposition of this root-derived C may lead to a decline in soil CO₂ efflux in late summer months and autumn (Kirschbaum 2004; Phillips et al. 2013). Therefore, it is assumed that the same depletion of easily decomposable substrate occurred within the trenched points.

It is very likely that both effects, CO₂ emissions from decomposing roots and depletion of easily decomposable substrates, occurred at the same time within the trenched points throughout the length of this experiment. Rather than assume that these cancelled each other, it is proposed that they have been minimised relative to the measured values, by the installation recovery period before measurements started, and by the moderate length of the study relative to decomposable pools present, so they are not large compared to other measurement uncertainties.

Conclusion

This is the first study partitioning soil respiration in afforested peatland ecosystems in temperate climate conditions and one of the few studies conducted on global forested peatlands. Although soil T measured at 10 cm depth was the main driver of temporal variation in soil respiration and its component fluxes, this study has demonstrated that the inclusion of WL in soil respiration models can improve their predictive capacity. The effect of WL on soil respiration was dependent on soil T, while all soil respiration components had different sensitivities and responses to changing soil T and WL values. Therefore, specific predictive models should be used for each one of the soil respiration components. In addition, the effect of WL on soil respiration, incorporated as a Gaussian function, showed that there is an optimum WL for soil respiration in afforested peatlands. The WL thresholds found (i.e. when soils are either too wet or too dry) have important implications in predicting soil CO₂ emissions in future climate change scenarios. In peatland forests, with wet soils and WL less than optimum, a decrease in precipitation would increase WL and is likely to increase soil CO₂ emissions. Moreover, this study has also provided relatively simple models able to simulate the temporal and the spatial variation of soil respiration. The accuracy of the models developed for the entire dataset have been cross-validated (Figure 6), and

although they do not provide the detail of the site-specific models, we propose they are suitable for calculating annual soil CO₂ emissions with high enough confidence. The combined model requires WL data in order to provide accurate soil CO₂ emissions. Therefore, a robust method to simulate WL in peatland forests, using commonly measured environmental variables, is needed. Despite this, if WL is not available, the temperature exponential models developed for the entire dataset may be used with confidence to scale up soil respiration and its component fluxes at a regional level.

Acknowledgements

We gratefully acknowledge the Department of Agriculture, Food and the Marine and the Forestry Research Programme for funding the Additions and refinements to the Irish forest carbon accounting and reporting tool (CForRep) project (grant No. 11/C/205), and Coillte for use of sites. We also thank Dr. Richard Lane for his assistance in setting up the study sites and also Síle-Caitriona O'Callaghan for helping with taking soil samples and conducting laboratory analysis.

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List of Figures

Figure 1 Site installation diagram a) microtopographies selected within each site and b) soil respiration treatment points established in each microtopography. The cut A-A' represents three treatment points established within the flat microtopography. This included one trenching collar with the litter removed representing peat respiration (R_P), one trenching collar with the litter left intact representing peat and litter respiration (R_{PL}), and one surface collar marking the area used to measure total soil respiration (R_{TOT}). This was repeated three times in the flat, two times in the furrow and two times in the ridge microtopographies at each site. The top and bottom of each collar are open

Figure 2 a) Mean hourly air temperature recorded at Mount Russell climatological station (about 35 km east of the study sites). b) Mean hourly soil temperature measured at 10 cm depth at the SS₂₄ (black line) and SS₄₄ (grey line) sites. c) Measured (symbols) and interpolated (solid lines) daily water table level at the 24 (black line) and 44 (grey line) year old Sitka spruce sites. Vertical bars represent daily rainfall recorded at Rokchapel weather station (about 2 km south of SS₂₄). Vertical dashed line separates the measurement time into the two study years. Year 1: 22/02/2014–21/02/2015 and year 2: 22/02/2015–21/02/2016. Only two sites are presented here as an example

Figure 3 Sites comparison of a) mean total soil respiration (R_{TOT}), c) mean peat respiration (R_P) e) mean autotrophic respiration (R_A) and, g) mean litter respiration (R_L). Also, mean hourly effluxes comparison between subsites within each site, of b) R_{TOT} , d) R_P , f) R_A and, h) R_L . Different letters between sites, and also between subsites within each site, indicate that they are significantly different (P value < 0.05)

Figure 4 Measured (symbols) and simulated (curves) peat respiration (R_P), peat and litter respiration (R_{PL}) and total soil respiration (R_{TOT}) at the eight study sites. Each

measured value is the mean value of seven manual measurements. Vertical dashed line separates the measurement time into two years. Year 1: 22/02/2014–21/02/2015 and year 2: 22/02/2015–21/02/2016. Sites SS₂₇ and SS₃₉ were clearfelled in June 2015 and therefore, only one year simulations are presented

Figure 5 a) Pooled measured data (symbols) from the eight study sites combined together to create a single model for the entire dataset. Simulated values (mesh) represent the multiplicative combined effect of soil temperature and water level on a) total soil respiration (R_{TOT}), c) peat and litter respiration (R_{PL}) and, e) peat respiration (R_P). Relationship between observed and modelled effluxes, correlation coefficients (r), model efficiency (MEF) and mean bias are presented for b) R_{TOT} , d) R_{PL} and, f) R_P . Solid lines indicate a 1:1 relationship between observed and modelled effluxes. Notice the different scales used for R_{TOT} , R_{PL} and R_P

Figure 6 Annual soil respiration originating from peat respiration (R_P), autotrophic respiration (R_A) and litter respiration (R_L). b) Contribution of soil respiration components to total soil respiration (R_{TOT}). Solid bars represent annual soil CO₂ emissions calculated using site-specific models (Table S1). Cross-hatching bars represent annual soil CO₂ emissions calculated using the models developed for the entire dataset (Table 4).

Supplementary Figures

Figure S1 Comparison of mean monthly water level (\pm SE) between a) sites b) subsites within each site. Different letters between sites, and also between subsites within each site, mean that they are significantly different (P value < 0.05)

Figure S2 Relationship between observed and modelled total soil respiration (R_{TOT}), peat and litter respiration (R_{PL}) and peat respiration (R_P) using site-specific models.

Correlation coefficients (r), model efficiency (MEF) and mean bias are presented. Solid lines indicate a 1:1 relationship between observed and modelled effluxes

Figure 1

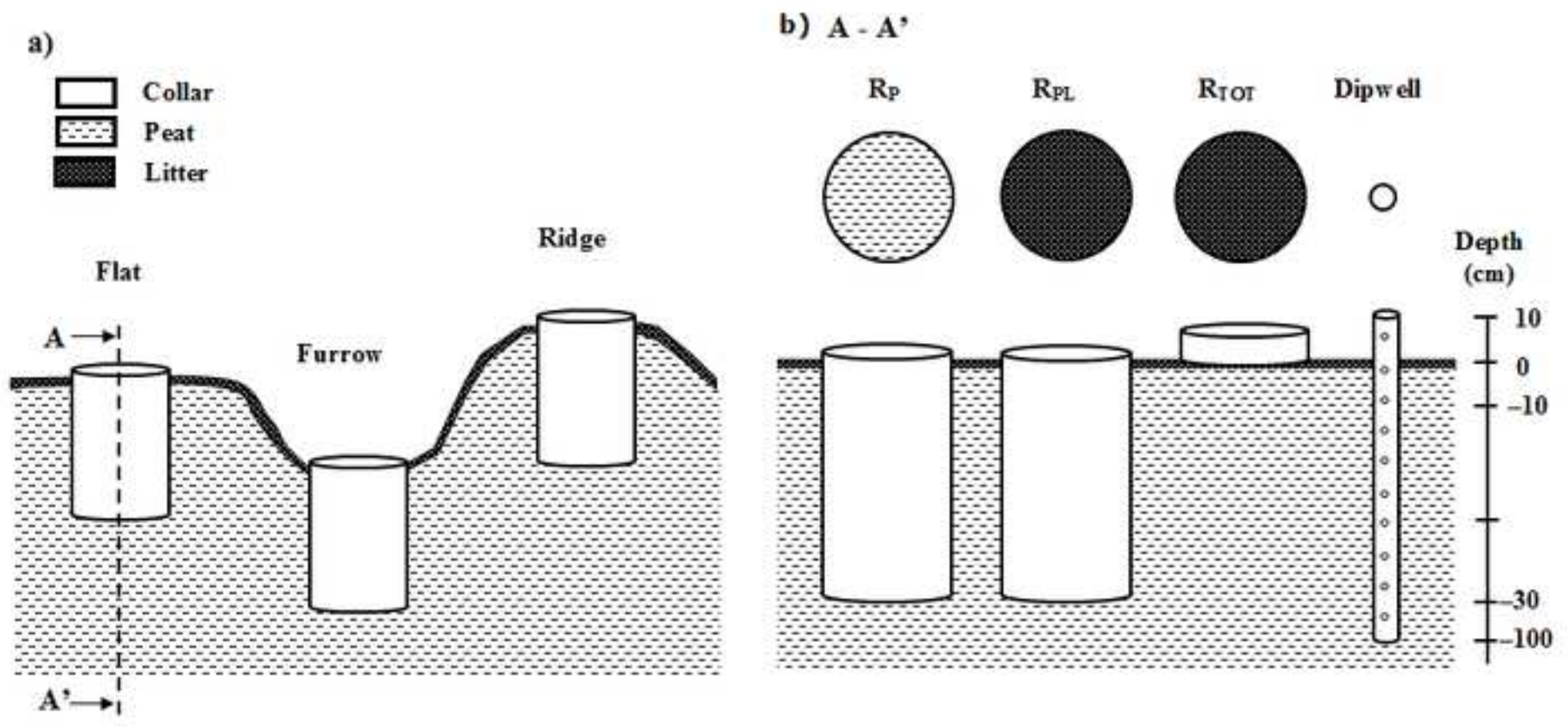


Figure 2

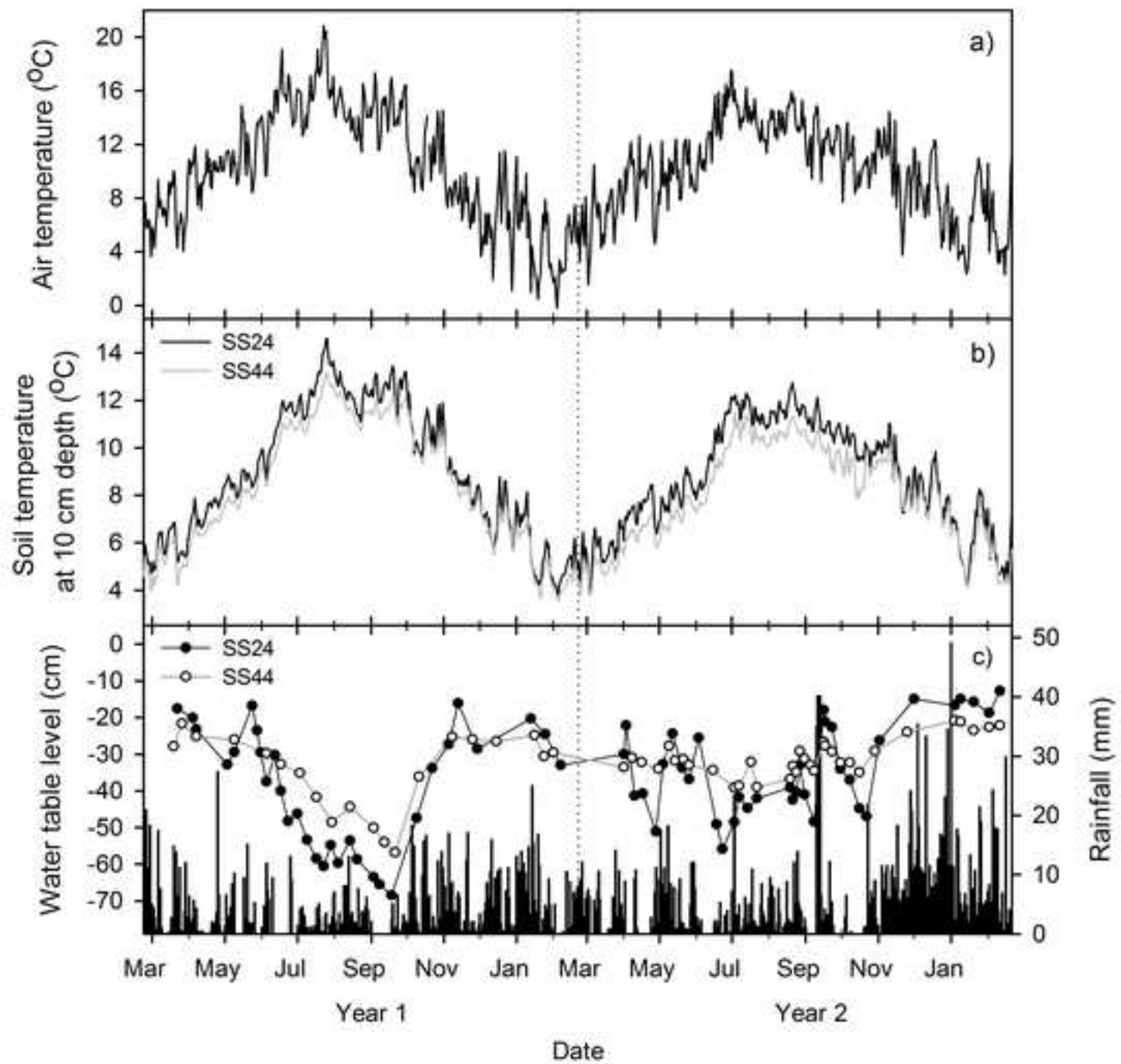


Figure 3

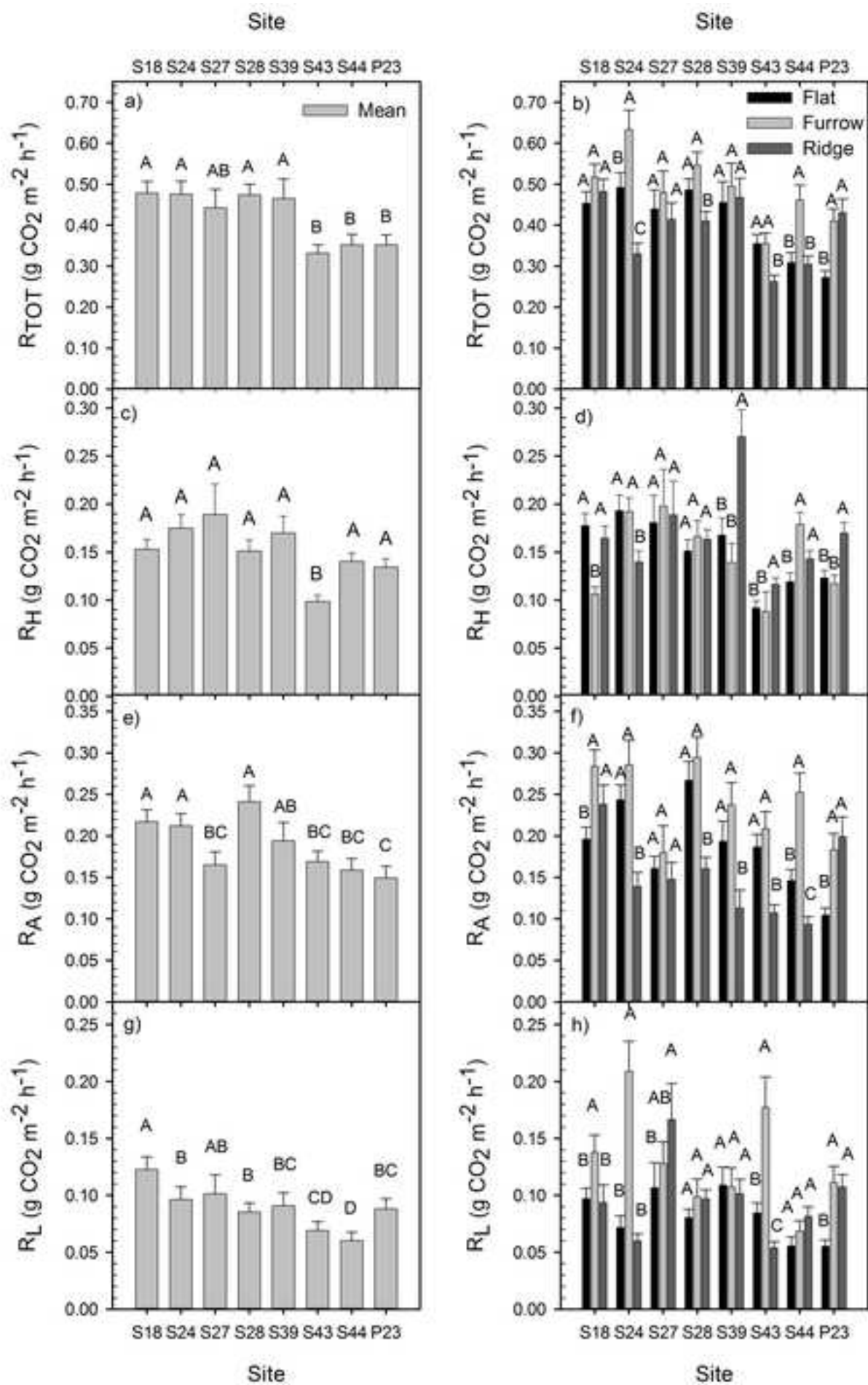


Figure 4

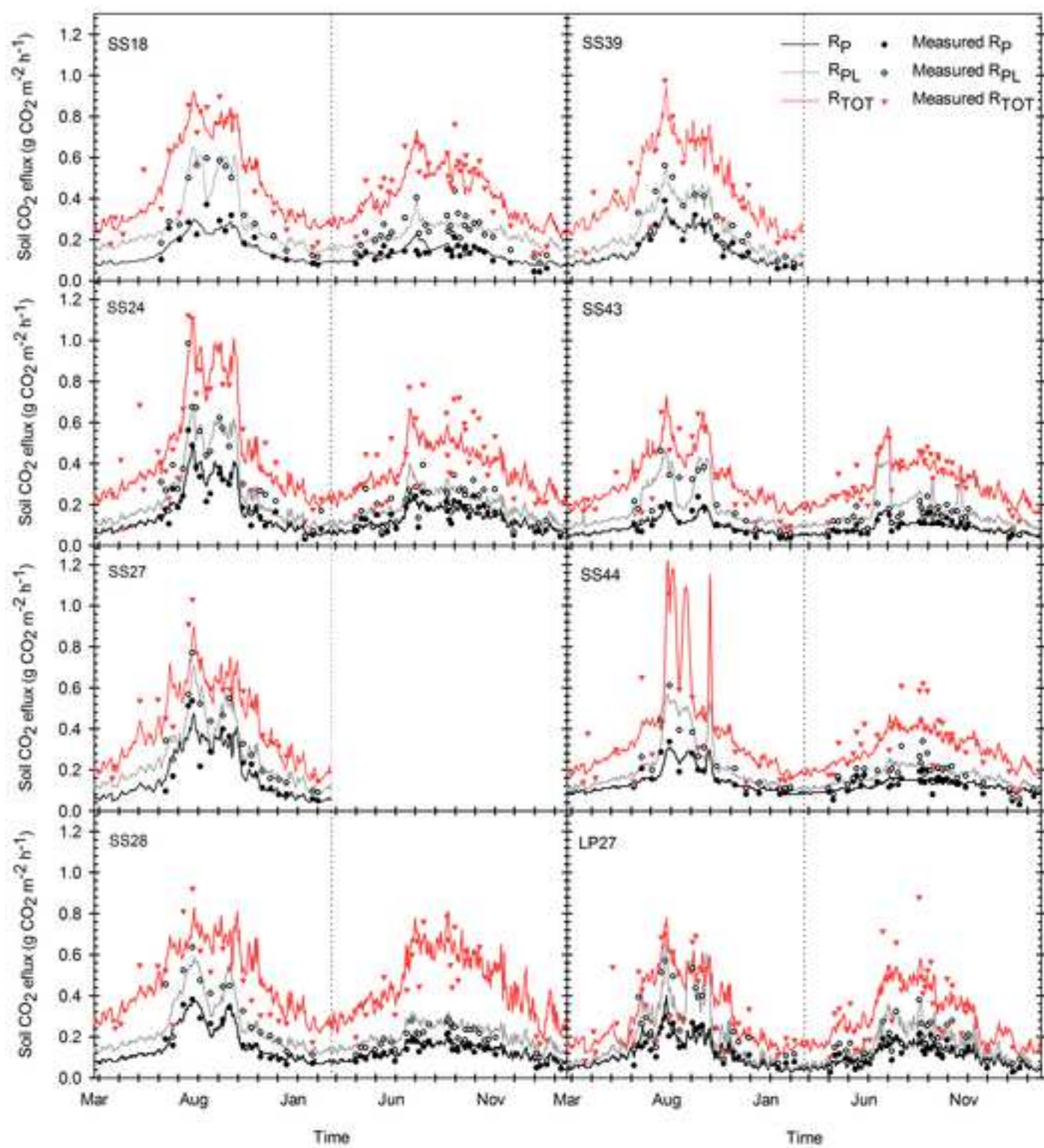


Figure 5

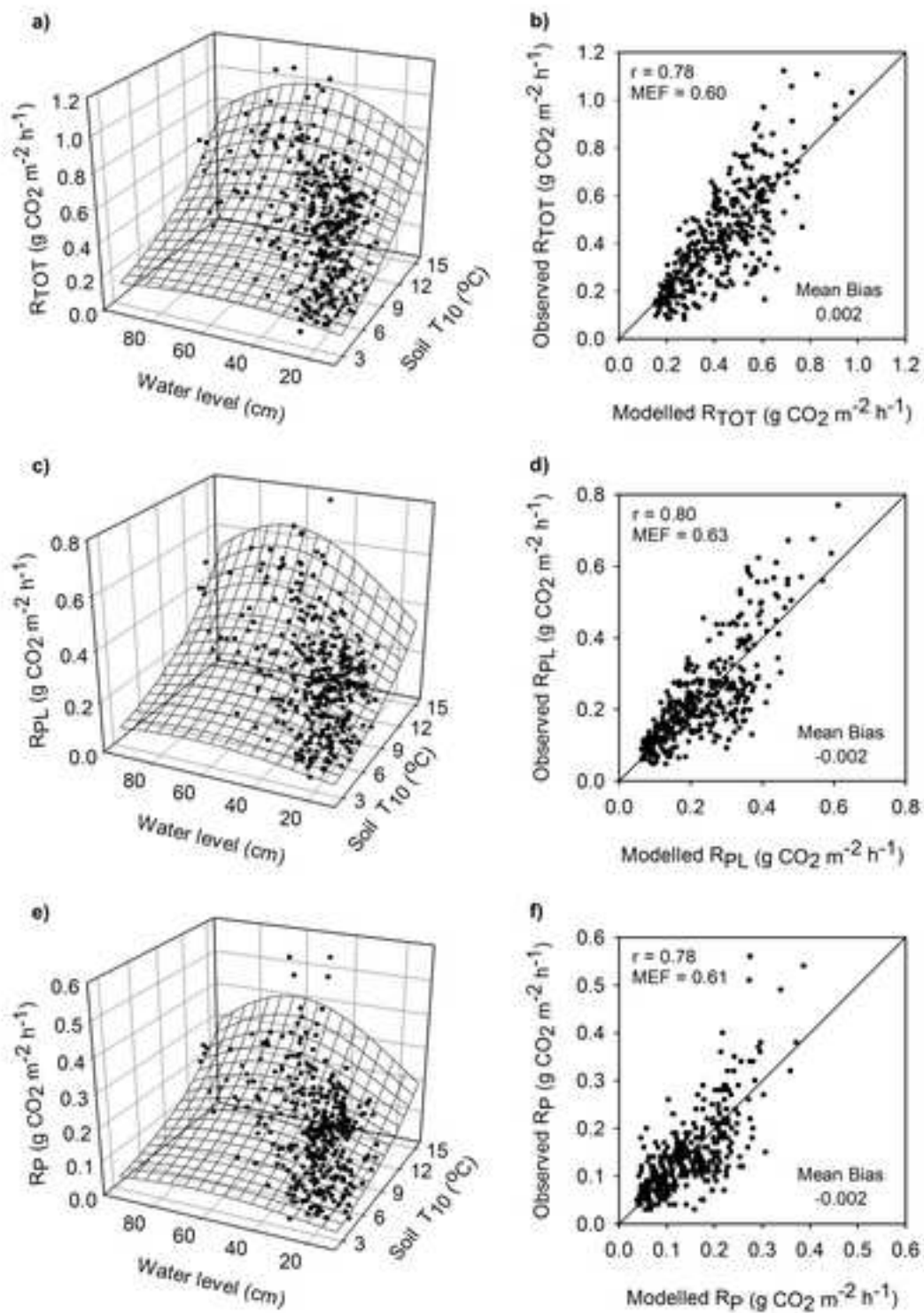


Figure 6

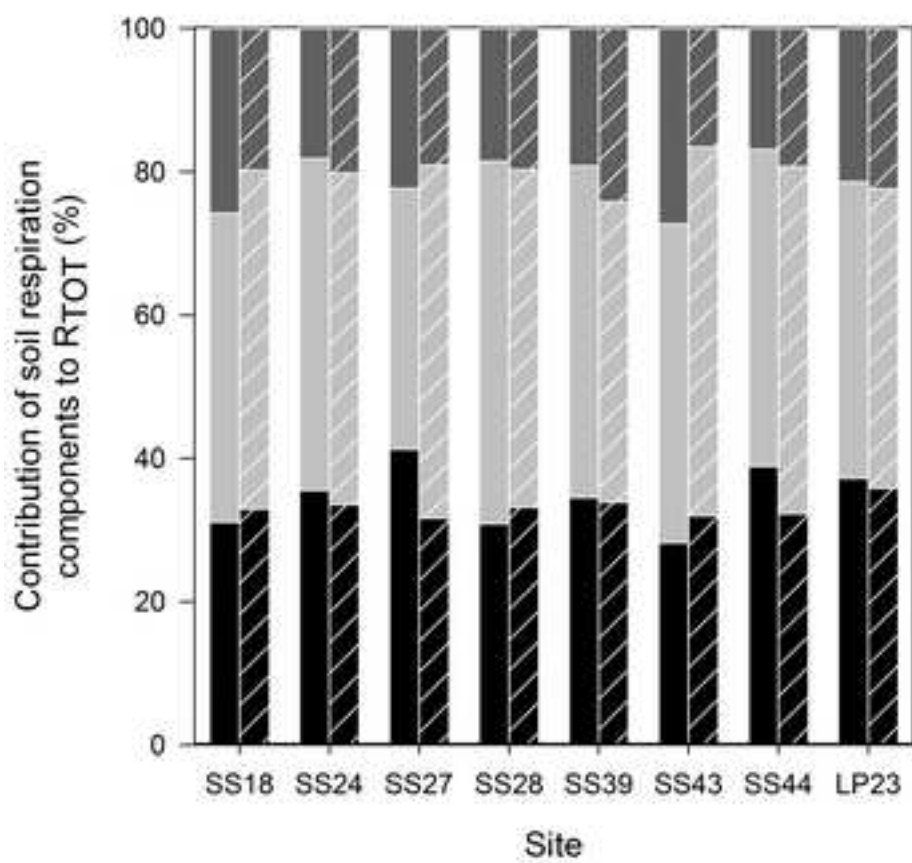
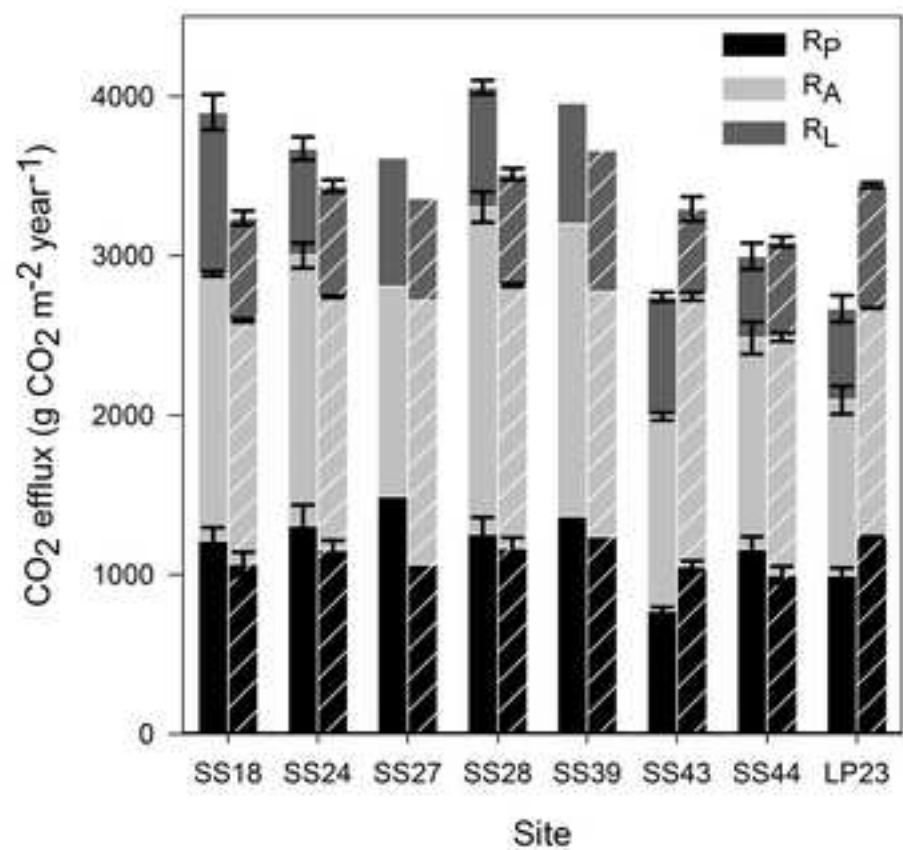


Table 1 General site features. Description included stand mean diameter at breast height (mean dbh) and stand basal area (ba).

Site code	Latitude (N)	Longitude (W)	Planting year	Ground preparation	Elevation (m.a.s.l.)	Age (in 2015)	Slope (%)	Density (trees ha ⁻¹)	Mean dbh (cm)	Mean ba (m ² ha ⁻¹)	Yield class (m ³ ha ⁻¹ year ⁻¹)	Area (ha)
SS ₁₈	52°20'43.20"	9°6'30.02"	1997	Mounded	360	18	2.1	3,000	13.6	43.5	16	2.4
SS ₂₄	52°18'00.85"	9°9'28.94"	1991	Mounded	293	24	4.4	2,767	15.4	51.8	14	20.2
SS ₂₇	52°19'58.01"	9°8'15.48"	1988	Double ploughed	243	27	4.6	2,469	18.2	63.9	16	22.7
SS ₂₈	52°19'04.50"	9°8'14.23"	1987	Single ploughed	319	28	4.8	1,733	26.2	93.4	20	18.8
SS ₃₉	52°17'57.06"	9°9'41.72"	1976	Double ploughed	288	39	4.1	2,345	n.d.	n.d.	14	9.6
SS ₄₃	52°20'43.20"	9°6'30.02"	1972	Double ploughed	317	43	2.3	2,133	18.3	55.8	10	3.2
SS ₄₄	52°19'50.40"	9°4'01.55"	1971	Single ploughed	358	44	2.2	1,733	20.5	72.6	10	3.8
LP ₂₃	52°18'16.60"	9°8'56.55"	1992	Mounded	287	23	1.8	2,500	16.4	52.5	12	4.2

n.d. – not determined; SS – Sitka spruce; LP – lodgepole pine. Subscript numbers under the site code correspond to number of years since planting (in 2015). Sites SS₂₇ and SS₃₉ were clearfelled unintentionally in June 2015

Table 2 Forest floor (litter and fermented layers) and peat properties (0–30 cm soil depth). Values in parentheses are standard error of the mean. Soil values were calculated for each 10 cm soil depth and then averaged for the top 30 cm of soil

Site	Depth (cm)	SOC (%)	N (%)	C/N	Ash content (%)	BD (g cm ⁻³)	SCS (t C ha ⁻¹)	pH
SS ₁₈	L/F	52.5 (0.1)	1.5 (0.0)	35.0	2.6 (0.0)	n.d.	47.5	n.d.
	0-30	55.1 (0.3)	1.7 (0.1)	32.4	3.7 (0.5)	0.12 (0.02)	205.1	3.41 (0.01)
SS ₂₄	L/F	54.2 (0.1)	1.7 (0.0)	31.9	3.5 (0.0)	n.d.	30.2	n.d.
	0-30	54.0 (2.2)	3.2 (0.1)	16.9	7.2 (2.6)	0.12 (0.01)	186.5	3.52 (0.04)
SS ₂₇	L/F	54.3 (0.0)	2.9 (0.0)	18.7	2.3 (0.0)	n.d.	25.6	n.d.
	0-30	55.5 (2.0)	2.5 (0.3)	22.2	7.4 (1.2)	0.15 (0.01)	256.7	4.54 (0.12)
SS ₂₈	L/F	53.0 (0.0)	1.9 (0.0)	27.9	5.5 (0.0)	n.d.	31.6	n.d.
	0-30	47.5 (1.4)	2.6 (0.2)	18.3	17.1 (2.5)	0.18 (0.02)	256.8	4.03 (0.13)
SS ₃₈	L/F	54.3 (0.2)	1.5 (0.0)	35.2	1.6 (0.0)	n.d.	54.3	n.d.
	0-30	55.1 (0.7)	2.4 (0.1)	23	7.4 (0.2)	0.24 (0.04)	395.6	4.22 (0.35)
SS ₄₃	L/F	53.5 (0.0)	1.6 (0.0)	33.4	1.5 (0.0)	n.d.	45.9	n.d.
	0-30	53.5 (0.4)	1.8 (0.1)	29.7	2.4 (0.3)	0.10 (0.01)	158.7	3.54 (0.04)
SS ₄₄	L/F	53.9 (0.1)	1.5 (0.0)	35.9	1.8 (0.0)	n.d.	53.3	n.d.
	0-30	56.5 (0.4)	1.7 (0.1)	33.2	2.7 (0.5)	0.12 (0.01)	210.4	3.43 (0.01)
LP ₂₃	L/F	53.8 (0.1)	1.6 (0.0)	33.6	2.3 (0.0)	n.d.	29.5	n.d.
	0-30	53.7 (0.6)	2.0 (0.1)	26.9	2.4 (0.5)	0.11 (0.01)	174.9	3.71 (0.01)

SOC – soil organic carbon; N – nitrogen; C/N – carbon and nitrogen ratio; BD – bulk density; SCS – soil carbon stocks; n.d. – not determined

Table 3 Results of the combined models (soil temperature and water level) comparison using the Akaike's Information Criterion (AICc) with a bias-adjustment for finite samples. Best models denoted by the lowest AICc are in bold. Values highlighted in italics mean that at least one of the model parameters was not statistically significant and therefore the model combination was discarded. Combined models consisted of pair combinations of the soil temperature exponential function (Eq. 3) with water level, in linear (Eq. 4), sigmoidal (Sig; Eq. 4) and Gaussian (Gauss; Eq.5) functions

Site	R _{TOT}			R _{PL}			R _P		
	Linear	Sig	Gauss	Linear	Sig	Gauss	Linear	Sig	Gauss
SS ₁₈	-217	-217	-217	-249	-249	-259	-289	-288	-287
SS ₂₄	-225	-233	-235	-283	-292	-295	-334	-339	-345
SS ₂₇	-116	n.c.	-117	-120	-117	-118	-108	-107	-110
SS ₂₈	-233	n.c.	-233	-256	-254	-253	-305	-320	-320
SS ₃₉	-87	-87	-87	-136	-134	-134	-154	-151	-151
SS ₄₃	-234	-232	-235	-286	-286	-293	-342	-353	-347
SS ₄₄	-200	-198	-216	-271	-268	-294	-310	-307	-315
LP ₂₃	-234	-233	-233	-287	-285	-294	-383	n.c.	n.c.
Entire dataset	-1406	-1407	-1415	-1730	-1742	-1747	-1230	-1228	-2042

n.c. model regression did not converge

Table 4 Models developed for the entire dataset that best fulfilled the model selection criteria. Model parameters \pm standard error of the estimates in brackets, coefficients of determinations (r^2) and number of measurements (n) for soil temperature exponential function (Eq. 3) and the combination of soil temperature and water table level Gaussian form equation (Eq. 6) simulating total soil respiration (R_{TOT}), peat and litter respiration (R_{PL}) and peat respiration (R_P). Each n value represents the mean value of seven measurements

Component	Model #	Parameters					r^2	n
		a_i	b_i	c_i	d_i	WL_i		
R_{TOT}	$y = a_i \exp^{b_i T}$	0.097 (0.008)	0.149 (0.007)	-	-	-	0.59	349
	$y = a_i \exp^{b_i T} \times \exp \left[-0.5 \left(\frac{WL - WL_i}{d_i} \right)^2 \right]$	0.123 (0.014)	0.134 (0.009)	-	55.99 (8.45)	55.21 (3.52)	0.60	
R_{PL}	$y = a_i \exp^{b_i T}$	0.037 (0.004)	0.183 (0.009)	-	-	-	0.57	348
	$y = a_i \exp^{b_i T} \times \exp \left[-0.5 \left(\frac{WL - WL_i}{d_i} \right)^2 \right]$	0.067 (0.009)	0.147 (0.010)	-	46.19 (4.95)	65.92 (3.51)	0.63	
R_P	$y = a_i \exp^{b_i T}$	0.023 (0.003)	0.184 (0.009)	-	-	-	0.57	349
	$y = a_i \exp^{b_i T} \times \exp \left[-0.5 \left(\frac{WL - WL_i}{d_i} \right)^2 \right]$	0.041 (0.006)	0.148 (0.011)	-	42.81 (4.62)	62.61 (2.86)	0.61	

Table 5 Annual contributions of peat respiration (R_P), litter respiration (R_L) and autotrophic respiration (R_A) to total soil respiration and their proportion calculated using site-specific models. Standard error (SE) of the mean (two years calculations) is presented in parenthesis. Sites without SE represent only one year simulations as they were clearfelled after one year

Site	Annual estimate (g CO ₂ m ⁻² year ⁻¹)				Percentage (%)			
	R _{TOT}	R _P	R _A	R _L	R _{TOT}	R _P	R _A	R _L
SS₁₈	3899 (209)	1214 (82)	1672 (14)	1013 (112)	100	31	43	26
SS₂₄	3672 (279)	1309 (129)	1693 (79)	670 (72)	100	36	46	18
SS₂₇	3614 (n.d)	1492 (n.d)	1314 (n.d)	808 (n.d)	100	41	36	23
SS₂₈	4057 (50)	1255 (103)	2049 (96)	753 (43)	100	31	51	18
SS₃₉	3958 (n.d)	1367 (n.d)	1831 (n.d)	760 (n.d)	100	35	46	19
SS₄₃	2742 (75)	774 (23)	1219 (24)	749 (29)	100	28	45	27
SS₄₄	2999 (261)	1162 (77)	1323 (101)	514 (83)	100	39	44	17
LP₂₇	2669 (42)	995 (46)	1100 (87)	574 (83)	100	37	41	22

n.d. not determined