Ecosystems (2017) 20: 796–812
DOI: 10.1007/s10021-016-0062-3

ECOSYSTEMS

# Inter-annual Variability of Soil Respiration in Wet Shrublands: Do Plants Modulate Its Sensitivity to Climate?

María T. Domínguez,[1,2]* Andrew R. Smith,[3] Sabine Reinsch,[1] and Bridget A. Emmett[1]

[1]Centre for Ecology and Hydrology Bangor, Natural Environment Research Council, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK; [2]Present address: Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS-CSIC), 10 Reina Mercedes Av, 41012 Seville, Spain; [3]School of Environment, Natural Resources and Geography, Bangor University, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK

## ABSTRACT

Understanding the response of soil respiration to climate variability is critical to formulate realistic predictions of future carbon (C) fluxes under different climate change scenarios. There is growing evidence that the influence of long-term climate variability in C fluxes from terrestrial ecosystems is modulated by adjustments in the aboveground–belowground links. Here, we studied the inter-annual variability in soil respiration from a wet shrubland going through successional change in North Wales (UK) during 13 years. We hypothesised that the decline in plant productivity observed over a decade would result in a decrease in the apparent sensitivity of soil respiration to soil temperature, and that rainfall variability would explain a significant fraction of the inter-annual variability in plant productivity, and consequently, in soil respiration, due to excess-water constraining nutrient availability for plants. As hypothesised, there were parallel decreases between plant productivity and annual and summer $CO_2$ emissions over the 13-year period. Soil temperatures did not follow a similar trend, which resulted in a decline in the apparent sensitivity of soil respiration to soil temperature (apparent $Q_{10}$ values decreased from 9.4 to 2.8). Contrary to our second hypothesis, summer maximum air temperature rather than rainfall was the climate variable with the greatest influence on aboveground biomass and annual cumulative respiration. Since summer air temperature and rainfall were positively associated, the greatest annual respiration values were recorded during years of high rainfall. The results suggest that adjustments in plant productivity might have a critical role in determining the long-term-sensitivity of soil respiration to changing climate conditions.

**Key words:** plant productivity; $Q_{10}$; soil C; climate change; drought; heathland; *Calluna vulgaris*.

## INTRODUCTION

Soil respiration represents a major flux of C to the atmosphere, estimated at 98 Pg C $y^{-1}$ and increasing by 0.1 Pg C $y^{-1}$ in response to a warming climate (Bond-Lamberty and Thomson 2010). Understanding the long-term responses of soil respiration to current fluctuations in climate and plant

---

Received 23 November 2015; accepted 21 August 2016;

**Electronic supplementary material:** The online version of this article (doi:10.1007/s10021-016-0062-3) contains supplementary material, which is available to authorized users.

**Author Contributions** BAE conceived and supervised the experiment. MTD, ARS and SR collected data and contributed to experimental maintenance. MTD led data analysis and wrote the paper. BAE, ARS and SR commented on the manuscript.

*Corresponding author; e-mail: maitedn@irnase.csic.es

productivity is therefore critical to formulate predictions of future C fluxes under the different climate change scenarios. For this purpose, long-term datasets containing climate, vegetation and $CO_2$ flux information are critically needed but generally unavailable due to the limited duration of most of studies.

Inter-annual variability in soil respiration is affected by an array of usually inter-related factors, including air temperature and rainfall, plant phenology and productivity and soil nutrient availability (reviewed in Luo and Zhou 2006). At a global scale, annual soil respiration correlates with mean annual air temperature (Raich and others 2002). However, analysis at the biome level suggests that variations in rainfall rather than in temperature drive the annual variability in soil respiration in many ecosystems, including evergreen broadleaf forests, wooded grasslands and open shrublands, where annual soil respiration positively correlates with rainfall (Raich and others 2002). This has been observed at the plot scale in some warm (tropical and subtropical) and arid ecosystems (Epron and others 2004; Thomas and others 2009; Wang and others 2011), as well as in subalpine forests (Scott-Denton and others 2003) which are seasonally exposed to conditions of low water availability. Often absent in these datasets are those ecosystems exposed to seasonal excess-water conditions, where soil organic matter (SOM) decomposition is constrained due to the low oxygen diffusion into enzymatic reaction sites (Freeman and others 2001). In these excess-water limited ecosystems, the occurrence of drought periods can lead to the release of large amounts of soil C due to the activation of a *biogeochemical cascade* under the increased oxygen availability, which accelerates SOM decomposition (Fenner and Freeman 2011). Here, we present an analysis of the decadal variability of soil respiration in a wet Atlantic shrubland, a typical ecosystem where soil C dynamics and plant productivity are limited by seasonal excess-water conditions.

Despite many studies showing a direct relationship between annual climate and soil respiration, there is growing evidence that the influence of long-term climate variability of C fluxes from terrestrial ecosystems is mediated by adjustments in aboveground–belowground couplings (Stoy and others 2009; Aanderud and others 2011; Shao and others 2014), which suggests that predicting long-term $CO_2$ fluxes from climate variables alone could lead to large inaccuracies (Richardson and others 2007; Stoy and others 2009; Migliavacca and others 2010). The tight coupling between plant photosynthetic activity and soil respiration has been demonstrated by a range of tree-girdling (Högberg and others 2001; Jing and others 2015), canopy clipping and shading experiments (Wan and Luo 2003; Jia and others 2014), which demonstrated that total soil respiration can be highly variable in response to changes in the supply of recently fixed C by plants. Further, several studies have shown that annual plant productivity is the most important factor driving the inter-annual variability of soil respiration over the years across a range of spatial scales, and that the direct effect of plant productivity can overrule the influence of climate (Janssens and others 2001; Reichstein 2003; Irvine and others 2008; Stoy and others 2009).

At seasonal and annual time scales, the links between plant productivity and soil respiration can be particularly tight in those temperate ecosystems with a marked seasonality, where the supply of photosynthates to soil microorganisms by the plant community follows strong seasonal patterns. Indeed, in these ecosystems, the seasonal temperature sensitivity of soil respiration (often indicated as $Q_{10}$ values) reflects the phenological stage of the plant community, which responds to air temperature and drives the patterns of C-fixation and belowground C allocation (Curiel-Yuste and others 2004; Sampson and others 2007; Davidson and Holbrook 2009; Wang and others 2010). Although the intrinsic or ''pure'' temperature sensitivity of ecosystem respiration seems to converge across climatic zones and ecosystem types (Mahecha and others 2010), the apparent temperature sensitivity of ecosystem or soil respiration spans over a much broader range across ecosystems (Davidson and Janssens 2006; Zhou and others 2009; Mahecha and others 2010). This broader range in apparent temperature sensitivity originates from the integration of, for example, plant productivity and soil C pool size on soil respiration, and illustrates the variety and complexity of responses of the respiratory fluxes to temperature depending on site properties. Recently, several works showed that the temperature sensitivity of microbial soil respiration is modulated by the supply of fresh C inputs by plants, with decreases in $Q_{10}$ correlated to a reduction of labile soil C availability (Curiel-Yuste and others 2010; Thiessen and others 2013). Thus, changes in plant productivity over time might play a critical role in the long-term sensitivity of soil respiration to a changing climate.

Wet temperate shrublands are an example of an ecosystem with a marked seasonality, where soil respiration strongly depends on photosynthesis (Larsen and others 2007) and where the intrinsic temperature sensitivity of respiration might be confounded by the effects of plant phenology on soil respiration and by the occurrence of excess-water conditions that limit SOM decomposition. These wet shrublands are often characterised by the presence of organo-mineral soils, which are seasonally exposed to excess-water conditions. In the UK, wet shrublands dominated by *Calluna vulgaris* with organo-mineral soils occupy 1.96 million ha (Hall and others 2014) and have one of the highest soil C densities across habitats (Reynolds and others 2013), with a potential C sequestration capacity that is more than the double of that of peatlands (Quin and others 2015). However, they might be more sensitive to inter-annual variations in rainfall due to the limited capacity of the soil to buffer drying events, in comparison to peatlands. To forecast future $CO_2$ emissions from these ecosystems under the different climate change scenarios, it is critical to analyse the contribution of plant and climate controls to soil respiration.

To address this question, we studied the inter-annual variability in soil respiration from a wet shrubland in North Wales (UK) during 13 years. Previously, we have shown, using a whole-ecosystem climate change experiment, that warming and summer droughts could lead to the destabilisation of large amounts of soil organic C in this shrubland through the stimulation of total soil respiration (Sowerby and others 2010; Domínguez and others 2015). Here, we analysed the response of soil respiration to ambient fluctuations of temperature, rainfall and plant productivity at a decadal time scale. We analysed the evolution of apparent temperature sensitivity of soil respiration and studied the response of this variable to changes in plant productivity. Specifically, our hypotheses were that:

(1) Changes in plant productivity would significantly affect the apparent sensitivity of respiration to soil temperature.
(2) Rainfall variability would explain a significant fraction of the inter-annual variability in plant productivity and consequently, of the inter-annual variability in soil respiration due to excess-water constraints on SOM mineralization and nutrient availability for plants (Emmett and others 2004).

## MATERIALS AND METHODS

### Site Description

The study was carried out near Clocaenog Forest at NE Wales, UK (53°03′19″N, 3°27′55″W), situated at 490 m a.s.l. Mean annual air temperature is 8.2°C and rainfall is 1411 mm (automated weather station located at the site, 2000–2012 period). Inter-annual variations of air temperature and rainfall are strongly influenced by the North Atlantic Oscillation (NAO), with high winter and spring temperatures and high rainfall during years of high (positive) NAO index and vice versa (Ottersen and others 2001). The ecosystem is an upland Atlantic heathland dominated by *C. vulgaris* (L.) Hull (>60% of plant biomass), with *Vaccinium myrtilus* L., *Empetrum nigrum* L. and *Deschampsia flexuosa* (L.) Trin. The ecosystem has remained unmanaged and undisturbed over at least the last 25 years and has moved from a ‘‘mature’’ to ‘‘degenerate’’ phase of heathland succession (Gimingham 1972).

The soil at the site can be classified as Ferric stagnopodzol in the Hafren Series in the Soil Survey of England and Wales (Cranfield University 2014). Organic matter content in the topsoil (0–10 cm) is 89%, with a C:N ratio of 37.4 and a bulk density of 0.09 g $cm^{-3}$. Soils at 18–20 cm (total depth of the soil) have organic matter content of 37% and bulk density of 0.41 g $cm^{-3}$. See (Robinson and others 2016) for further details on soil properties at the site.

### Soil Respiration Measurements

Soil respiration rates ($CO_2$ efflux from soil surface to atmosphere) were measured in three experimental plots of 4 × 5 m, which had a 0.5-m buffer strip around the perimeter (Beier and others 2004). These were the control plots in a field-scale experimental manipulation that aimed to study the vulnerability of the ecosystem to warming and summer drought (Sowerby and others 2010; Domínguez and others 2015). In these control plots no treatment was applied, and thus the plots were under ambient temperature and rainfall conditions. The plots were established in 1999, and soil respiration has been monitored from summer 1999 to date.

Soil respiration results presented here were measured fortnightly between January 2000 and December 2012 within permanent PVC collars of 10 cm diameter, inserted 5 cm into the soil. Three collars per plot were used (a total of 9 collars); these collars did not exclude roots and therefore measurements of $CO_2$ efflux included both heterotrophic respiration from soil microorganisms, as well as autotrophic respiration from roots within the collars. Measurements were taken in the afternoon, between 12:00 and 15:00, using portable infrared gas analysers (EGM-2, PP Systems until 2008 and LI-8100 automated soil $CO_2$ flux system onwards) coupled to soil respiration chambers. Due to technical limitations, during 2005 measurements were restricted to the spring and summer seasons.

## Abiotic Variables

Meteorological conditions (air temperature and humidity, rainfall and wind speed) have been monitored by an automated weather station located at the site, with hourly recordings, starting in 1999 to date. Data collection was incomplete during 2006 and 2007 due to technical problems, and climate data for missing dates were gathered from the Alwen Dam MET station, located 6 km away from our experimental site (Met Office 2012). Monthly NAO index values, representing the difference between the normalised sea level pressure over Gibraltar and the normalised sea level pressure over Southwest Iceland (Jones and others 1997), were gathered from a public data repository (http://www.cru.uea.ac.uk/cru/data/nao/).

At the plot level, soil temperature was continuously measured at 5 cm soil depth by Reference Thermistor sensors (Probe 107, Campbell Scientific, Logan, UT, USA). Due to technical problems, the soil temperature dataset for 2001, 2007 and 2008 was incomplete. Soil moisture (0–10 cm depth) was measured at every routine visit to the site using a theta probe (ML-2, Delta-T, Cambridge, UK) and a soil moisture meter (HH2, Delta-T) until 2009. In 2009, TDR probes (CS616, Campbell Scientific, Logan, UT, USA) were inserted into the soil at 5 cm for a continuous monitoring of soil moisture (hourly recordings).

## Vegetation Data

Plant community composition and biomass were monitored most years, excepting 2004–2006, at the end of the growing season using the pin-point method. In each plot three permanent 0.5 × 0.5 $m^2$ subplots were established and a grid of 100 pins was lowered through the vegetation. Every touch of vegetation was recorded to the nearest 1 cm indicating the species, the plant part (leaf, flower, or stem) and its status (green, dry, dead). Calibration between pin-point measurements and plant biomass was conducted using a destructive sampling outside the experimental plots in 2000, and relationships between pin-point measurements and plant biomass were established for each plant species.

All datasets are available from CEH́s Environmental Information Platform (https://eip.ceh.ac.uk/). See Supplementary Material for links to archived data.

## Data analysis

For each date, we calculated the number of growing-degree days (GDD) from air temperature data, according to Roltsch and others (1999): $GDD_i = (T_{max_i} + T_{min_i})/2 - T_{low}$, where $T_{max}$ and $T_{min}$ are the maximum and minimum air temperatures for each single day *i*, respectively, and $T_{low}$ is the lower threshold temperature for plant growth, which was set to 5°C (Beier and others 2004). Upper threshold temperature for growth ($T_{high}$) was set to 25°C. $GDD_i$ was set to zero, if $GDD_i < 1$ or if $GDD_i > (T_{high} - T_{low})$.

Annual and seasonal cumulative $CO_2$ emissions were calculated assuming that the routine measurements taken in the afternoon represented the daily maximum rate of $CO_2$ efflux, as described in (Domínguez and others 2015). Based on a diurnal study conducted in 2002, we calculated the daily average respiration rates as 87% of that maximum. Then, average seasonal rates were calculated, and finally the seasonal cumulative $CO_2$ emissions were obtained by multiplying the seasonal rates by the number of days in each season. Annual emissions were calculated as the sum of all the seasonal emissions. Spring, summer, autumn and winter seasons correspond to March–May, June–August, September–November and December–February, respectively.

The apparent temperature sensitivity of soil respiration was assessed for each year using two models (excluding 2005 due to limited respiration data available, and 2007 and 2008 due to incomplete soil temperature datasets). In the first model, respiration data was fitted against soil temperature (at 5 cm depth) using an exponential function: $SR = ae^{bT}$, where SR is soil respiration, T is soil temperature, and *a* and *b* are fitted constants. $Q_{10}$ values were calculated as: $Q_{10} = e^{10b}$ (Suseela and others 2012).

In the second model, the square root of the respiration data was fitted against soil temperature using a lineal relationship: $SR^{1/2} = a(T - T_{min})$, where SR is soil respiration, *a* is a fitted constant, *T* is soil temperature, and $T_{min}$ is the apparent minimum temperature for microbial activity (Ratkowsky and others 1982). This "square-root model" is frequently used to describe microbial activity below the optimum temperature for growth, and it better describes the sensitivity of heterotrophic respiration when the temperature range is below 25°C, in comparison to the Arrhenius equation (Pietikäinen and others 2005). $T_{min}$ can be calculated from the slope and intercept of the models; this parameter is frequently used to compare the capacity to grow at low temperatures across different microbial communities (Pietikäinen and others 2005; Rinnan and others 2009, 2011).

We applied additive mixed models to analyse whether climate and soil moisture, temperature and respiration rates followed any significant time trend over the 13-year period, using the mgcv package in R 3.2.3. Each time series was modelled as a function of two smoothing factors as fixed terms. The first term, accounting for annual cycles, was a function of the Julian day of each measurement and used cyclic penalised cubic regression spline smooth. The second term, accounting for possible decadal time trends, was a function of the cumulative number of days since the date of the first measurement in each series (January 2000), using thin-plate regression spline or cubic regression spline smooths. We followed the recommendations by (Zuur and others 2009) to account for the proper temporal autocorrelation structure. First, we fitted a model without autocorrelation structure, using restricted maximum likelihood. This model was compared against different alternative models which considered different autocorrelation structures (compound symmetry, continuous autocorrelation structure of order 1, moving average correlations of different orders, spherical and exponential correlation). The optimal model was selected based on Akaike Information Criteria (AIC). Validation of the selected model included graphical examination of normalised residuals to check for homogeneity and independency. For soil moisture, the 2000–2008 and the 2009–2012 periods were analysed separately, due to the different periodicity of measurements in each dataset. Details of the selected models for each time series are given in Supplementary Material, Table S1.

The relationships among climate and vegetation variables were first explored using bivariate scatterplots and principal component analyses (PCA). As many climate variables were mutually correlated, we selected some key variables to be used as predictors for soil $CO_2$ emissions, based on the three first factors extracted by a PCA analysis of climate data. Selected variables include (1) average of summer daily maximum air temperatures (highly correlated with annual and spring maximum temperatures, and winter minimum air temperatures), (2) spring minimum air temperature and (3) summer rainfall (used as an index of rainfall variability, significantly related to annual and spring rainfall). Likewise, vegetation information was reduced to the total aboveground biomass and the abundance of C-fixing (photosynthetically active) biomass of the dominant plant species (*C. vulgaris*), as a surrogate for productivity of the plant community. This variable was highly correlated with bryophyte biomass.

A PCA was then applied to the selected climate and vegetation variables together with annual soil respiration, summer average soil temperature and summer average soil moisture to explore the patterns of covariation among climate, vegetation and respiration. To assess the influence of the selected climate predictors (summer maximum air temperatures, spring minimum temperatures and summer rainfall) on summer and annual $CO_2$ emissions, we applied linear mixed models, using the nlme package in R 3.2.3. First, we fitted a model that included the three climate predictors as fixed terms without any temporal autocorrelation structure, using restricted maximum likelihood. This model was compared against different alternative models which considered different autocorrelation structures, in which the year of measurement was included as a repeated measures factor. The model with the best autocorrelation structure was selected based on AIC. Then, we evaluated the optimal structure of the fixed terms, by applying a sequential backwards deletion of the fixed terms included in this model, using the maximum likelihood as fit method. The optimal model was selected based on AIC and refitted using restricted maximum likelihood. Model validation included graphical examination of normalised residuals to check for homogeneity and normality. We verified the independency of predictors included in the final model (variance inflation factor $< 2$).

Similarly, linear mixed models that considered the temporal autocorrelation of vegetation and respiration measurements over the years were applied to check for significant relationships between the number of GDDs in each summer season and the plant productivity variables (total aboveground biomass and *C. vulgaris* C-fixing biomass), as well as to study the relationships between $CO_2$ emissions, apparent sensitivity of soil respiration to soil temperature and plant productivity.

## RESULTS

### Climate and Vegetation Variability

Over the 13 years, some climate variables followed a significant time trend. The additive mixed model for average daily temperatures explained a 70% of the variance, decomposing air temperature time series into seasonal cycle and long-term trend (Figure 1 a, b; Table S1). The smooth function for the long-term trend revealed an upward pattern in air temperatures between 2004 and 2006 (1000–2200 days after the start of the study), followed by a downward trend between 2006 and 2012 (Figure 1b). This decline was more evident for maximum summer air temperatures, which decreased between 2006 and 2012 following the downward trend of the NAO over that period (lower summer NAO index values, in comparison to the 2000–2005 period, Figure 2a). The additive mixed model for daily rainfall explained a very limited proportion of its variance (4%, Table S1), but suggested some downward trend between 2000 and 2006 (Figure 1d). This trend was more evident when cumulative winter rainfall for each year was calculated (Figure 2b).

The fitted additive mixed model for soil temperature (0–5 cm) explained an 86% of its variance and revealed a strong seasonal pattern, with maximum temperatures reached by mid-August (Figure 3a, b, Table S1). Summer and winter inter-annual averages were 11.1 and 3.4°C, respectively (Figure 3a). Temperatures were particularly low during the winters of 2001, 2010 and 2011, when they remained below 2°C. In agreement with the records of air temperatures, an upward trend in soil temperature was observed between 2004 and 2006 (1000–2200 days after the start of the study, Figure 3c). However, the downward trend detected for air temperature between 2006 and 2012 was not observed for soil temperature. Soil moisture seasonal variation was much more irregular than that of soil temperature (Figure 3d). Soils were particularly wet in winter 2000 and 2010. The lowest moisture records ($< 0.2$ m$^3$ m$^{-3}$) were observed in summer 2006. Since 2010 seasonal differences decreased, soils being wetter during the summer. The fitted additive models did not perform well at describing seasonal or long-term trends in soil moisture, in particular for the 2008–2012 period (Table S1).

Aboveground biomass showed a 14% inter-annual variability (average ± standard deviation of 3.4 ± 0.48 kg m$^{-2}$), which was closely linked to the variability in summer minimum and maximum temperatures, indicated by the number of growing-degree days (Figure 4a, Table S2). Consequently, there was a trend for a reduction in total aboveground biomass at the site between 2006 and 2012. Likewise, the productivity of the plant community, measured by the abundance of C-fixing biomass of

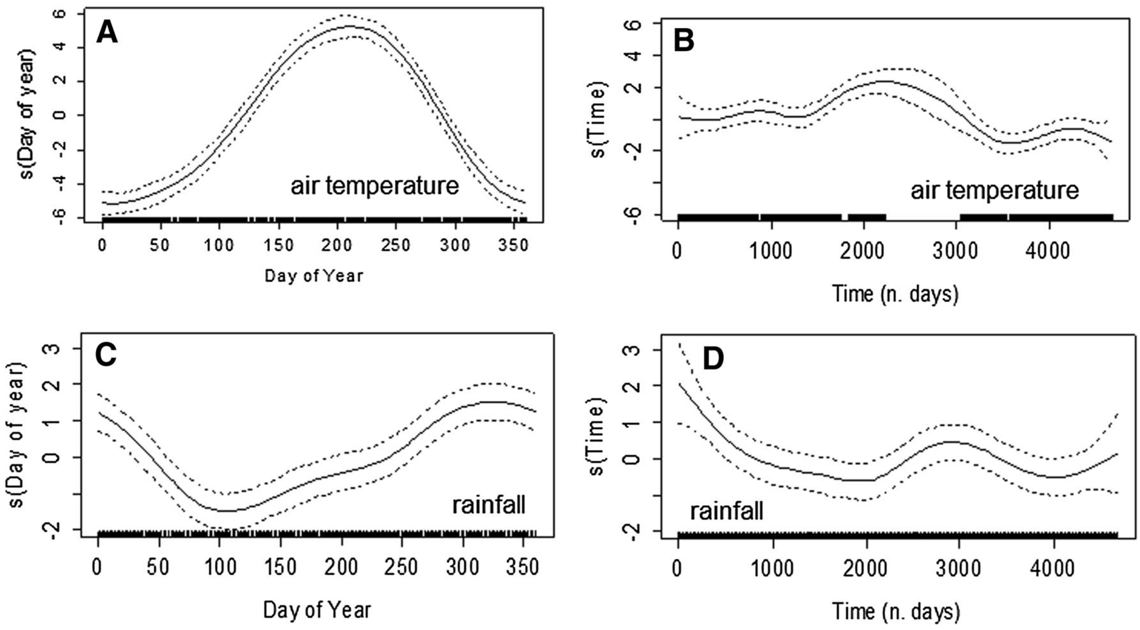

**Figure 1.** Smooth functions resulting from the application of additive mixed models to air temperature and rainfall time series. Each time series was modelled as a function of two smoothing terms. The first term, accounting for annual cycles, was a function of the Julian day of each measurement (**a**, **c**) and used cyclic penalized cubic regression spline smooth. The second term, accounting for possible decadal time trends, was a function of the cumulative number of days since the date of the first measurement (January 2000), using plate regression spline or cubic regression spline smooths (**b**, **d**). See Table S1 for a summary of model results.

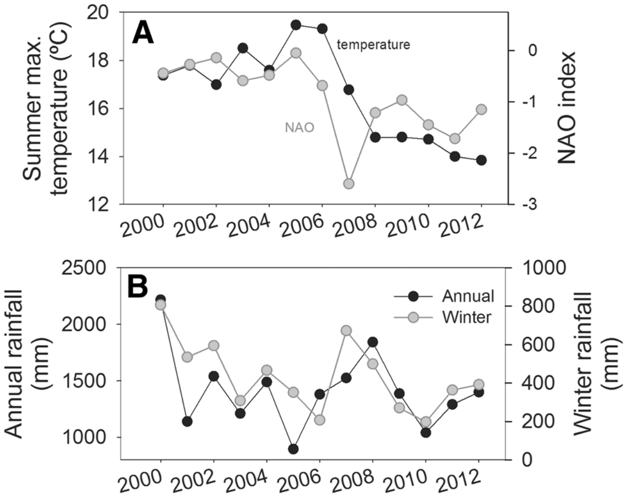

**Figure 2.** **a** Variation in summer air temperatures (average of daily maximum values) and the North Atlantic Oscillation Index (NAO index) of the summer seasons for the 2000–2012 period. Annual and winter rainfall is also shown (**b**).

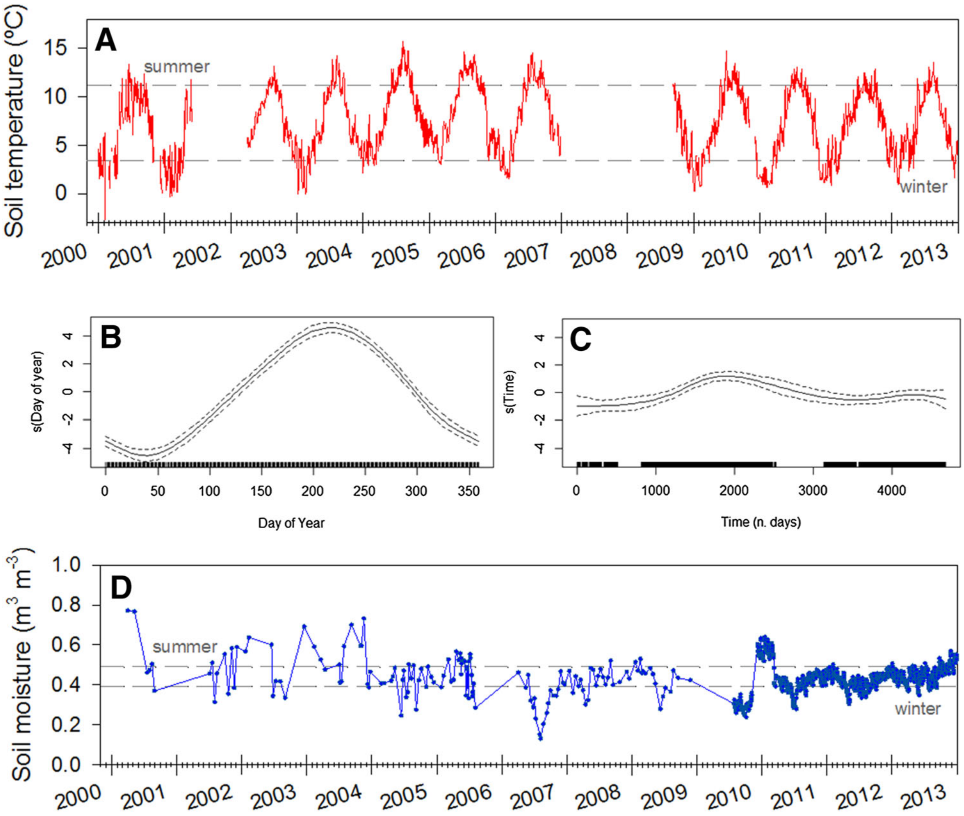

**Figure 3.** **a** Soil temperature over the course of the study (0–5 cm soil depth, daily average, mean of three plots). Inter-annual winter and summer average values are indicated for reference. **b**, **c** Smooth functions resulting from the application of an additive mixed model to soil temperature time series. The first smoother (**b**), accounting for annual cycles, was a function of the Julian day of each measurement and used cyclic penalized cubic regression spline smooth. The second smoother (**c**), accounting for possible decadal time trends, was a function of the cumulative number of days since the date of the first measurement (January 2000), using cubic regression spline smooth. See Table S1 for a summary of model results. **d** Soil moisture over the course of the study (0–5 cm soil depth, mean of three plots).

dominant *C. vulgaris*, was significantly related to summer air temperatures (Figure 4b, Table S2). When this index was expressed in terms of deviation from the inter-annual average, a clear pattern of decreased plant productivity at the site was observed over the studied decade, in particular be-

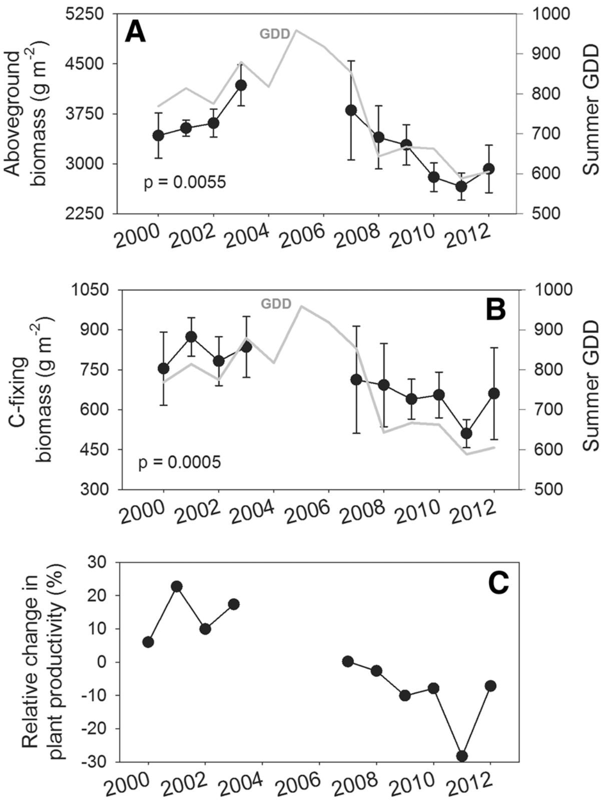

**Figure 4.** **a** Aboveground biomass of the plant community over the 2000–2012 period (symbols, mean ± standard error, *left* axis) and number of growing-degree days (GDD) during the summer seasons (*grey line*, *right* axis). **b** C-fixing biomass of the dominant plant species (*Calluna vulgaris*) over the studied period (symbols, mean ± standard error, *left* axis) and number of growing-degree days (GDD) during the summer seasons (*grey line*, *right* axis). In both graphs, *p* values correspond to the linear positive relationship between total aboveground plant biomass or *C. vulgaris* C-fixing biomass, and summer season cumulative Growing-Degree-Days (GDD). These linear mixed models included an autocorrelation structure term to account for repeated measures of plant productivity on the same plots over the 13-year period (autoregressive order 1 for total biomass; plot identity as random factor for *C.vulgaris* C-fixing biomass). See Table S2 for a summary of model results. **c** Relative changes in *C. vulgaris* C-fixing biomass (index of plant productivity) over the 2000–2012 period (percentage of change from inter-annual average). C-fixing biomass estimated by pin-point calibration, from the number of hits of green *C. vulgaris* leaves.

tween 2006 and 2011 when productivity decreased by a 30% (Figure 4c).

## Soil Respiration Variability

Soil respiration in this shrubland followed a strong seasonal pattern, with winter rates usually lower than 50 mg C m$^{-2}$ h$^{-1}$ and peaks of greater than 200 mg C m$^{-2}$ h$^{-1}$ during the summer months (June, July and August) coinciding with the maximum plant phenological development (Figure 5a, b). The fitted additive model revealed a clear downward trend in soil respiration rates over the 13-year period (Figure 5c, Table S1). Consequently, there was a decline in annual emissions, ranging from 904 g C m$^{-2}$ in 2000 to 275 g C m$^{-2}$ in 2011, with an average of 490 g C m$^{-2}$ for the 2000–2012 period and a 42% inter-annual variability (Figure 5c). Summer and autumn respiration accounted for 42 and 29% of annual $CO_2$ emissions, respectively, while spring and winter respiration only represented 18 and 13% of annual respiration, respectively. The downward trend in annual cumulative respiration was caused by strong declines in spring, summer and autumn respiration rates (Figure 6). The decline in summer respiration was remarkable, being reduced by more than 50% between 2000 and 2012. This change occurred without a concurrent decrease in average soil temperatures during the summer season (Figure 6), which resulted in a decline in *apparent* temperature sensitivity, indicated by the $Q_{10}$ values (Figure 7a). The two models used to describe apparent temperature sensitivity (the $Q_{10}$ and the ‘‘square-root model'') gave similar results, explaining similar percentages of the annual variance of the soil respiration rates and showing similar decreases in apparent temperature sensitivity over time. We therefore used the $Q_{10}$ model for all further analysis.

For those years for which the comparison between plant biomass and temperature sensitivity of soil respiration was possible (8 out of 13 years), we found that *apparent* temperature sensitivity was positively related to aboveground plant biomass (Figure 7b, Table S3). Maximum *apparent* temperature sensitivity ($Q_{10} > 9$) was recorded during the first studied years, when aboveground biomass was greater than 4 kg m$^{-2}$.

## Influence of Climate on Soil Respiration

In the multivariate analysis, summer maximum air temperatures and the abundance of *C. vulgaris* C-fixing biomass were closely associated to annual cumulative soil respiration (Figure 8). Interestingly, annual respiration was decoupled from average summer soil temperature. Instead, there was a trend for a positive association between summer soil moisture and annual respiration (Figure 8).

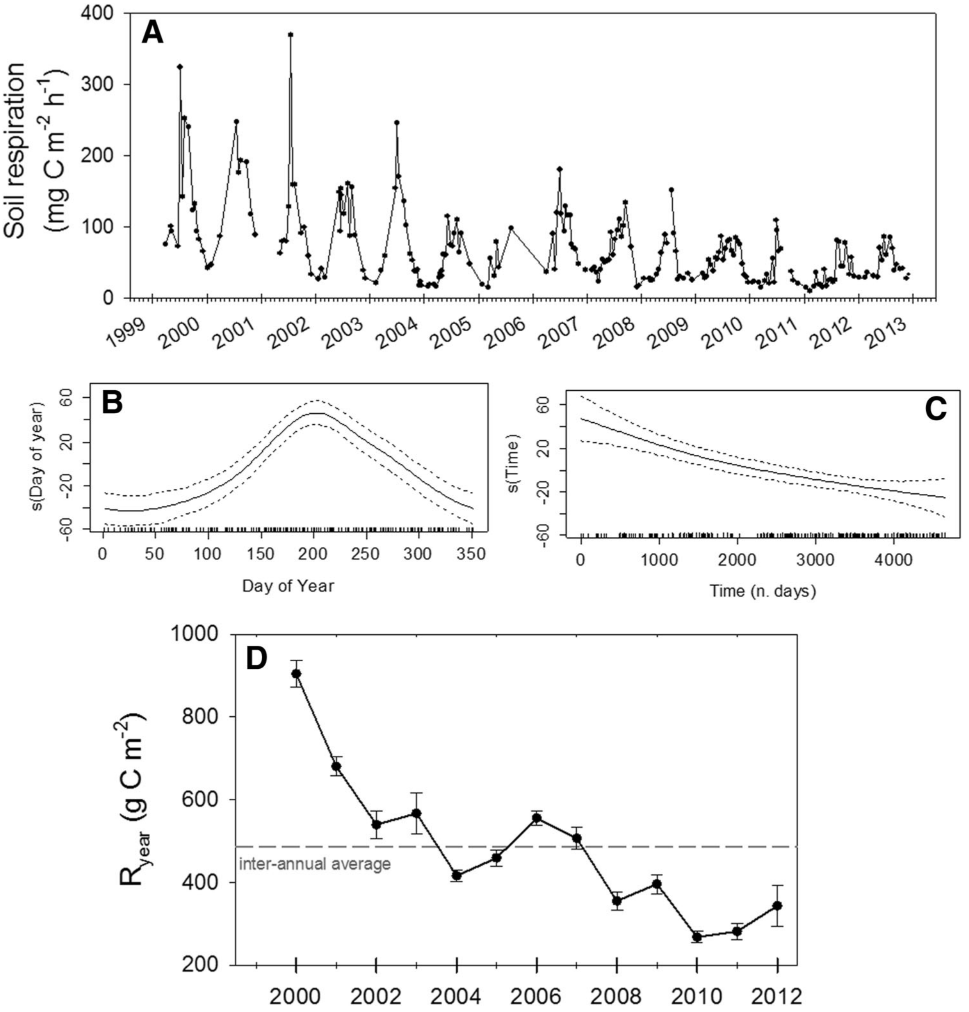

**Figure 5. a** Soil respiration rates (average of the three experimental plots for each date, $N = 3$ per plot). **b, c** Smooth functions resulting from the application of an additive mixed model to soil respiration time series. The first smoother, accounting for annual cycles (**b**), was a function of the Julian day of each measurement and used cyclic penalized cubic regression spline smooth. The second smoother (**c**), accounting for possible decadal time trends, was a function of the cumulative number of days since the date of the first measurement (January 2000), using thin-plate regression spline smooth. See Table S1 for a summary of model results. **d** Cumulative annual soil respiration ($R_{year}$, mean ± standard error for three plots) for the 2000–2012 period. Inter-annual average is indicated.

Table 1 shows the results of the mixed models applied to summer and annual cumulative $CO_2$ emissions, with a selection of climate variables (summer maximum temperatures and rainfall, and spring minimum temperatures) as predictors. For both summer and annual emissions, the model with the highest empirical support (lowest AIC) included summer maximum temperatures as the only fixed factor, and a spherical temporal autocorrelation structure. The graphical examination of the response of annual respiration to summer temperatures suggested a non-linear pattern, with a peak in annual cumulative respiration when the average of daily maximum temperatures during the summer season was around 18°C and slight decreases during warmer years (Figure 9b). Therefore, we fitted a non-linear additive mixed model, using a smooth function of summer temperatures as predictor for annual cumulative respiration. This model was significant, but had slightly lower empirical support (higher AIC) than the linear mixed model (data not shown).

In contrast to one of our initial hypotheses, no pattern of covariation between seasonal or annual respiration and rainfall was detected, neither between plant productivity and rainfall (data not shown). No significant relationship was observed between average soil temperature during the

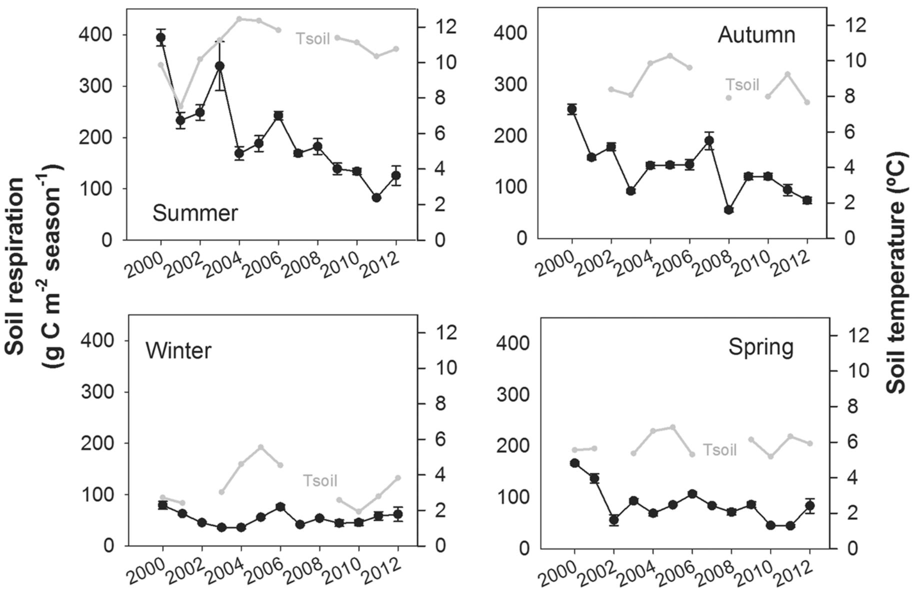

**Figure 6.** Seasonal soil respiration rates for the 2000–2012 period (mean ± standard error). Average soil temperatures (0–5 cm depth) during the seasons are also shown (*grey line, right axis*).

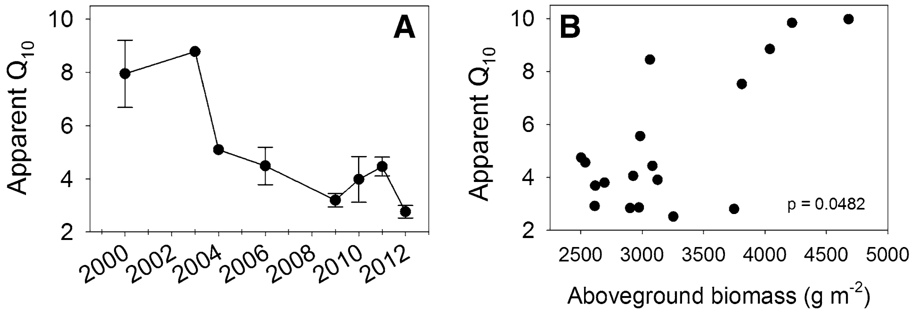

**Figure 7.** **a** *Apparent* sensitivity of soil respiration to soil temperature (indicated by *apparent* $Q_{10}$ values) over the study period (average ± standard error of the three experimental plots for each year). **b** Relationship between *apparent* temperature sensitivity and aboveground plant biomass (individual plots). *p* value corresponds to the linear positive relationship between apparent temperature sensitivity and total aboveground plant biomass. This linear mixed model included an autocorrelation structure term to account for repeated measures of plant productivity on the same plots over the 13-year period (spherical autocorrelation). See Table S3 for a summary of model results. Soil temperature ranged from 1.2 to 15.6°C.

summer season and summer or annual cumulative respiration (data not shown).

As plant productivity was significantly related to summer air temperatures, summer soil respiration was also associated with aboveground plant biomass, although this relationship was marginally significant ($p = 0.059$, Table 2). The relationship between plant biomass and annual respiration was non-significant (Table 2).

## DISCUSSION

Wet shrublands dominated by *Calluna vulgaris* have a high potential capacity for C sequestration (Quin and others 2015). In our studied wet shrubland, experimental climate manipulations have shown that soil respiration in this type of ecosystem has a particular sensitivity to warming and recurrent summer droughts, which does not attenuate, but instead increases at decadal time scales (Domínguez and others 2015), suggesting that the current predictions of climate change might result in the release of a significant amount of the organic C stored in the soil in these ecosystems. Long-term datasets covering periods of inter-annual variability in climate and plant productivity are needed to understand the drivers of soil respiration in these ecosystems and to improve the predictions of potential soil C losses under the projected climate change scenarios. Our work provides unique information about the response of soil respiration to climate fluctuations in these ecosystems.

Annual fluxes of $CO_2$ from the soil to the atmosphere ranged from 904 to 275 g C $m^{-2}$, with an average of 490 g C $m^{-2}$ for the 2000–2012 period, and 45% inter-annual variability. This inter-annual average is equivalent to 13.5% of the organic C stored in the top 5 cm of the soil at our site (estimated at 3.6 kg C $m^{-2}$). This value agrees with other studies of $CO_2$ fluxes in shrubland ecosystems across Europe, estimating that annual soil respiration represents 3–12% of the soil organic C pool (Beier and others 2009). The relatively high losses of C to the atmosphere through soil respiration are related to the size of the soil organic C pool; organo-mineral soils in these wet shrublands contain large organic C stocks, much of which becomes accessible to soil microbes under appropriate temperature and moisture conditions, which leads to high rates of heterotrophic respiration (Beier and others 2009). In addition, in wet (hydric) shrublands the relative belowground C allocation is by far greater than in mesic and dry (xeric) shrublands (Beier and others 2009), which results in high root respiration rates. In spite of the size of the respiration fluxes, wet *C. vulgaris* shrublands are net C sinks, sequestering between 1.26 and 3.50 t C $ha^{-1}$ $y^{-1}$ (Beier and others 2009; Quin and others 2015), although the recurrence of extreme climate events such as summer droughts may turn these ecosystems into C sources (Sowerby and others 2010).

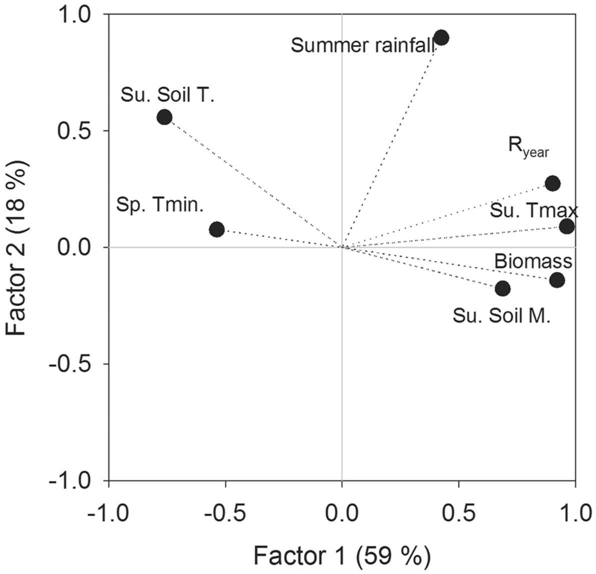

**Figure 8.** Result of a principal components analysis applied to the inter-annual variations of annual soil respiration ($R_{year}$) and a selection of climate and vegetation variables. The percentage of variance explained by each factor is indicated in their axes. Biomass: abundance of C-fixing biomass of the dominant plant species in the community (*C. vulgaris*), as an index of plant productivity; *Su.* $T_{max}$ average of daily maximum air temperatures during the summer season. *Su. Soil M* average soil moisture during the summer season, *Su. Soil T* average soil temperature during the summer season, *Sp.* $T_{min}$ average of daily minimum air temperatures during the spring season.

## Influence of Climate on Soil Respiration

Over the studied period air temperature was determined by a large-scale climatic pattern, the NAO. Inter-annual variability of soil respiration (both annual and summer emissions) was significantly related to summer air temperatures, and therefore summer and annual emissions declined markedly between 2006 and 2012 coinciding with a downward trend of the NAO. However, the parallel decreases in annual respiration and plant productivity (Figures 4c, 5d), the positive association between plant biomass and the apparent sensitivity of soil respiration to soil temperature (Figure 7b) and the decoupling between summer or annual cumulative respiration and average summer soil temperature over the studied period (Figures 6 and 8) suggest that the climate effect on soil respiration could be mediated by the back-

**Table 1.** Results of the Selected Linear Mixed Models Applied to Summer and Annual Cumulative $CO_2$ Emissions as Response Variables, and a Selection of Climate Variables as Predictors

| Response variable | AIC | ΔAIC | Intercept | Predictors | Estimated parameter | St. error | *t* value | *p* value |
|---|---|---|---|---|---|---|---|---|
| Summer $CO_2$ emissions | 405.5 | −9.12 | −392.08 | Summer Tmax. | 36.56 | 9.44 | 3.87 | 0.0004 |
| Annual $CO_2$ emmisions | 466.5 | −8.92 | −274.88 | Summer Tmax. | 43.47 | 12.58 | 3.45 | 0.0015 |

*Both models included a spherical autocorrelation structure term to account for temporal autocorrelation. The model for summer emissions also included a variance covariate term (dependent on summer maximum temperatures), needed to improve the structure of model residuals. The increase in goodness of fit (decrease in AIC values) from null models (which assume no influence of any climate predictors on summer or annual emissions) is indicated. Summer Tmax: average of daily maximum air temperatures during the summer season.*

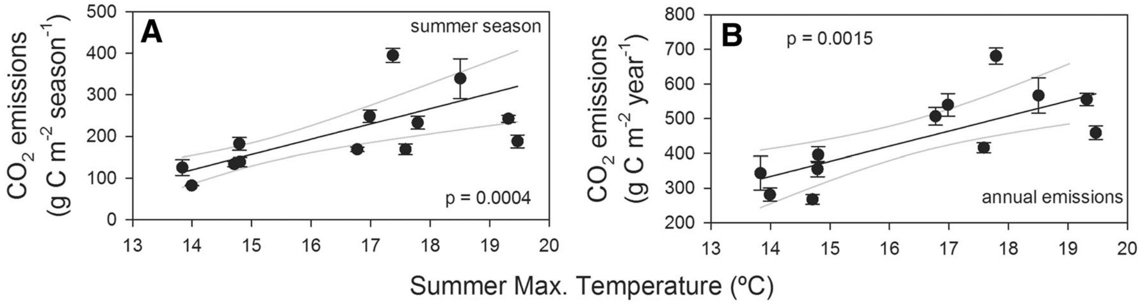

**Figure 9.** Summer (**a**) and annual (**b**) cumulative respiration predicted by the linear mixed models applied to $CO_2$ emissions, with average of summer daily maximum temperatures as climate predictor (*black lines*). 95% confidence intervals (*grey lines*) and *p* values are also shown. These linear mixed models included an autocorrelation structure term to account for repeated measures of soil respiration on the same plots over the 13-year period (spherical autocorrelation). See Table 1 for a summary of model results. Measured summer and annual cumulative respiration is also shown (symbols, average ± standard error of the three experimental plots for each year).

**Table 2.** Results of the Linear Mixed Models Applied to Summer and Annual Cumulative $CO_2$ Emissions as Response Variables, and Aboveground Plant Biomass as Predictor

| Response variable | AIC | ΔAIC | Intercept | Predictor | Estimated parameter | St. error | *t* value | *p* value |
|---|---|---|---|---|---|---|---|---|
| Summer $CO_2$ emissions | 303.87 | -1.21 | 63.85 | Aboveground biomass | 0.038 | 0.019 | 1.97 | 0.0592 |
| Annual $CO_2$ emmisions | 325.68 | 0.62 | 286.62 | Aboveground biomass | 0.043 | 0.027 | 1.64 | 0.114 |

*Both models included a spherical autocorrelation structure term to account for temporal autocorrelation. The increase in goodness of fit (decrease in AIC values) from null models (which assume no influence of plant biomass on summer or annual emissions) is indicated.*

ground relationship between climate and plant productivity.

In temperate *C. vulgaris* shrublands, soil and ecosystem respirations depend strongly on photosynthesis (Larsen and others 2007). Root respiration is coupled with photosynthetic activity (Kuzyakov and Gavrichkova 2010), and because heterotrophic microbes may preferably use short-lived C pools (Trumbore 2000), heterotrophic respiration also depends primarily on plant inputs. (Högberg and others 2001; Irvine and others 2005; Knohl and others 2005) and therefore, indirectly on site productivity. Thus, plant productivity might have a critical role in determining the impact of a changing climate on soil respiration from these wet shrublands. Our results agree with recent findings that suggest that ecosystem respiration and net ecosystem exchange strongly respond to environmental variability at short (daily, weekly) time scales, whereas at longer (annual, decadal) time scales, the biological responses to climate variability or ecosystem development (such as changes in plant productivity or functional diversity, and variations in the soil C pools), rather than the climate variability *per se,* determine the C fluxes (Richardson and others 2007; Stoy and others 2009; Mahecha and others 2010; Marcolla and others 2011; Delpierre and others 2012; Shao and others 2014; Knapp and others 2015). In any case, our study is merely observational, and therefore the observed relationships between plant productivity and respiration might not be causal. Further experimental work (for instance, simultaneous manipulations of air temperatures and plant productivity in a factorial design) would be needed to confirm the role of plant productivity in the response of soil respiration to climate variability at our site.

Annual emissions reached their maximum when average maximum summer temperature was around 18°C, with slight decreases at warmer temperatures. Those years with summer maximum temperatures above 18°C (2003, 2005 and 2006) were anomalous hot years, particularly 2003 when the heat and drought caused a Europe-wide reduction in primary productivity (Ciais and others 2005). Instead, the studied wet shrubland responded to the heat and drought of 2003 with an increase in biomass and a decrease in litterfall (Peñuelas and others 2007). Given the common positive relationship between litter accumulation and soil respiration (Maier and Kress 2000; Sulzman and others 2005; Liu and others 2009), the slight decrease in soil respiration might be caused by a reduction in litter accumulation during the warmest years. Soil moisture limitation during these warm years is not likely to be the reason for this pattern, as experimental manipulation of rainfall in this ecosystem has shown that the reduction of soil moisture enhances respiration and that the stimulation of respiration can be sustained with soil moisture reductions as high as 30% (Domínguez and others 2015).

In contrast to one of our initial hypotheses, we found no pattern of covariation between annual or seasonal rainfall and respiration, despite our experimental manipulation of rainfall showed that summer drought clearly stimulates respiration, with the heterotrophic component likely being more responsive to drought (Sowerby and others 2008; Domínguez and others 2015). As climate at our site is determined by the NAO, high winter/spring temperatures and high rainfall values are associated during years of high (positive) NAO index and vice versa. Therefore, maximum values of annual soil respiration were recorded during years of high precipitation (Figure 8), leading to an apparent disagreement with the results from the experimental climate manipulations at our site, which considered air temperature and rainfall as separate factors. Interestingly, there was a decoupling between average summer soil temperatures and summer soil $CO_2$ emissions. It is likely that during the warm and wet summers, the high soil water content had a thermal buffering effect, soils being less exposed to fluctuations in air temperature. Indeed, soil drying in wet organic soils increases the sensitivity of SOM decomposition to air temperature and intensifies the losses of soil organic C during drying events (Ise and others 2008). The frequent positive association between summer temperatures and rainfall at our site might prevent greater losses of soil C through respiration during the summer seasons.

## Plant Productivity and Apparent Temperature Sensitivity

Annual apparent $Q_{10}$ values were high, considerably above the range of mean apparent $Q_{10}$ for different biomes (1.43–2.03, Zhou and others 2009). These high $Q_{10}$ values are typical for high latitude (Zhou and others 2009) and other ecosystems with a marked seasonality, where the $Q_{10}$ reflects the response of soil respiration to the phenological stage of the plant community, which drives the supply of recently assimilated C compounds to roots and soil microbes (Curiel-Yuste and others 2004; Davidson and Holbrook 2009; Wang and others 2010). Our soil respiration measurements included autotrophic root respiration and therefore seasonal soil respiration rates were strongly influenced by seasonality and plant activity, which confound the ‘‘pure’’ or intrinsic temperature response of microbial respiration. High apparent $Q_{10}$ values may also be indicative of the large contribution of the autotrophic component to soil respiration (Wei and others 2010), which might be due to the relatively high partitioning of biomass into the root system in hydric *C. vulgaris* shrublands, in comparison to other mesic and xeric shrublands (Beier and others 2009).

Over the duration of the study, there was a decline in the apparent sensitivity of soil respiration to temperature, which was significantly related to the decrease in the standing aboveground biomass (Figure 7). The observed decrease in plant productivity might result in a decline in soil respiration due to a reduction, not only in the autotrophic fraction, but also in the heterotrophic component, as discussed above. Our results suggest that the supply of labile C substrates by plant roots might play a key role in regulating the sensitivity of the soil C efflux to soil temperature. This idea is supported by recent experimental works showing that the temperature sensitivity of microbial respiration is modulated by the supply of labile C substrates, with decreases in $Q_{10}$ values under a shortage of fresh C inputs by plants (Curiel-Yuste and others 2010; Thiessen and others 2013) and increases in the $Q_{10}$ of SOM decomposition by rhizophere priming effects (Zhu and Cheng 2011). Some theoretical models and soil incubation studies have shown that the mineralization of chemically recalcitrant or structurally complex substrates have a higher $Q_{10}$ than the mineralization of more labile substrates (Knorr and others 2005; Fierer and others 2006), and therefore we could have expected an increase in temperature sensitivity as the relative abundance of labile, plant-derived C inputs to soil decreases. However, under field conditions, the complexity of the processes involved in SOM decomposition often results in deviations from these theoretical models (Davidson and Janssens 2006). Fresh plant C inputs have been shown to stimulate the mineralization of more complex, recalcitrant organic C pools through microbial priming (Bader and Cheng 2007; Dijkstra and Cheng 2007; Fontaine and others 2007; Zhu and Cheng 2011; Thiessen and others 2013). Thus, it is necessary to consider not only the relative sizes of C pools of varying recalcitrance, but also how they interact to fully understand the response of SOM decomposition to temperature (Kirschbaum 2004; Knorr and others 2005).

In addition to the observed decline in maximum summer temperatures between 2006 and 2012, which was linked to a decline in plant productivity, the process of ageing of the plant community could also partly explain the decrease in site productivity over the 13 years and consequently, the decline in apparent temperature sensitivity and annual soil respiration. Our studied shrubland has remained unmanaged and undisturbed over at least the last 25 years and has moved from a ''mature'' to ''degenerate'' phase of heathland succession, as described by Gimingham (1972). Management of *C. vulgaris* heathlands usually includes grazing and periodical burning and cutting, to maintain a mosaic landscape comprised of *C. vulgaris* at multiple life stages. These management disturbance regimes are used to maintain a healthy stand for recreational purposes resulting in higher productivity than in mature or degenerate stands. The interruption of these practices has a pronounced impact on the ecosystem C balance over time (Quin and others 2015). In mesic heathlands, the proportion of autotrophic respiration decreases as the ecosystem ages (Kopittke and others 2013), which could partly explain the observed reduction in apparent temperature sensitivity over the years, given the positive relationship between the relative contribution of autotrophic respiration to soil C efflux and apparent temperature sensitivity, detected at global scales for forest ecosystems (Wei and others 2010). Similar reductions in temperature sensitivity during secondary succession have been observed in other ecosystems (Tang and others 2006; Yan and others 2009).

## CONCLUSIONS

Our work showed that annual soil $CO_2$ emissions and plant productivity from wet shrublands are highly variable in a decadal time scale, and that they are tightly coupled to summer air temperatures, with a limited influence of rainfall variability on these variables. The decoupling between summer soil temperature and respiration inter-annual variabilities, the parallel declines in soil respiration and plant productivity and the positive association between plant productivity and the apparent sensitivity of soil respiration to soil temperature suggest that the effect of summer temperatures on soil $CO_2$ efflux is mediated by a strong control of plant productivity on soil respiration. As plant productivity does not depend only on climate conditions, but also on other ecological factors (such as land management, stage during the processes of ecosystem development or secondary succession), it seems essential to consider some measurements of plant productivity to understand long-term variability in soil $CO_2$ emissions. Further experimental work, however, would be needed to confirm whether plant productivity has such key role in the response of soil respiration to climate variability, as suggested by our observational study.

## ACKNOWLEDGEMENTS

We thank all the CEH staff members who have contributed to the experiment establishment and maintenance over the years, in particular Alwyn Sowerby and David Williams. This research was funded by the EU projects CLIMOOR, VULCAN and INCREASE FP7-INFRASTRUCTURE-2008-1 (Grant Agreement No. 227628)—the INCREASE project. M.T.D was supported by two postdoctoral fellowships awarded by the Spanish Government (National Science and Technology Foundation and Juan de la Cierva fellowship). We thank two anonymous reviewers for their suggestions on previous versions of the manuscript.

## REFERENCES

Aanderud ZT, Schoolmaster DR Jr, Lennon JT. 2011. Plants mediate the sensitivity of soil respiration to rainfall variability. Ecosystems 14:156–67.

Bader NE, Cheng W. 2007. Rhizosphere priming effect of *Populus fremontii* obscures the temperature sensitivity of soil organic carbon respiration. Soil Biol Biochem 39:600–6.

Beier C, Emmett B, Gundersen P, Tietema A, Peñuelas J, Estiarte M, Gordon C, Gorissen A, Llorens L, Roda F, Williams D. 2004. Novel approaches to study climate change effects on terrestrial ecosystems in the field: drought and passive nighttime warming. Ecosystems 7:583–97.

Beier C, Emmett BA, Tietema A, Schmidt IK, Peñuelas J, Láng EK, Duce P, De Angelis P, Gorissen A, Estiarte M, de Dato GD, Sowerby A, Kröel-Dulay G, Lellei-Kovács E, Kull O, Mand P, Petersen H, Gjelstrup P, Spano D. 2009. Carbon and nitrogen balances for six shrublands across Europe. Global Biogeochemical Cycles 23.

Bond-Lamberty B, Thomson A. 2010. Temperature-associated increases in the global soil respiration record. Nature 464:579–82.

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend AD, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–33.

Cranfield University. 2014. The Soils Guide. Available: www.landis.org.uk. Cranfield University, UK. (http://www.landis.org.uk/services/soilsguide/series.cfm?serno=755). Accessed on 18 November 2014.

Curiel-Yuste J, Janssens IA, Carrara A, Ceulemans R. 2004. Annual Q10 of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Glob Change Biol 10:161–9.

Curiel-Yuste J, Ma S, Baldocci DD. 2010. Plant-soil interactions and acclimation to temperature of microbial-mediated soil respiration may affect predictions of soil $CO_2$ efflux. Biogeochemistry 98:38–127.

Davidson EA, Holbrook NM. 2009. Is temporal variation of soil respiration linked to the phenology of photosynthesis? In: Noormets A, Ed. Phenology of ecosystem processes-applications in global change research. New York: Springer. p 187–99.

Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–73.

Delpierre N, Soudani K, François C, Le Maire G, Bernhofer C, Kutsch W, Misson L, Rambal S, Vesala T, Dufrêne E. 2012. Quantifying the influence of climate and biological drivers on the interannual variability of carbon exchanges in European forests through process-based modelling. Agric For Meteorol 154–155:99–112.

Domínguez MT, Sowerby A, Smith A, Robinson D, Van Baarsel S, Mills RE, Marshall M, Koller E, Lebron I, Hall J, Emmett B. 2015. Sustained impact of drought on wet shrublands mediated by soil physical changes. Biogeochemistry 122:151–63.

Dijkstra FA, Cheng W. 2007. Interactions between soil and tree roots accelerate long-term soil carbon decomposition. Ecol Lett 10:1046–53.

Emmett BA, Beier C, Estiarte M, Tietema A, Kristensen HL, Williams D, Peñuelas J, Schmidt I, Sowerby A. 2004. The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. Ecosystems 7:625–37.

Epron D, Nouvellon Y, Roupsard O, Mouvondy W, Mabiala A, Saint-André L, Joffre R, Jourdan C, Bonnefond J-M, Berbigier P, Hamel O. 2004. Spatial and temporal variations of soil respiration in a Eucalyptus plantation in Congo. For Ecol Manag 202:149–60.

Freeman C, Ostle N, Kang H. 2001. An enzymic 'latch' on a global carbon store. Nature 409:149.

Fenner N, Freeman C. 2011. Drought-induced carbon loss in peatlands. Nature Geosci 4:895–900.

Fierer N, Colman BP, Schimel JP, Jackson RB. 2006. Predicting the temperature dependence of microbial respiration in soil: A continental-scale analysis. Glob Biogeochem Cycles 20:GB3026.

Fontaine S, Barot S, Barre P, Bdioui N, Mary B, Rumpel C. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–80.

Gimingham CH. 1972. Ecology of heathlands. London: Chapman Hall.

Hall J, Curti C, Dore T, Smith R. 2014. Methods for the calculation of critical loads and their exceedances in the UK, draft report to UK Department of Environment and Rural Affairs-DEFRA. http://nora.nerc.ac.uk/505595/. Accessed 7 September 2015.

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Lofvenius M, Read DJ. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–92.

Irvine J, Law BE, Martin JG, Vickers D. 2008. Interannual variation in soil $CO_2$ efflux and the response of root respiration to climate and canopy gas exchange in mature ponderosa pine. Glob Change Biol 14:2848–59.

Ise T, Dunn AL, Wofsy SC, Moorcroft PR. 2008. High sensitivity of peat decomposition to climate change through water-table feedback. Nat Geosci 1:763–6.

Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grünwald T, Montagnani L, Dore S, Rebmann C, Moors EJ, Grelle A, Rannik Ü, Morgenstern K, Oltchev S, Clement R, Guðmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen NO, Vesala T, Granier A, Schulze E-D, Lindroth A, Dolman AJ, Jarvis PG, Ceulemans R, Valentini R. 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. Glob Change Biol 7:269–78.

Jia X, Zhou X, Luo Y, Xue K, Xue X, Xu X, Yang Y, Wu L, Zhou J. 2014. Effects of substrate addition on soil respiratory carbon release under long-term warming and clipping in a tallgrass prairie. PLoS ONE 9:e114203.

Jing Y, Guan D, Wu J, Wang A, Jin C, Yuan F. 2015. An experimental comparison of two methods on photosynthesis driving soil respiration: girdling and defoliation. PLoS ONE 10:e0132649.

Jones PD, Jonsson T, Wheeler D. 1997. Extension to the North Atlantic oscillation using early instrumental pressure observations from Gibraltar and south-west Iceland. Int J Climatol 17:1433–50.

Kirschbaum MUF. 2004. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Glob Change Biol 10:1870–7.

Knohl A, Werner R, Brand W, Buchmann N. 2005. Short-term variations in $\delta^{13}C$ of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. Oecologia 142:70–82.

Knapp A, Carroll CW, Denton E, La Pierre K, Collins S, Smith M. 2015. Differential sensitivity to regional-scale drought in six central US grasslands. Oecologia 177:949–57.

Kopittke GR, van Loon EE, Tietema A, Asscheman D. 2013. Soil respiration on an aging managed heathland: identifying an appropriate empirical model for predictive purposes. Biogeosciences 10:3007–38.

Knorr W, Prentice IC, House JI, Holland EA. 2005. Long-term sensitivity of soil carbon turnover to warming. Nature 433:298–301.

Kuzyakov Y, Gavrichkova O. 2010. Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Glob Change Biol 16:3386–406.

Larsen KS, Ibrom A, Beier C, Jonasson S, Michelsen A. 2007. Ecosystem respiration depends strongly on photosynthesis in a temperate heath. Biogeochemistry 85:201–13.

Liu L, King JS, Booker FL, Giardina CP, Lee Allen H, Hu S. 2009. Enhanced litter input rather than changes in litter chemistry drive soil carbon and nitrogen cycles under elevated $CO_2$: a microcosm study. Glob Change Biol 15:441–53.

Luo Y, Zhou X. 2006. Soil respiration and the environment. Burlington: Academic Press.

Mahecha M, Reichstein M, Carvalhais N, Lasslop G, Lange H, Seneviratne SI, Vargas R, Ammann C, Arain MA, Cescatti A, Janssens IA, Migliavacca M, Montagnani L, Richardson AD. 2010. Global convergence in the temperature sensitivity of respiration at ecosystem level. Science 329:838–40.

Maier CA, Kress LW. 2000. Soil $CO_2$ evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Can J For Res 30:347–59.

Marcolla B, Cescatti A, Manca G, Zorer R, Cavagna M, Fiora A, Gianelle D, Rodeghiero M, Sottocornola M, Zampedri R. 2011. Climatic controls and ecosystem responses drive the inter-annual variability of the net ecosystem exchange of an alpine meadow. Agric For Meteorol 151:1233–43.

Met Office. 2012. Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current). NCAS British Atmospheric Data Center.

Migliavacca M, Reichstein M, Richardson AD, Colombo R, Sutton MA, Lasslop G, Tomelleri E, Wohlfahrt G, Carvalhais N, Cescatti A, Mahecha MD, Montagnani L, Papale D, Zaehle S, Arain A, Arneth A, Black TA, Carrara A, Dore S, Gianelle D, Helfter C, Hollinger D, Kutsch WL, Lafleur PM, Nouvellon Y, Rebmann C, Da Rocha HR, Rodeghiero M, Roupsard O, Sebastiá MT, Seufert G, Soussana JF, Van Der Molen MK. 2011. Semiempirical modeling of abiotic and biotic factors controlling ecosystem respiration across eddy covariance sites. Glob Change Biol 17:390–409.

Ottersen G, Planque B, Belgrano A, Post E, Reid PC, Stenseth NC. 2001. Ecological effects of the North Atlantic Oscillation. Oecologia 128:1–14.

Peñuelas J, Prieto P, Beier C, Cesaraccio C, De Angelis P, De Dato G, Emmett BA, Estiarte M, Garadnai J, Gorissen A, Láng EK, Kröel-Dulay G, Llorens L, Pellizzaro G, Riis-Nielsen T, Schmidt IK, Sirca C, Sowerby A, Spano D, Tietema A. 2007. Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. Glob Change Biol 13:2563–81.

Pietikäinen J, Pettersson M, Bååth E. 2005. Comparison of temperature effects on soil respiration and bacterial and fungal growth rates. FEMS Microbiol Ecol 52:49–58.

Quin SLO, Artz RRE, Coupar AM, Woodin SJ. 2015. Calluna vulgaris-dominated upland heathland sequesters more $CO_2$ annually than grass-dominated upland heathland. Sci Total Environ 505:740–7.

Raich JW, Potter CS, Bhagawati D. 2002. Interannual variability in global soil respiration, 1980–94. Glob Change Biol 8:800–12.

Ratkowsky DA, Olley J, McMeekin TA, Ball A. 1982. Relationship between temperature and growth rate of bacterial cultures. J Bacteriol 149:1–5.

Reichstein M. 2003. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. Glob Biogeochem Cycles 17:1104.

Reynolds B, Chamberlain PM, Poskitt J, Woods C, Scott WA, Rowe EC, Robinson DA, Frogbrook ZL, Keith AM, Henrys PA, Black HIJ, Emmett BA. 2013. Countryside Survey: National ''Soil Change'' 1978–2007 for Topsoils in Great Britain—acidity, carbon, and total nitrogen status. Vadose Zone J 12.

Richardson AD, Hollinger DY, Aber JD, Ollinger SV, Braswell BH. 2007. Environmental variation is directly responsible for short- but not long-term variation in forest-atmosphere carbon exchange. Glob Change Biol 13:788–803.

Rinnan R, Rousk J, Yergeau E, Kowalchuk GA, Bååth E. 2009. Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: predicting responses to climate warming. Glob Change Biol 15:2615–25.

Rinnan R, Michelsen A, Bååth E. 2011. Long-term warming of a subarctic heath decreases soil bacterial community growth but has no effects on its temperature adaptation. Appl Soil Ecol 47:217–20.

Robinson DA, Jones SB, Lebron I, Reinsch S, Domínguez MT, Smith AR, Jones DL, Marshall MR, Emmett BA. 2016. Experimental evidence for drought induced alternative stable states of soil moisture. Sci Rep 6:20018.

Sampson DA, Janssens IA, Curiel-Yuste J, Ceulemans R. 2007. Basal rates of soil respiration are correlated with photosynthesis in a mixed temperate forest. Glob Change Biol 13:2008–17.

Scott-Denton LE, Sparks KL, Monson RK. 2003. Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest. Soil Biol Biochem 35:525–34.

Shao J, Zhou X, He H, Yu G, Wang H, Yi Luo, Chen J, Gu L, Li B. 2014. Partitioning climatic and biotic effects on interannual variability of ecosystem carbon exchange in three ecosystems. Ecosystems 17:1186–201.

Stoy PC, Richardson AD, Baldocchi DD, Katul GG, Stanovick J, Mahecha MD, Reichstein M, Detto M, Law BE, Wohlfahrt G, Arriga N, Campos J, McCaughey JH, Montagnani L, Paw UKT, Sevanto S, Williams M. 2009. Biosphere-atmosphere exchange of $CO_2$ in relation to climate: a cross-biome analysis across multiple time scales. Biogeosciences 6:2297–312.

Sowerby A, Emmett BA, Williams D, Beier C, Evans CD. 2010. The response of dissolved organic carbon (DOC) and the ecosystem carbon balance to experimental drought in a temperate shrubland. Eur J Soil Sci 61:697–709.

Sulzman EW, Brant JB, Bowden RD, Lajtha K. 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil $CO_2$ efflux in an old growth coniferous forest. Biogeochemistry 73:231–56.

Suseela V, Conant RT, Wallenstein MD, Dukes JS. 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Glob Change Biol 18:336–48.

Tang X-L, Zhou G-Y, Liu S-G, Zhang D-Q, Liu S-Z, Li J, Zhou C-Y. 2006. Dependence of soil Respiration on soil Temperature and soil moisture in successional forests in Southern China. J Integr Plant Biol 48:654–63.

Thiessen S, Gleixner G, Wutzler T, Reichstein M. 2013. Both priming and temperature sensitivity of soil organic matter decomposition depend on microbial biomass—an incubation study. Soil Biol Biochem 57:739–48.

Thomas CK, Law BE, Irvine J, Martin JG, Pettijohn JC, Davis KJ. 2009. Seasonal hydrology explains interannual and seasonal variation in carbon and water exchange in a semiarid mature ponderosa pine forest in central Oregon. J Geophys Res 114.

Trumbore S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecol Appl 10:399–411.

Wan S, Luo Y. 2003. Substrate regulation of soil respiration in a tallgrass prairie: results of a clipping and shading experiment. Glob Biogeochem Cycles 17.

Wang X, Piao S, Ciais P, Janssens IA, Reichstein M, Peng S, Wang T. 2010. Are ecological gradients in seasonal $Q_{10}$ of soil respiration explained by climate or by vegetation seasonality? Soil Biol Biochem 42:1728–34.

Wang Y, Li Q, Wang H, Wen X, Yang F, Ma Z, Liu Y, Sun X, Yu G. 2011. Precipitation frequency controls interannual variation of soil respiration by affecting soil moisture in a subtropical forest plantation. Can J For Res 41:1897–906.

Wei W, Weile C, Shaopeng W. 2010. Forest soil respiration and its heterotrophic and autotrophic components: global patterns and responses to temperature and precipitation. Soil Biol Biochem 42:1236–44.

Yan J, Zhang D, Zhou G, Liu J. 2009. Soil respiration associated with forest succession in subtropical forests in Dinghushan Biosphere Reserve. Soil Biol Biochem 41:991–9.

Zhou T, Shi P, Hui D, Luo Y. 2009. Global pattern of temperature sensitivity of soil heterotrophic respiration ($Q_{10}$) and its implications for carbon-climate feedback. J Geophys Res 114.

Zhu B, Cheng W. 2011. Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition. Glob Change Biol 17:2172–83.

Zuur A, Ieno EN, Walker N, Saveliev A, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.