Soil Respiration in European Grasslands in Relation to Climate and Assimilate Supply

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Abstract

Soil respiration constitutes the second largest flux of carbon (C) between terrestrial ecosystems and the atmosphere. This study provides a synthesis of soil respiration (R_s) in 20 European grasslands across a climatic transect, including ten meadows, eight pastures and two unmanaged grasslands. Maximum rates of R_s ($R_{s_{max}}$), R_s at a reference soil temperature (10°C; R_{s10}) and annual R_s (estimated for 13 sites) ranged from 1.9 to 15.9 µmol CO_2 m^{-2} s^{-1}, 0.3 to 5.5 µmol CO_2 m^{-2} s^{-1} and 58 to 1988 g C m^{-2} y^{-1}, respectively. Values obtained for Central European mountain meadows are amongst the highest so far reported for any type of ecosystem. Across all sites $R_{s_{max}}$ was closely related to R_{s10}.

Assimilate supply affected R_s at timescales from daily (but not necessarily diurnal) to annual. Reductions of assimilate supply by removal of aboveground biomass through grazing and cutting resulted in a rapid and a significant decrease of R_s. Temperature-independent seasonal fluctuations of R_s of an intensively managed pasture were closely related to changes in leaf area index (LAI). Across sites R_{s10} increased with mean annual soil temperature (MAT), LAI and gross primary productivity (GPP), indicating that assimilate supply overrides potential acclimation to prevailing temperatures. Also annual R_s was closely related to LAI and GPP. Because the latter two parameters were coupled to MAT, temperature was a suitable surrogate for deriving estimates of annual R_s across the grasslands studied. These findings contribute to our understanding of regional patterns of soil C fluxes and highlight the importance of assimilate supply for soil CO_2 emissions at various timescales.

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Keywords

soil CO_2 efflux; temperature; moisture; gross primary productivity; leaf area index; soil carbon; land use

Introduction

Soil respiration is the major source of CO_2 released by terrestrial ecosystems and constitutes the second largest flux of carbon between ecosystems and the atmosphere (Raich and Schlesinger 1992). Current global estimates indicate that soils emit 68–80 Pg C per year (Raich and Potter 1995; Raich and others 2002), which exceeds emission rates from fossil fuel combustion by a factor of more than 10 (Schlesinger and Andrews 2000). In view of a growing interest concerning the role of ecosystems in the terrestrial carbon cycle and its feedbacks to climate change, increasing numbers of studies have explored soil respiration in relation to environmental factors and across bioclimatic gradients. Whilst soil respiration (R_s) has been well characterized for a range of forest ecosystems (for example, recent syntheses for bioclimatic transects by Janssens and others 2001; Kane and others 2003; Reichstein and others 2003; Hibbard and others 2005; Rodeghiero and Cescatti 2005), comparatively little is known for grasslands.

Depending on definition, grasslands cover 20–40% of the land surface. In Europe, grasslands play an important role in areas where climate and topography restrict a highly productive use of crops. Therefore, grasslands are frequent in mountain areas of Central, Southern and Eastern Europe and the uplands at higher latitudes. There is limited evidence that soil CO_2 efflux from grasslands may be about 20% higher than that from comparable forest stands (Raich and Tufekcioglu 2000). Unfortunately, however, most annual estimates of soil CO_2 efflux from temperate grasslands date back to the 1970s (compare reviews by Raich and Schlesinger 1992; Raich and Potter 1995), when primarily static-chamber methods were applied, which have been shown to underestimate R_s rates when fluxes are high (for example, Norman and others 1997). Recent estimates for annual R_s in grasslands based on dynamic chambers are largely restricted to seasonally dry, C4 dominated grasslands in North and South America (for example, Luo and others 1996; Bremer and others 1998; Davidson and others 2000; Wan and Luo 2003). These grassland systems are mostly unfertilized and prone to extended periods of water stress, and may therefore exhibit lower rates of R_s than could be expected, for example, for managed grasslands in temperate climates. Up to now no comparative study on R_s is available for temperate grasslands across a latitudinal transect. Thus, it is an aim of the present paper to provide an overview of soil CO_2 efflux from differently managed and unmanaged temperate grasslands along a climatic gradient. We explore the hypotheses that with increasing mean annual temperature (1) annual soil CO_2 efflux increases in the absence of extended droughts and (2) soil respiration at a reference temperature decreases, indicating a temperature acclimation of respiratory processes (as suggested by recent studies by Janssens and others 2003 and Rodeghiero and Cescatti 2005).

A second objective of this study is to analyze possible effects of assimilate supply on R_s at timescales from diurnal to annual. A number of recent studies have shown that assimilate supply may strongly affect R_s. Temperature-independent diurnal variations of R_s under trees have been suggested to result from changes in photosynthesis (Tang and others 2005; Baldocchi and others 2006; Liu and others 2006). An interruption of the transport of assimilates to the soil by tree girdling results in a substantial decrease of soil CO_2 efflux (Högberg and others 2001). Likewise, reductions in assimilate supply by shading and/or clipping have been shown to reduce grassland R_s (for example, Craine and others 1999;

Wan and Luo 2003; Bahn and others 2006). Estimates of the temperature sensitivity of R_s are often confounded by unidentified processes of substrate supply (compare reviews by Davidson and others 2006; Davidson and Janssens 2006). At an annual timescale R_s in forests is closely related to gross primary productivity (GPP) and leaf area index (LAI) (Janssens and others 2001; Reichstein and others 2003; Hibbard and others 2005), indicating a coupling between the amounts of CO_2 assimilated by forest canopies and released from the soil. We expected that, similarly, in grasslands soil respiration responds to assimilate supply (1) at the diurnal scale, rates at a given temperature being higher during daytime than at night, (2) at the daily to weekly scale in relation to grassland management (cutting and grazing), and (3) at the annual scale in relation to GPP and LAI.

Methods

Sites

The sites were studied within the EU-Framework Program 5 projects CarboMont (Cernusca and others 2008) and GreenGrass (Soussana and others 2007) and cover a latitudinal transect from 41 °90′ N to 67°72′ N and an altitudinal range from 50 m (Carlow, Ireland) to almost 2000 m a.s.l. (Stubai, Austrian Alps) (Table 1), mean annual air and soil temperatures ranging from −1.0 to 10.1°C and from 3.3 to 11.8°C, respectively. Mean annual precipitation ranges from 500 to 1760 mm. Grasslands include meadows that are fertilized and cut at least twice a year (intensive use; Oensingen 2, Stubai 1), lightly used meadows that are unfertilized or slightly fertilized, cut once a year and are mostly grazed during short periods late in the season (all other meadows), a fertilized intensive pasture that is cut for silage and is grazed extensively from then onwards (Carlow), moderately grazed pastures, abandoned and natural (unmanaged) grassland. For details on site characteristics refer to Table 1.

Soil Respiration Measurements

The two major systems used in this study were the LI 6400-09 soil respiration chamber combined with a LI 6400 IRGA (Li-Cor, Lincoln, NE, USA) and the upgraded SRC-1 chamber in combination with an IRGA of the same company (EGM 1, 2 and 4, CIRAS-1) (PPSystems, Hitchin, Herts, UK) (Table 1). On several occasions these two systems were cross-compared (October 2002, Stubai Valley; April 2004, Innsbruck; August 2004, Seebodenalp; September 2004, Monte Bondone; summer 2005, Viterbo), indicating a good agreement (on the average less than 5% difference) between the systems applied on the same collars. At the Berchtesgaden sites a manually operated closed system (home-made system as described by Velthof and Oenema 1995, combining a chamber with a vent with IRGAs (Li-800 and Li-6262, Licor, Lincoln, NE, USA) was applied (compare also Pumpanen and others 2004). At Polana a home-made chamber was attached to an infrared gas analyzer (Li 6250, Li-Cor, USA). At Alinya and at the Stubai sites in addition to the closed chamber systems home-made open systems were installed. For measurements, all chambers were placed on collars, which had been inserted into the soil at least 24 h prior to measurement (Bahn and others 2008). Aboveground vegetation was removed from inside the collars before measurements were started. In parallel to soil respiration measurements soil temperature (using soil temperature probes) and soil moisture (using TDR probes) were recorded.

Additional Site Parameters

Continuous half-hourly means of soil temperature and moisture were obtained with microclimate stations using soil thermocouples and TDR sensors. Soil carbon stocks were measured on at least nine cores per sites, except at Värriö where fewer large soil monoliths were excavated. Sieved and root-free soil samples were analyzed for C using elemental

analyzers. Leaf area index and standing biomass and were measured from samples cut at the soil surface. Leaf area was determined using leaf area meters. For biomass estimates samples were oven-dried at 70–80°C. Gross primary productivity was estimated from eddy covariance measurements, as described by Wohlfahrt and others (2008) and Gilmanov and others (2007).

Annual Totals of Soil Respiration

Annual totals of soil respiration were estimated by applying the following functions, which were fitted against the measured values.

$$R_s = a / (1 + b * \exp(-k * T_s)) \quad (1)$$

where R_s denotes soil respiration rate (μmol CO_2 m^{-2} s^{-1}); a, b and k are fitting parameters and T_s is soil temperature (°C) (compare Rodeghiero and Cescatti 2005).

$$R_s = R_{s_{10}} * \exp(E_o * (1/56.02 - (1/T_s + 46.02))) \quad (2)$$

where R_{s10} is the soil respiration rate at 10°C and E_o is the activation energy (Lloyd and Taylor 1994, Eqn. 1).

For the sites Alinya, Monte Bondone and Carlow inclusion of soil water content as a separate parameter resulted in a distinctly better model fit; therefore, a Gompertz function (Janssens and others 2003) was added to Eqn. 2:

$$R_s = R_{s_{10}} * \exp(E_o * (1/56.02 - (1/T_s + 46.02)) * \exp(-\exp(c - d * M_s))$$

where a and b are fitting parameters and M_s is the soil moisture (relative volumetric soil water content, %).

A nonlinear estimation least squares method (STATISTICA, StatSoft, Inc., 2005) was used to fit the models and derive model parameters. For estimating the generalization error of the applied models (Eqs. 1, 2, 3), and testing their performance, we applied a holdout validation method (Shao 1993). For each site the original dataset was separated in two datasets called the "training set" and the "testing set". The testing set was selected by randomly sampling 20% of the original data, according to their temperature frequency distribution. The remaining 80% of the data belonging to the training set was used for model fitting and to derive the model parameters with a nonlinear estimation least square method (STATISTICA, Statsoft, Inc., 2005). We preferred the holdout validation method to a more complex k-fold cross validation (Shao 1993), because the datasets were large enough to allow for extraction of 20% of the data, leaving at the same time enough data for model fitting (more than 21; Table 2). Table 2 summarizes the model parameters and r^2, as well as linear regression statistics of the validation. At all sites residuals of predicted versus observed values of R_s were plotted against M_s, r^2 values of the linear regressions are reported in Table 2. The models (1)–(3) were compared with respect to r^2, mean absolute error (MAE) and model efficiency (ME) (compare for example, Medlyn and others 2005; Richardson and Hollinger 2005), and the best performing model was selected for estimating annual totals of soil respiration for each site (Table 2).

Annual soil CO_2 efflux was calculated as the sum of single half-hourly fluxes obtained from model outputs based on continuously recorded soil temperature and moisture data. There are several approaches to estimating the uncertainty of modelled annual totals of fluxes, including Monte Carlo and bootstrap simulations (Richardson and Hollinger 2005). We

decided to adopt a simpler approach, which is more conservative than the ones mentioned above and thus likely provides comparatively higher uncertainty estimates. We binned the data to equally sized T_s classes. For each class the average and the 95% confidence interval of R_s were calculated, which were each used for parameterizing the equation previously applied for the site (compare Lavigne and others 1997) and calculating annual R_s and its confidence interval as described above. Following this approach the uncertainty estimate for a selected site (Stubai 1) is approximately five times higher (11.2%, Table 2) than when applying a bootstrap analysis (2.2%), and about half the value when the bootstrap analysis is combined with a Monte Carlo simulation (assuming a Gaussian uncertainty of 20%) of soil temperature (24%).

Results

Rates of soil respiration at a reference temperature of 10°C (R_{s10}) ranged from 0.25 to 5.49 μmol m^{-2} s^{-1} (Table 1) and increased with increasing mean annual soil temperature, C content of the upper soil layers, peak leaf area index and annual gross primary productivity across sites (Figure 1A–D). Maximum R_s exceeded 14 μmol m^{-2} s s^{-1} for a number of Central European sites, reaching values of up to 15.9 μmol m^{-2} s^{-1} on warm summer days (Table 1, Figure 2). Across sites maximum R_s rates were not correlated with associated soil temperatures, but generally increased with increasing R_{s10} of a site (Figure 2A, B). The temperature sensitivity of R_s (Q_{10}) based on the pooled data sets and calculated for a common temperature range (at 5 cm depth) from 10 to 15°C ranged from 2.0 to 4.9 and was not related to mean annual soil temperature ($r^2 = 0.01$; not shown).

Soil moisture constrained R_s at higher soil temperatures at most sites. This is reflected by the logistic model, whose sigmoid shape levels R_s at higher T_s when limitations due to low soil moisture are frequent, and the Lloyd and Taylor model combined with a Gompertz-function, which modifies the temperature response of R_s in relation to soil moisture. Reductions of R_s by low soil moisture were most pronounced at the Spanish site Alinya, which—with the exception of the northernmost site Värriö—was characterized by the lowest amounts of annual precipitation (Table 1). Two time series illustrate the course of R_s at Alinya during two summer periods immediately before and after short rainfall events. In July 2003 R_s was low and its diurnal variation was minor until after a rain event when soil moisture increased from less than 10 to more than 20 vol%. After a short time lag following the rain pulse soil CO_2 efflux doubled and then followed a distinct diurnal pattern (Figure 3A). As soil moisture dropped below 10 vol% during the subsequent days, R_s was again reduced to values occurring before the rain, with a decreasing response to T_s fluctuations. In June 2004, soil moisture never decreased to less than 20 vol%, and an increase in soil moisture after rain did not alter R_s rates and their response to T_s (Figure 3B).

The temperature response of R_s was not only influenced by thresholds of soil moisture, but varied under non-limiting water supply in the course of the day. This was particularly obvious on clear days, when a hysteresis effect occurred, which became more apparent when relating soil CO_2 efflux to temperature at increasing soil depth (Figure 4A–C). When related to a given T_s at 1 cm soil depth R_s was higher in the late afternoon as compared to the morning hours (Figure 4A), whereas in relation to a given T_s at deeper soil layers R_s was highest during morning hours and lowest at night (Figure 4B–C). On a cloudy day at a given T_s at 1 cm evening and early night-time values of R_s were slightly higher than during the rest of the day (Figure 4D), whereas no clear temperature response and temperature-independent pattern of R_s were observed in relation to temperatures at deeper soil layers (Figure 4E–F).

At a daily to weekly timescale land use affected R_s and its response to T_s. At Monte Bondone R_s of clipped plots was reduced by approximately 10% relative to adjacent unclipped plots, and recovered after about 2 weeks (data not shown). At Amplero clipping resulted in a reduction of R_s by more than 50% at two periods during August, and by almost 30% later in the season, whereas it caused an increase in soil temperature during all periods (Figure 5). Additional grazing caused a further significant reduction of R_s only in late August (Figure 5). At Carlow a silage cut early in the season followed by subsequent extensive grazing resulted in distinct seasonal fluctuations of LAI, which explained much of the variation of observed versus predicted R_s values, as based on the seasonal relationship between T_s and R_s (Figure 6).

Annual soil CO_2 efflux from the grasslands ranged from 58 to 1988 g C m^{-2} y^{-1} (Table 2), the average being 1108 g C m^{-2} y^{-1}. The highest values were found for meadows in the Alps (Oensingen, Stubai Valley, Monte Bondone), the lowest occurred at the northernmost site in Finland (Värriö). The uncertainty of the annual estimates was 9–25% for most sites, but as high as 40 to almost 90% for three sites in different parts of the European transect (Table 2). Across sites annual R_s was closely related to mean annual T_s (Figure 7A). Without the two Mediterranean sites (Amplero, Alinya), whose annual totals were distinctly below the regression line, r^2 of the regression increased from 0.81 to 0.92 ($P < 0.001$). Across sites annual R_s increased with increasing soil C content in the upper soil layers ($r^2 = 0.65$; not shown) and peak leaf area index (Figure 7B, without values for Auchencorth Moss $r^2 = 0.77$), and was very well correlated with gross primary productivity (Figure 7C), but exhibited no relationship with peak aboveground biomass ($r^2 = 0.02$; not shown).

Land use of the grasslands studied was generally related to mean annual soil temperature (Figure 7A), which decreased from meadows (mean annual T_s across sites 9.5 ± 0.6°C) to pastures (8.3 ± 0.7°C), and the natural grasslands (5.1 ± 1.8°C). Thus it is not possible to separate effects of land use on annual R_s from those related to temperature. Average annual R_s pooled for meadows, pastures and natural grasslands was 1520 ± 151, 865 ± 155 and 293 ± 236 g C m^{-2} y^{-1}, respectively.

Discussion

Soil Respiration in Relation to Climate and Site Productivity

Raich and Schlesinger (1992) and Raich and Potter (1995) showed that at a global scale temperature is the single best predictor of annual R_s in the absence of water stress. More recently, several authors have pointed out that a consideration of productivity (for example, gross primary productivity, GPP) or surrogates of productivity (for example, peak leaf area index, LAI) improves predictions of annual R_s of forests (Janssens and others 2001; Reichstein and others 2003; Hibbard and others 2005), especially in cases when GPP does not increase consistently with temperature (Janssens and others 2001). Dornbush and Raich (2006) have demonstrated for central Iowa grasslands that, in contrast, aboveground net primary productivity (ANPP) is less suited for predicting intra-annual variations of R_s than soil temperature.

All these observations are well supported by our data. We found that across sites annual R_s was closely related to GPP and LAI (Figure 7C, D). At the same time peak standing biomass, a proxy for ANPP, did not explain intersite variations of annual R_s. This, however, was not unexpected, as peak standing biomass underestimates productivity in grasslands that are cut more than once a year or that are intensively grazed, and it likely overestimates productivity in unmanaged sites. Moreover, estimates of site productivity from aboveground biomass may be strongly biased, as they ignore belowground productivity as well as dying and decomposing biomass. Mean annual T_s was a very good predictor of annual R_s across

sites, except for the two Mediterranean mountain grasslands, which exhibited distinctly lower annual R_s than expected from its relationship to mean annual T_s. For these two cases proxies or direct measures of soil moisture (compare Table 2; Figure 3) would need to be included in models accounting for the variability of R_s at larger scales (Raich and others 2002; Reichstein and others 2003). The fact that the slope of the temperature–respiration relationship of the grasslands studied (Figure 7A) was best described by a power rather than a linear (Raich and Schlesinger 1992) function may be explained by the fact that land use changed from pastures to more productive, fertilized meadows as annual temperatures increased.

There is some disagreement between studies on whether (Smith 2003; Rodeghiero and Cescatti 2005) or not (Janssens and others 2003; Reichstein and others 2003) soil C content influences R_s. Rodeghiero and Cescatti (2005) suggested that a lack of standardized protocols for soil C sampling and a confusion of the terms concentration and content may obscure a possible relationship of soil C content and respiration. Our data indicate an increase in annual R_s with soil C content in the uppermost soil layers. It should, however, be noted that sites with high soil C content were also characterized by higher productivity. The degree to which soil efflux is coupled to soil C content may be largely determined by the proportions of labile versus recalcitrant C (Gu and others 2004; Davidson and Jansssens 2006), as well as priming effects on soil organic matter decomposition through fresh organic C from litter-fall and root exudation (Kuzyakov 2002; Pendall and others 2003; Subke and others 2004), which may be coupled to short-term assimilate supply as related to gross primary productivity.

Soil respiration at a reference temperature ($R_{s\text{ref}}$) has often been used as an input for temperature dependent models of R_s and as a key parameter for comparing R_s across bioclimatic transects (Janssens and others 2003; Reichstein and others 2003; Hibbard and others 2005; Rodeghiero and Cescatti 2005). Our study indicates that $R_{s\text{ref}}$ is also well suited for predicting maximum rates of R_s occurring across sites (Figure 2B). Recently some authors interpreted an observed decrease of $R_{s\text{ref}}$ with increasing mean annual temperature along bioclimatic transects as an indication of acclimation of the respiration of roots and microorganisms (Janssens and others 2003; Rodeghiero and Cescatti 2005). This interpretation is not supported by our results, which show that $R_{s\text{ref}}$ increases with mean annual T_s (Figure 1A). As $R_{s\text{ref}}$ increased with site productivity (GPP, LAI) across all these mentioned studies (compare also Reichstein and others 2003; Hibbard and others 2005) it appears that site productivity rather than acclimation to a mean annual temperature determines $R_{s\text{ref}}$, indicating that substrate supply overrides potential acclimation.

Magnitude of Grassland Soil Respiration and Its Significance for Partitioning Ecosystem Carbon Fluxes

Soil CO_2 efflux varied considerably across the grasslands studied. Peak values, as regards instantaneous maximum flux rates, rates at a reference temperature and annual totals, were amongst the highest reported in the literature (Table 3). Especially Central European meadows exhibited distinctly higher rates and annual totals of soil CO_2 efflux than has previously been documented for most forests and grasslands (Table 3). These meadows are characterized by comparatively high T_s during summer coupled with only minor restrictions due to low soil moisture, by fertilization and, in consequence, by a comparatively high peak leaf area index and gross primary productivity. Comparatively low values of CO_2 efflux of less than 1 μmol m^{-2} s^{-1} during winter were compensated by very high respiration rates during summer (up to 14–16 μmol m^{-2} s^{-1}) yielding annual totals in the range of 1743–1988 g C m^{-2} y^{-1} (Tables 1, 2). For a lightly grazed grassland on the Tibetan plateau a similarly high annual soil CO_2 efflux was estimated (Cao and others 2004, Table 3).

Attempts to quantify soil CO_2 emissions at scales from ecosystems to the globe (Raich and Schlesinger 1992; Raich and Potter 1995; Schlesinger and Andrews 2000; Raich and others 2002) rely very much on the accuracy of estimates of annual totals and their underlying parameters. However there is still a considerable uncertainty in such estimates (for example, Hibbard and others 2005; this study), which may result from inevitable tradeoffs between temporal and spatial data coverage (Savage and Davidson 2003), the large amount of abiotic and biotic drivers and their interactions that may vary, and often co-vary, in the course of the year (for example, Davidson and others 2006) and interannually (Raich and others 2002) and the vast diversity of C substrates and enzymes, which so far constrain mechanistic approaches to modelling soil respiration (Davidson and Janssens 2006). Such uncertainties not only reduce the value of estimates of the magnitude of individual fluxes, but also limit their usefulness for partitioning ecosystem carbon fluxes. A particularly critical aspect concerning estimates of ecosystem CO_2 component fluxes is related to systematic differences between different methods. This is a major constraint when, for example, relating absolute values of annual R_s (based on chamber measurements) to those of GPP (derived from eddy covariance measurements) (Table 1, Figure 7D). Generally, chamber-based estimates of fluxes (as mostly applied for soil respiration measurements) tend to yield distinctly (20–40%) higher values than those based on eddy covariance measurements (for example, Goulden and others 1996; Lavigne and others 1997; Drewitt and others 2002; Bolstad and others 2004; Wohlfahrt and others 2005a). There are a number of major reasons for these discrepancies. These include: (1) differences in spatial sampling/footprint area (Lavigne and others 1997; Drewitt and others 2002; Davidson and others 2002); (2) overestimation of dynamic chamber-based fluxes through underpressure created in chamber headspace by surface wind (Bain and others 2005); (3) underestimation of EC-based respiration fluxes through advection or insufficient turbulence/mixing at night (Goulden and others 1996; Lavigne and others 1997). (4) Daytime respiration rates may be overestimated when extrapolating from EC-based nighttime data respiration fluxes due to a neglected reduction of leaf respiration in light (Atkin and others 1997; Amthor and Baldocchi 2001; Wohlfahrt and others 2005b). (5) Daytime respiration rates extrapolated from nighttime data usually do not account for possible temperature-independent effects on R_s (Tang and others 2005; Liu and others 2006; this study, but see discussion below). Therefore, care should be taken when using soil respiration data based on chamber measurements for partitioning ecosystem, regional or global fluxes of CO_2, which are based on different methodologies.

Soil Respiration and Short-Term Changes in Assimilate Supply

In recent years it has become increasingly evident that soil respiration is closely related to canopy photosynthesis at various timescales. As discussed above, GPP and its surrogate LAI are generally well correlated with annual R_s. Also at the seasonal timescale we observed in an intensively managed pasture that the residuals of the temperature–respiration relationship could be well explained by changes in LAI (Figure 6). Likewise, Reichstein and others (2003) found that across a range of forest ecosystems residual R_s (based on a model using temperature and precipitation as a predictor) was closely related to LAI. Bremer and Ham (2002) found for an intensively grazed Konza prairie that LAI needed to be considered to obtain realistic estimates of annual R_s. Our cutting and grazing experiments indicate that removal of the leaf mass may result in a significant reduction of R_s (Figure 5) and its temperature sensitivity. This is in agreement with observations from tallgrass prairies and a pasture on the Tibetan plateau (Bremer and others 1998; Johnson and Matchett 2001; Wan and Luo 2003; Cao and others 2004). In contrast, it has also been observed that soil warming following clipping may override effects of reduced assimilate supply and lead to an increase in R_s (Bahn and others 2006). However, when corrected for such temperature effects R_s is consistently reduced by clipping within 1–2 days (Wan and Luo 2003; Bahn and others

2006; this study), which is arguably the effect of a lack of assimilate supply by photosynthesis.

These findings strongly favor the view of a close short-term coupling of photosynthesis and R_s. Evidence also comes from isotopic studies demonstrating that in forests R_s is largely driven by freshly produced photosynthates and that time-lags for the isotopic signal from tree photosynthesis to appear in R_s are in the range of 1–10 days (Ekblad and Högberg 2001; Bowling and others 2002; Ekblad and others 2005; Steinmann and others 2004). It remains, however, somewhat speculative to what extent R_s is affected by photosynthesis at a diurnal timescale. Recently, it has been shown that temperature-independent diel variations of R_s occur, which have been interpreted as modulating effects of photosynthesis (Tang and others 2005; Baldocchi and others 2006; Liu and others 2006). Our results indicate, similarly, that there is a diurnal hysteresis in the temperature–R_s relationship (Figure 4). However, especially on sunny days the pattern changes depending on the soil depth at which temperature is measured (Figure 4A–C). Such a diel hysteresis, which can also be depicted by the residuals of observed versus predicted values of the temperature–respiration relationship (Liu and others 2006), may be determined by a number of factors that produce a time lag between the rate of CO_2 flux emitted from the soil and the T_s at a given depth, the most predominant ones being (1) shifts in phase and amplitude of soil temperature with depth, (2) diurnal changes of soil moisture close to a critical threshold value, (3) time lags between CO_2 production in various soil layers and the diffusion of CO_2 out of the soil (which may be more relevant when soil moisture is high) and (4) possible effects of diurnal changes in the supply of newly produced photosynthates on root and rhizosphere respiration. In the case of Figure 4 soil moisture is unlikely to have determined the observed hystereses (compare Figure 3 and section "Results"). However, it is not possible to clearly separate potential effects of progressive changes in T_s and of photosynthesis. Even when assuming (1) a constant basal respiratory activity and (2) a constant temperature response across all soil layers as well as (3) no short-term effects of photosynthesis on soil respiration, a diurnal hysteresis in the relationship between soil temperature at any fixed depth and soil respiration would occur, because shifts in phase and amplitude of soil temperature with depth during the day create time lags in the relationship (Reichstein and others 2005). However, it is likely that respiratory activity and its temperature response are not evenly distributed in the soil, being higher in soil layers with high root activity and lower in deeper soil layers where little or no rhizosphere priming of the soil organic matter decomposition occurs (for example, Boone and others 1998; Kuzyakov 2002; Pendall and others 2003; Fontaine and others 2004). In that case effects will be much more confounded and preclude a clear interpretation of an apparent diurnal relationship of canopy photosynthesis versus soil respiration (as described for example, by Tang and others 2005). A way forward in understanding the short-term coupling between canopy photosynthesis and R_s would be to monitor diurnal changes in CO_2 production in the main rooting horizon together with the associated T_s and moisture, together with canopy photosynthesis, and/or to carry out factorial manipulation experiments including isotopic pulse labelling.

Conclusions

This study provides the first synthesis of soil respiration in temperate (mostly mountain) grasslands along a climatic transect, documenting that soil CO_2 efflux from Central European meadows is amongst the highest so far reported for any type of ecosystem. The study indicates that in and across grasslands soil respiration is closely related to assimilate supply for time scales from daily (but not necessarily diurnal) to annual. Across sites R_{s10} increased with mean annual soil temperature (MAT), LAI and gross primary productivity (GPP) indicating that assimilate supply overrides potential acclimation to prevailing temperatures. Also annual R_s was closely related to LAI and GPP. Because the

latter two parameters were coupled to MAT, temperature was a suitable surrogate for deriving estimates of annual R_s across the grasslands studied. Thus, our study contributes to an understanding of regional patterns of soil C fluxes, and highlights the importance of assimilate supply as a major driver of soil CO_2 emissions and the necessity of future work examining more explicitly a direct short-term coupling between canopy photosynthesis and soil respiratory fluxes.

Acknowledgments

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Zhou X, Wan S, Luo Y. Source components and interannual variability of soil CO2 efflux under experimental warming and clipping in a grassland ecosystem. Glob Chang Biol. 2007; 13:761–75.

Figure 1.
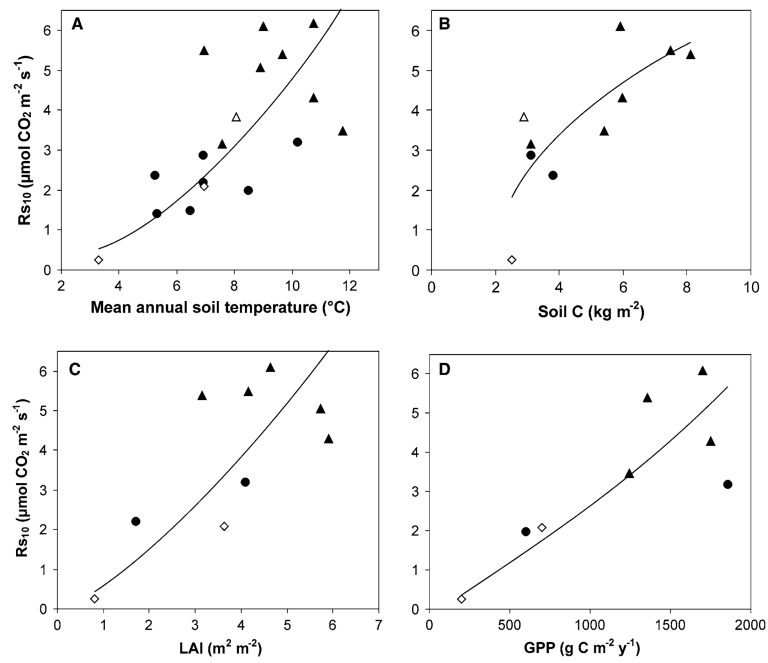Soil respiration at a reference temperature (10°C) in relation to **A** mean annual soil temperature ($r^2 = 0.69$, $P < 0.001$), **B** soil C content in the uppermost 20–25 cm of the soil ($r^2 = 0.50$, $P < 0.05$), **C** peak leaf area index ($r^2 = 0.55$, $P < 0.01$) and **D** annual gross primary productivity ($r^2 = 0.88$, $P = 0.001$). Meadows (▲), pastures (●), unmanaged Northern grasslands (◇).

Figure 2.
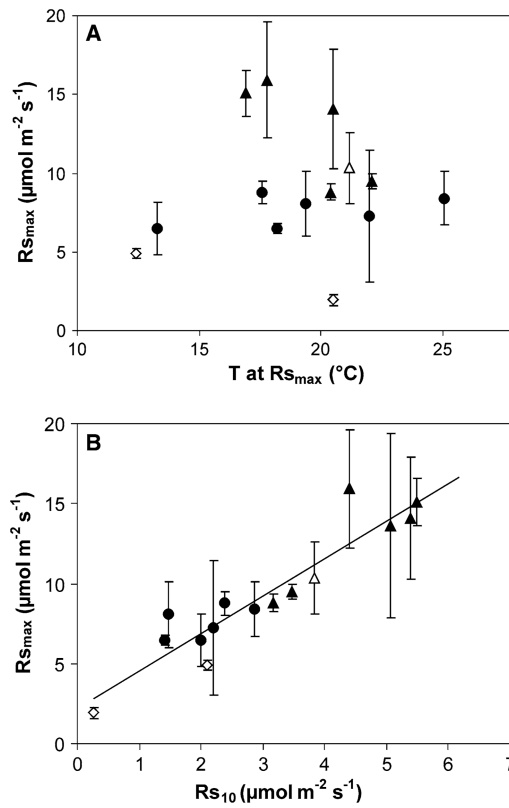Maximum rates of soil respiration in relation to **A** the associated soil temperature and **B** soil respiration at a reference temperature (10°C) ($r^2 = 0.87$, $P < 0.001$). Meadows (▲), pastures (●), unmanaged Northern grasslands (◇). *Error bars* denote standard deviations obtained for the highest spatially replicated soil respiration rates ($n = 3$–9) recorded at a single point of time.
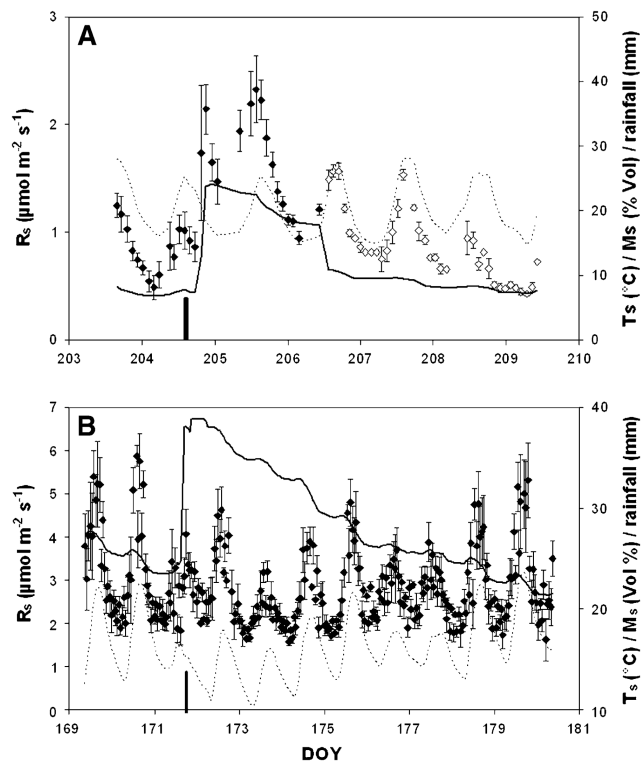
Figure 3.
Soil respiration (◆), soil temperature (*dashed line*) and soil moisture (*solid line*) before and after rainfall during summer periods in **A** 2003 and **B** 2004 at Alinya. *Bars* indicate the timing and the amount rainfall. Soil respiration was measured using a continuous system on five collars, which were changed on DOY 206 in 2003, as indicated by different symbols. Note the different scales in **A** and **B**.
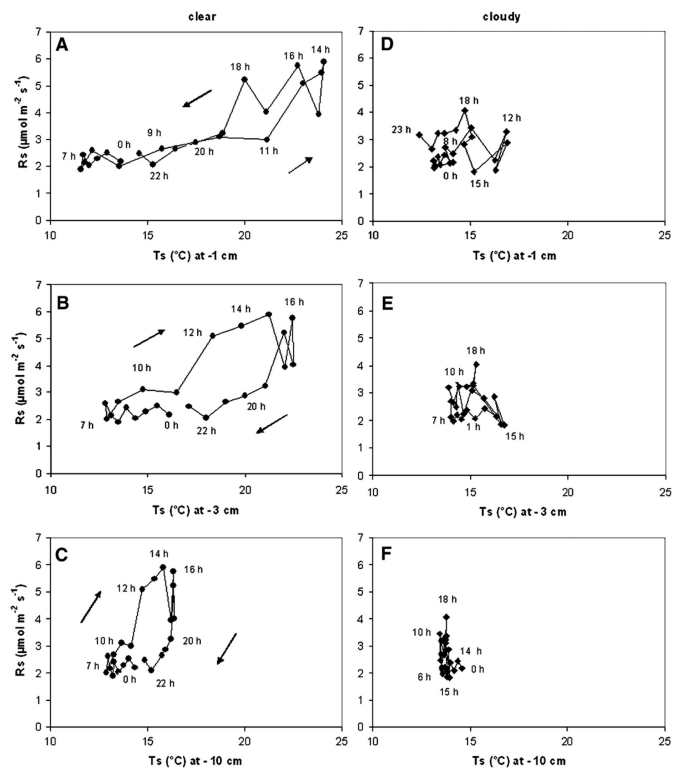
Figure 4.
Diurnal changes of soil respiration (R_s) in response to temperature at 1, 3 and 10 cm soil depth on a clear (18 June 2004; **A–C**) and a subsequent cloudy day (19 June 2004; **D–F**) at Alinya. Consecutive hourly means have been connected by lines, inserts indicate time of the day. For further details on the time course of soil respiration, soil temperature and soil water content refer to Figure 3B.
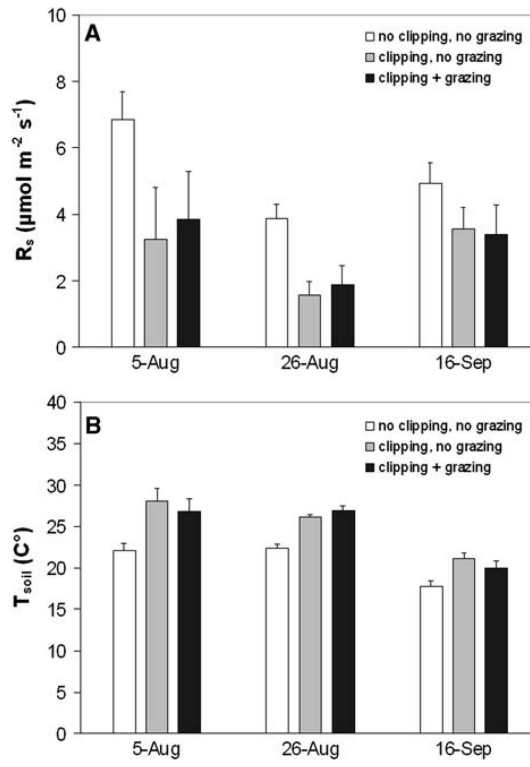
Figure 5.
Effects of clipping and grazing on **A** soil CO_2 efflux and **B** soil temperature at Amplero during the summer of 2004 (for each treatment $n = 9$).
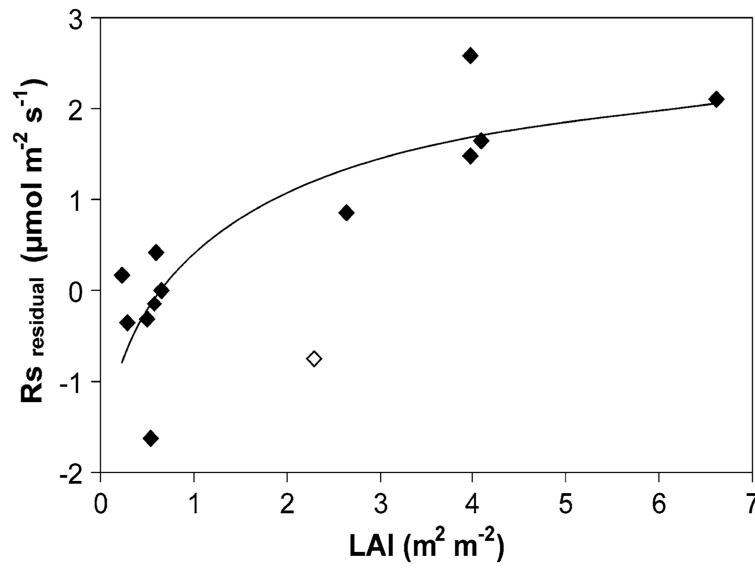
Figure 6.
Residuals of observed minus predicted values of soil respiration at Carlow in relation to seasonal values of leaf area index (LAI) in 2003 ($r^2 = 0.70$, $P < 0.001$, when excluding the data point indicated with an open symbol from the regression).

Figure 7.
Annual soil respiration in relation to **A** mean annual soil temperature ($r^2 = 0.81$, $P < 0.001$), **B** peak leaf area index ($r^2 = 0.74$, $P < 0.001$) and **C** annual gross primary productivity ($r^2 = 0.94$, $P < 0.001$). Meadows (▲), pastures (●), unmanaged Northern grasslands (◇).

Table 1

Site Characteristics and Data Acquisition

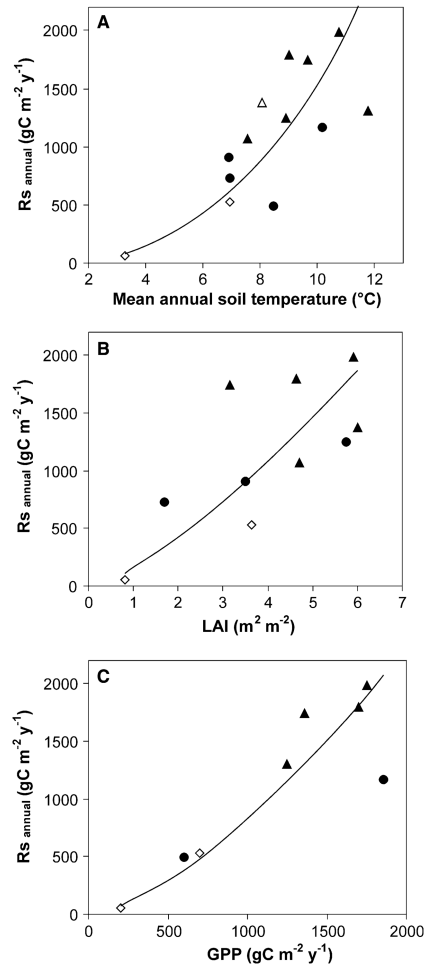| Site	Land use	Location (latitude/longitude)	Altitude (m)	MAT air/soil (°C)	MAP (mm)	Soil type	Soil texture	Soil pH
Amplero, Abruzzi (I)	Mc1g	41°54′ N 13°36′ E	900	$10.0/11.8_{(5)}$	1365	Haplic phaeozem	C	6.4
Alinya (E)	P	42°12′ N 1°27′ E	1765	$6.5/8.5_{(5)}$	700	Lythic cryrendoll	SC	7.4
Monte Bondone (I)	Mc1	46°02′ N 11°07′ E	1550	$5.5/9.7_{(5)}$	1189	Hapludalf	fine L	5.3
Passo Brocon (I)	P	46°07′ N 11°41′ E	1750	5.8/n.a.	1200	Alfisol	SL	n.a.
Seebodenalp (CH)	Mc1g	47°05′ N 8°45′ E	1025	7.3/n.a.	1061	Stagnic cambisol	n.a.	n.a.
Oensingen extensive (CH)	Mc3[1]	47°17′ N 7°44′ E	450	$9.0/10.5_{(5)}$	1200	Stagnic cambisol	SL	7.5
Stubai 1 (A)	Mc3f	47°17′ N 11°32′ E	970	$6.3/9.0_{(5)}$	850	Fluvisol	SL	6.8
Stubai 2 (A)	Mc1fg	47°17′ N 11°32′ E	1750	$3.0/6.9_{(5)}$	1097	Dystric cambisol	fine L	5.5
Stubai 3 (A)	P	47°17′ N 11°32′ E	1960	$3.0/6.9_{(5)}$	1097	Dystric cambisol	fine L	6.8
Berchtesgaden 1 (D)	Ma[2]	47°37′ N 12°35′ E	620	$8.3/8.1_{(5)}$	1665	Cambisol	n.a.	5.8
Berchtesgaden 2 (D)	P	47°37′ N 12°35′ E	620	$8.3/6.9_{(5)}$	1665	Cambisol	n.a.	6.6
Berchtesgaden 3 (D)	Mc2fg	47°37′ N 12°35′ E	620	$8.3/7.6_{(5)}$	1665	Cambisol	n.a.	6.6
Berchtesgaden 4 (D)	P	47°37′ N 12°35′ E	1420	$5.6/5.2_{(5)}$	1761	Rendzina	n.a.	6.3
Berchtesgaden 5 (D)	P	47°37′ N 12°35′ E	1425	$5.6/5.3_{(5)}$	1761	Rendzina	n.a.	6.7
Berchtesgaden 6 (D)	Pr[3]	47°37′ N 12°35′ E	1430	$5.6/6.5_{(5)}$	1761	Rendzina	n.a.	6.7
Polana (SK)	Mc1g	48°38′ N 19°32′ E	850	5.8/n.a.	853	Eutric cambisol	LS	4.7
Carlow (IRL)	Pic1f	52°85′ N, 6°54′ W	50	10.1/10.2	974	Calcic luvisol	SCL	7.3
Auchencorth Moss (GB)	U	55°79′ N 3°24′ W	270	$8.0/6.9_{(5)}$	970	Histosol	Peat	n.a.
Cow Park (GB)	Mc1f	55°52′ N 3°12′ W	200	$8.3/8.9_{(10)}$	849	Gleysol	CL	6.4
Varriö (FIN)	U	67°72′ N 29°60′ E	480	$-1.0/3.3_{(1)}$	500	n.a.	S	n.a.

Site	Soil C (kg m^{-2})	LAI (m^{-2} m^2)	Biomass (g m^{-2})	R_{s10} (µmol m^{-2} s^{-1})	R_{smax} (µmol m^{-2} s^{-1})	GPP (g C m^{-2} y^{-1})	System used	Data set
Amplero, Abruzzi (I)	5.42	1.93	125	3.47	9.5	1246	CP4	2002–4
Alinya (E)	n.a.	n.a.	515	1.99	6.5	600	OH, CP4	2003–4

Site	Soil C ($kg\ m^{-2}$)	LAI ($m^{-2}\ m^2$)	Biomass ($g\ m^{-2}$)	R_{S10} ($\mu mol\ m^{-2}\ s^{-1}$)	R_{Smax} ($\mu mol\ m^{-2}\ s^{-1}$)	GPP ($g\ C\ m^{-2}\ y^{-1}$)	System used	Data set
Monte Bondone (I)	8.12	3.2	286	5.39	14.1	1358	CL	2002–4
Passo Brocon (I)	n.a.	n.a.	n.a.	3.94	14.8	n.a.	CP2	2002–3
Seebodenalp (CH)	n.a.	5.0	n.a.	n.a.	14.2	n.a.	CL	2003
Oensingen extensive (CH)	5.99	5.9	490.0	3.58	n.a.	1750	CL	2003–4
Stubai 1 (A)	5.89	4.6	449	4.39	15.9	1697	CP4	2002–6
Stubai 2 (A)	7.49	4.2	431	5.49	15.1	n.a.	CP4	2002–4
Stubai 3 (A)	n.a.	1.7	157	2.20	7.3	n.a.	OH, CP4	2002–4
Berchtesgaden 1 (D)	2.90	6.0	699	3.83	10.3	n.a.	CH	2003
Berchtesgaden 2 (D)	3.10	3.5	207	2.86	8.4	n.a.	CH	2003
Berchtesgaden 3 (D)	3.10	4.7	299	3.16	8.8	n.a.	CH	2003
Berchtesgaden 4 (D)	3.80	5.7	411	2.37	8.8	n.a.	CH	2003
Berchtesgaden 5 (D)	5.50	4.1	275	1.42	6.5	n.a.	CH	2003
Berchtesgaden 6 (D)	n.a.	4.6	438	1.48	8.1	n.a.	CH	2003
Polana (SK)	7.56	3.1	415	n.a.	12.0	n.a.	CH	2004
Carlow (IRL)	n.a.	4.1	680	3.19	8.4	1856	CPC1	2002–4
Auchencorth Moss (GB)	n.a.	3.6	n.a.	2.09	4.9	698	CP3	2003–4
Cow Park (GB)	n.a.	5.7	540.4	5.06	13.6	n.a.	CP2	2003
Varrió (FIN)	2.50	0.8	n.a.	0.25	1.9	200	CP4	2002–3

Land use: M(eadow); P(asture); U(nmanaged); number of cuts: c1–5, f(ertilized), g(razed) late in the season; [1]… sown in 2001; [2]a(bandoned) in 2002; [3]… reintroduced in 2002. MAT…mean annual air/ soil temperature (in 2003, at the soil depth given in parentheses). MAP…Mean annual precipitation. Soil type according to FAO classification. Soil texture: c(lay), s(ilt), l(oam). Soil carbon (C) content refers to the uppermost 20–25 cm of the soil, leaf area index (LAI) and aboveground biomass refer to peak values. R_{S10} (soil respiration at 10°C), R_{Smax} (maximum soil respiration rates). GPP…gross primary productivity (in 2003). Soil respiration system used: C(losed system), O(pen System), L(ICOR 6400-09) or P(PSystems upgraded SRC-1, EGM)2–4 or C(iras)1, H(omemade, compare text). Data set: 2002–4 refers to the years when soil respiration was measured.

Table 2

Annual Soil Respiration: Model Parameters, r^2 of Model Fit, Number of Observations, Validation (r^2, Slopes and Intercepts of Linear Fits between Modelled and Independently Observed Rates of Soil Respiration), Mean Absolute Error (MAE) and Model Efficiency (ME), r^2 of Residuals of Modelled Versus Observed Soil Respiration in Relation to Soil Water Content (SWC), Modelled Annual Soil Respiration Based on Single and on Bin-Averaged Data and Confidence Interval of Annual Soil Respiration (CI, in % Percent of Annual Total Obtained from Bin-Averaged Data)

Site	Model	Model parameters	r^2	n	Validation			MAE	ME	Residuals versus SWC r^2	Annual R_s (g m^{-2} y^{-1}) Total	CI (%)
					r^2	Slope	Intercept					
Amplero	1	$a = 6.05$, $b = 18.18$, $k = 0.32$	0.37	120	0.39	1.35	−0.71	1.59	0.37	0.29	1305	40.9
Alinya	3	$R_{s10} = 1.99$, $E_o = 236.9$, $c = -11.187$, $d = 0.859$	0.47	806	0.50	0.82	0.36	7.85	0.35	0.00	494	17.1
Monte Bondone	3	$R_{s10} = 5.39$, $E_o = 384.3$, $c = -0.0059$, $d = 0.035$	0.74	430	0.82	1.09	−0.70	7.55	0.68	0.01	1743	17.1
Oensingen 1	1	$a = 14.84$, $b = 17.22$, $k = 0.17$	0.45	131	0.44	1.02	1.38	2.76	0.75	0.00	1988	87.4
Stubai 1	1	$a = 12.69$, $b = 23.29$, $k = 0.25$	0.66	380	0.71	1.01	−0.10	1.22	0.97	0.04	1792	11.2
Stubai 3	1	$a = 5.33$, $b = 8.95$, $k = 0.18$	0.48	1066	0.51	1.03	−0.15	0.81	0.83	0.10	729	9.4
Berchtesgaden 1	2	$R_{s10} = 3.83$, $E_o = 310.2$	0.80	55	0.68	0.86	0.77	0.95	0.96	0.03	1378	22.0
Berchtesgaden 2	2	$R_{s10} = 2.86$, $E_o = 260.2$	0.77	68	0.67	0.93	0.34	0.82	0.97	0.05	907	32.0
Berchtesgaden 3	2	$R_{s10} = 3.16$, $E_o = 288.7$	0.77	55	0.84	0.98	0.65	0.90	0.96	0.01	1070	19.7
Carlow	3	$R_{s10} = 3.19$, $E_o = 269.8$, $c = -7.109$, $d = 0.422$	0.44	69	0.34	0.90	0.22	8.70	0.50	0.06	1166	69.7
Auchencorth Moss	2	$R_{s10} = 2.09$, $E_o = 541.3$	0.65	22	0.47	0.69	0.53	0.46	0.91	0.06	529	62.9
Cow Park	1	$a = 5.65$, $b = 520.23$, $k = 0.84$	0.23	1044	0.19	0.81	0.98	1.84	0.82	0.09	1246	12.5
Varrió	1	$a = 1.71$, $b = 17.15$, $k = 0.11$	0.45	26	0.39	0.88	0.08	0.13	0.83	n.a.	58	23.9

Model numbers refer to Eqs. 1-3 for logistic function, Lloyd and Taylor function and Lloyd and Taylor function combined with a Gompertz-function, respectively, as described in the section "Methods".

Table 3

Soil Respiration at a Reference Temperature, Maximum and Annual Soil Respiration in Grasslands from Different Regions in Relation to Ranges Reported for Forests Compared Along Bioclimatic Transects, and Some Selected Forest Sites

Ecosystem type, region	R (at T_{ref}) (μmol m^{-2} s^{-1})	R_{max} (μmol m^{-2} s^{-1})	R_{annual} (g C m^{-2} y^{-1})	References
Grasslands				
Temperate grasslands			187–830[2]	Various sources in Raich and Schlesinger (1992)
Tropical grasslands and savannas			380–900[2]	Various sources in Raich and Schlesinger (1992)
Tropical pastures (Amazonia)	5.1 (25°)	11.0[1]	1000–1500	Davidson and others (2000)
Tallgrass prairie (North America)		9.5	1090–1347	Bremer and others (1998), Bremer and Ham (2002)
Tallgrass prairie (North America)	3 (18°)[1]		1100[1]	Wan and Luo (2003)
Tallgrass prairie (North America)			1700	Mielnick and Dougas (2000)
Konza prairie (North America)		15 (18–22)[3]	1300–2100	Knapp and others (1998); Harper and others (2005)
Central Iowa C$_3$ grassland (North America)			730	Dornbush and Raich (2006)
Central Iowa C$_4$ grassland (North America)			1300	Dornbush and Raich (2006)
California grassland (North America)		3.8	344–485	Luo and others (1996)
Shortgrass steppe (North America)		4.6	530	Pendall and others (2003)
Great Basin western wheatgrass–cheatgrass	0.5–6.5[1] (15°)	3.3–5.7	400–650[1]	Hibbard and others (2005)
Oklahoma grassland (North America)			704–881	Zhou and others (2007)
Pasture (lightly–heavily grazed) (Tibet)	1.7–3.9 (10°)	3.2–6.5	1533–2035	Cao and others (2004)
Meadows, latitudinal transect (Europe)	3.2–5.5 (10°)	9.5–15.9	1070–1988	This study (range, for details refer to Tables 1 and 2)
Pastures, latitudinal transect (Europe)	1.4–3.2 (10°)	6.5–14.8	494–1166	This study (range, for details refer to Tables 1 and 2)
Ungrazed, Northern Europe	0.3–2.1 (10°)	1.9–4.9	58–529	This study (range, for details refer to Tables 1 and 2)
Forests				
Forests, latitudinal transect (Europe)	0.7–4.9 (10°)		281–1456	Janssens and others (2001, 2003)
Forests, latitudinal transect (Europe, US)		1.7–12.5	427–1805	Hibbard and others (2005) and sources therein
Temperate forests			250–1414[2]	Various sources in Raich and Schlesinger (1992)[2]
Tropical forests			345–1450[2]	Various sources in Raich and Schlesinger (1992)[2]
Tropical forest, Amazonia		11.6[1]	2000	Davidson and others (2000)
Douglas-fir forest			1920	Drewitt and others (2002)

[1] Estimated from figure.

[2] Most data based on closed static chambers.

[3] Peak fluxes after rainfall.