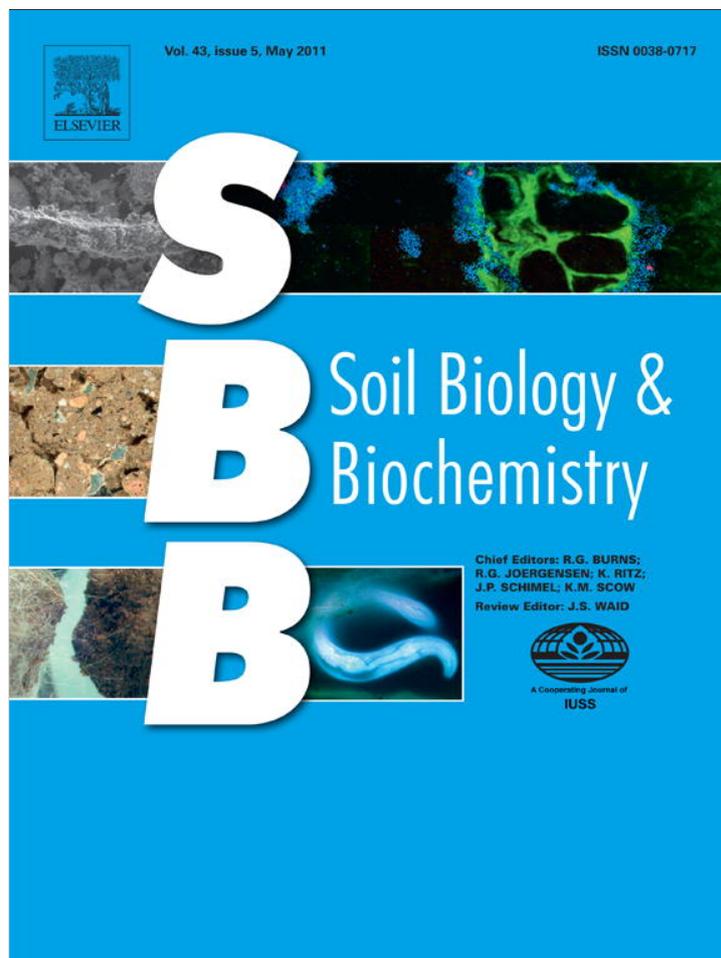


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Dependence of soil respiration on soil moisture, clay content, soil organic matter, and CO₂ uptake in dry grasslands

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ABSTRACT

The effects of abiotic and biotic drivers on soil respiration (R_s) were studied in four grassland and one forest sites in Hungary in field measurement campaigns (duration of studies by sites 2–7 years) between 2000 and 2008. The sites are within a 100 km distance of each other, with nearly the same climate, but with different soils and vegetation. Soil respiration model with soil temperature (T_s) and soil water content (SWC) as independent variables explained larger part of variance (range 0.47–0.81) than the Lloyd and Taylor model (explained variance: 0.31–0.76). Direct effect of SWC on R_s at much smaller temporal and spatial scale (1.5 h, and a few meters, respectively) was verified.

Soil water content optimal for R_s (SWC_{opt}) was shown to significantly (positively) depend on soil clay content, while parameter related to activation energy (E_0) was significantly (negatively) correlated to the total organic carbon content (TOC) in the upper 10 cm soil layer. Dependence of model parameters on soil properties could easily be utilized in models of soil respiration. The effect of current (a few hours earlier) assimilation rates on soil respiration after removing the effect of abiotic covariates (i.e. temperature and water supply) is shown. The correlation maximum between the R_s residuals ($R_{s,res}$, from the R_s (SWC, T_s) model) and net ecosystem exchange (NEE) was found at 13.5 h time lag at the sandy grassland. Incorporating the time-lagged effect of NEE on R_s into the model of soil respiration improved the agreement between the simulated vs. measured R_s data. Use of SWC_{opt} and E_0 parameters and consideration of current assimilation in soil respiration models are proposed.

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1. Introduction

In the last decades, a strong interest has arisen in soil respiration, due to widely used eddy flux studies and its problems on partitioning NEE. Eddy flux partition methods require simple but effective models in which main abiotic and biotic drivers of R_s are both taken into account.

At an annual scale, soil respiration (R_s) contributes 60–80% of ecosystem respiration (R_{eco} , Raich and Schlesinger, 1992) or 40–60% of gross primary production (GPP, Janssens et al., 2002). As a biochemical process, respiration is governed by temperature, and has been studied and described extensively (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001). The dependence of soil respiration on temperature is generally utilized when partitioning R_{eco} (Campbell et al., 2004; Bahn et al., 2008). However, temperature dependence of R_{eco} has been shown to be strongly different between active and

inactive periods due to the higher overall (active leaves and fine roots) activity of the vegetation in active periods (Reichstein et al., 2005). In other cases R_{eco} was shown to be connected only weakly to temperature, leading to problems with eddy data gap filling (Falge et al., 2001). These uncertainties in R_{eco} could arise from uncertainties in the estimation of soil respiration.

In addition to the temperature response, R_s was proven to be significantly limited both by low (Wan et al., 2007) and high (Davidson et al., 1998; Byrne et al., 2005; Saiz et al., 2007) soil water contents (SWC). Taking SWC into account is important when modeling the process of soil respiration in water limited ecosystems (Xu and Baldocchi, 2004; Jia et al., 2007; Nagy et al., 2007; Li et al., 2008). Simultaneous use of soil temperature (T_s) and SWC as independent driving variables in empirical models (Bahn et al., 2008) is straightforward in water limited cases (Wu et al., 2010). The importance of water filled pore space and tortuosity has already been elucidated in studies investigating physical soil properties and diffusion of solutes and gases in the soil (Moldrup et al., 1999; Jassal et al., 2004; Reth et al., 2008). One of the most difficult modeling tasks is the estimation of the effect of temporal

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precipitation distribution on R_s (Reth et al., 2008). On the one hand, greater ratio of microbial respiration and enhanced root death after prolonged drought stress have been reported (Harper et al., 2005), on the other hand, enhanced vegetation activity (root growth and germination) after larger precipitation events (Baldocchi et al., 2006) has been observed.

Temporally integrative biotic factors including leaf area index (Suyker and Verma, 2001), absolute growth rate (Jia and Zhou, 2009) and root biomass (Han et al., 2007) have also been considered as factors that strongly influence soil respiration rates and are thus used for modeling. Plant diversity may also affect R_s through increased productivity and C-input into the soil. Dias et al. (2010) reported positive relationship between diversity and soil respiration.

Photosynthesis stimulates R_s after translocation of the recent photosynthate to the roots and root-associated soil microbes (Moyano et al., 2007), with a few hours of time lag between the two processes (Tang et al., 2005; Bahn et al., 2009). However, based on numerous studies, different time lags have been documented in grasses and in trees, hours of time lag in the first and days of time lag in the latter (Kuzakov and Gavrichkova, 2010). This above effect decouples soil respiration from temperature (Tang et al., 2005). The magnitude of this effect and the fast response (short time lags) clearly show why it is important to consider recent photosynthesis in soil respiration modeling and carbon balance studies. The diurnal CO_2 exchange data sets are available at eddy-covariance sites, therefore they can be easily used in R_s estimations.

One aim of the present study was to describe the dependence of R_s on both SWC and T_s in different soils. The study has been conducted on five sites with soils strongly differing in soil total organic carbon (TOC) content and soil mechanical composition (clay content). These two parameters are usually available for most sites, thus we have also investigated their applicability as parameters in soil respiration models.

Another objective of the study was to separate the influence of recent photosynthesis on R_s from covariate effect of abiotic factors. This separation has been achieved at one study site where parallel eddy covariance and soil respiration data were available. These methods are expected to provide information which can be utilized to improve soil and ecosystem respiration models used in eddy flux studies.

2. Materials and methods

2.1. Site descriptions

Soil respiration measurements were undertaken within the framework of research projects that estimate the C-balance of Hungarian grasslands. The sites include four *Festuca* grasslands and one deciduous woodland which have evolved under nearly the same climate, yet differ in vegetation composition and soil structure. Two of the *Festuca* grasslands (Bugac and Mátra) are eddy-covariance sites. The sites' main characteristics are shown in Table 1.

The vegetation at site Bugac (B) is semi-arid sandy grassland dominated by *Festuca pseudovina* Hack. ex Wiesb., *Carex stenophylla* Wahlbg. and *Salvia pratensis* L. The study site is a part of the Kiskunság National Park and has been under extensive management (grazing) for the last 20 years. Grazing pressure was about 0.75 animal ha⁻¹ during the study. CO_2 flux measurements (eddy covariance) have been started in 2002. The grassland can turn into a source of carbon in dry years (Nagy et al., 2007), with annual sums of NEE between -186 and $+105$ gC m⁻².

The Mátra site (M) is situated at the edge of the Mátra Mountains. The site has a slight (<1%) slope exposed to west. The climate is characterized by a slightly higher than average annual precipitation sum (Table 1). Dominant species in the grassland include *Festuca rupicola* Heuff., other frequent species are *Arrhenaterum elatius* L., *Poa pratensis* L., *Plantago lanceolata* L. CO_2 flux measurements (eddy covariance) have been started in 2003, yearly sum of NEE ranged between -133 and $+64$ gC m⁻² (Pintér et al., 2008).

The Isaszeg (I) site is an abandoned pasture situated on a hill with a slope (about 20%) exposed to the west. The grassland is vertically well structured (60–80 cm height), species-rich, with several exhibiting broad-leaved dicotyledonous. This grassland is dominated by *F. rupicola* Heuff., *Bromus inermis* Leyss. and *Brachypodium rupestre* (Host.) Roem. et Schult. Other characteristic taxa were *Salvia nemorosa* L., *Euphorbia pannonica* Pall., *Seseli osseum* Cr. and *Galium verum* L. Modeled NEE based on chamber measurements (Balogh et al., 2005b) and measured variability in soil respiration (Fóti et al., 2008) suggest the highest carbon exchange rates of the investigated grasslands.

Table 1
Site characteristics.

Site	B (Bugac)	M (Mátra)	I (Isaszeg)	V (Vácrátót)	G (Gödöllő)
Location	46.69 N, 19.6 E	47.50 N, 19.43 E	47.34 N, 19.2 E	47.16 N, 19.16 E	47.36 N, 19.26 E
Altitude, asl., (m)	114	300	230	180	220
Annual precipitation (mm)	562	622	550	507	550
Mean annual temperature (°C)	10.4	10.2	9.1	10.5	11
Vegetation	Sand grassland	Mountain pasture	Loess grassland	Open sand grassland	Maple-oak forest
Soil type	Chernozem type sandy soil; (FAO: chernozem)	Brown soil with high clay content (FAO: vertisol)	Chernozem type loess soil. (FAO: chernozem)	Sandy soil (FAO: arenosol)	Brown forest soil with high clay content (FAO: cambisol)
Soil texture ^a	Sandy loam	Silty clay loam	Loam	Loamy sand	Clay loam
Soil pH _{KCl} ^a	7.3	6.2	7.6	7.6	6.9
Bulk density (g cm ⁻³) ^a	0.99	1.3	0.97	1.29	0.8
Clay content (g kg ⁻¹) ^a	128	346	184	17	311
TOC (g kg ⁻¹) ^a	51.5	15.4	24.6	17.7	35.6
TN (g kg ⁻¹) ^a	3.8	1.5	2.1	0.7	2.5
SWC (vol%) ^b	2.2–29	14.6–42	4.1–39.6	3.1–11.7	11.4–40
T_s (°C) ^b	–1.4–31.5	–1.6–34.8	–1.14–28.6	7.7–24.7	–1–20.5
R_s (μmol CO ₂ m ⁻² s ⁻¹) ^b (measurement dates)	0.17–18.6 (20/2/2006, 27/6/2008)	0.101–14.7 (11/8/2004, 1/8/2008)	0.24–15.6 (3/3/2006, 27/2/2008)	0.226–2.59 (4/4/2001, 3/5/2004)	2.44–10.56 (3/4/2008, 16/7/2008)
Land use	Extensive grazing Natural reserve	Extensive pasture	Abandoned (grazed ~10 years before)	Natural reserve	Natural reserve
Number of measurement years	7	3	3	3	2

^a Values given are representative for 0–10 cm soil depth.

^b Measured maximum and minimum of SWC, T_s and R_s respectively, during the experimental period.

The community at Vácrátót (site V) is a natural reserve grassland dominated by *Festuca vaginata* W. et K. and *Stipa borysthenica* Klokov. The average cover by vascular plants is 40–50% and non-vascular plants (mainly *Tortula ruralis* Hedw. and *Cladonia convoluta* (Lam.) Anders.) contribute about 20% to the total cover. The temperature of the sandy surface regularly reaches 60 °C at noon in summer. This grassland has the lowest carbon sequestration potential of the considered ecosystems (Balogh et al., 2005a).

Soil respiration was measured also in the *Aceri campestris-Quercetum roboris* forest at Gödöllő (G) in the Botanical Garden of Szent István University.

2.2. Soil samples

Six replicates of soil cores of 5 cm diameter were collected from two depths (0–10 and 10–30 cm). Soil sampling was performed within the framework of different research projects aimed to study the carbon balance in November 2002, May 2004 and September 2004 at sites B and I, in May 2003 and September 2003 at site M, and in March 2006 at sites G and V, respectively. While the sampling dates differ, the clay content and total organic matter contents are considered to be conservative enough within this time frame to allow comparison.

Soil pH was determined by KCl method and soil bulk density was measured using the volumetric core method. Soil textures were determined according to the NF X31-107 standard at INRA LAS (Lille, France) for the B, M and I sites, and according to the Hungarian Standard (MSZ-08-0205:1978) for the samples from the V and G sites in the lab of Forest Research Institute (FRI, Sárvár, Hungary).

Total organic carbon content (TOC) of the samples was determined by sulfochromic oxidation (NF ISO 14235), total nitrogen content (TN) was determined by the Kjeldahl method (NF ISO 11261) at INRA LAS for samples from the first three (B, M and I) sites and by automatic element analyzer EA3000 (Eurovector, Milan, Italy) for samples from V and G sites in the lab of FRI.

2.3. CO₂ flux measurements

Soil respiration was measured from 2001 to 2004 using a LI-6200 (Li-Cor Inc., NE, USA) IRGA with a hemisphere closed chamber ($d = 20$ cm, Balogh et al., 2005a) and from 2005 by a LICOR 6400 IRGA connected to a 6400-09 type soil chamber (Li-Cor Inc., NE, USA). Chambers were placed on the ground without using collars to prevent disturbance of the soil structure or the assimilate supply to the roots (Wang et al., 2005). Soil respiration measurements were made in the years 2002–2008 at site B, in 2003, 2004 and 2008 at site M, in 2001, 2007 and 2008 at site I, in 2000 and 2001 at site V and in 2008 and 2009 at site G, respectively. Measurements were done on several months both in growing and dormant periods in every year. During daytime measurement campaigns R_s was recorded in every 2–3 h with 3–5 spatial replications. Spatial replications distributed in a 20 m × 20 m large area - situated in the eddy flux footprint at B and M sites - were used at all sites in all campaigns. No permanent plots were used. Diurnal soil respiration courses were measured 7 times during 2006 and 2007 growing seasons (27/4/2006, 16/5/2006, 14/6/2006, 28/6/2006, 13/9/2006, 2/10/2006, 16/4/2007) at the Bugac sandy grassland site (B) studying the effect of assimilation on R_s .

Response of soil respiration to spatial variability in soil water content was also studied 3 times in 2007 growing season (16/4/2007, 2/8/2007, 2/10/2007). One and half hours were necessary to take the 75 measurements spaced every 20 cm along a 15 m long transect. As these measurements were taken within a short period around noon, R_s variation was probably not influenced by diurnal

rhythms (e.g. assimilate supply). These studies were conducted to investigate the possibility of a direct effect of SWC on R_s , independently of other factors.

Volumetric soil water content (SWC) was measured at the time (and place) of R_s measurements by time domain reflectometer (ML2, Delta-T Devices Co., Cambridge, UK) in 0–6 cm layer, T_s was measured at 5 cm depth by a digital soil thermometer.

Net ecosystem exchange (NEE) was measured by the eddy-covariance technique at the Bugac and at the Mátra sites. Both stations are equipped with a CSAT3 sonic anemometer (Campbell Sci., UK) and a LI-7500 open path IRGA (Li-cor Inc., NE, USA) to measure eddy fluxes of sensible and latent heat and CO₂ and several other sensors to measure micrometeorological variables (Nagy et al., 2007). Data processing is described by Pintér et al. (2008). Half-hourly averages of NEE were used for studying the time lag between NEE and R_s .

2.4. Modeling

Soil respiration data, containing both the autotrophic and heterotrophic components from the five different sites were fitted using the Lloyd–Taylor model (Lloyd and Taylor, 1994).

$$R_s = R_{10} e^{E_0 \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right)} \quad (1)$$

where R_{10} is the respiration rate at 10 °C, T is the soil temperature at 5 cm in Kelvin degrees, E_0 is the parameter related to the activation energy (in K). R_{10} and E_0 were allowed to vary according to Reichstein et al. (2005). This model was modified after Byrne et al. (2005) with SWC (Eq. (2)). With this modification it was possible to fit values of R_{10} , E_0 and the optimal soil water content for soil respiration (SWC_{opt} , % by volume, in Eq. (2)) simultaneously:

$$R_s = R_{10} e^{E_0 \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right)} \left[-0.5 \ln \left(\frac{SWC}{SWC_{opt}} \right) \right]^2 \quad (2)$$

Direct dependence of R_s data on SWC was described by Eq. (3):

$$R_s = R_{opt} e^{[-0.5 \ln \left(\frac{SWC}{SWC_{opt}} \right)]^2} \quad (3)$$

where R_{opt} is a free parameter. To study the effect of assimilation on soil respiration R_s data were fitted using Eq. (2) using the whole soil

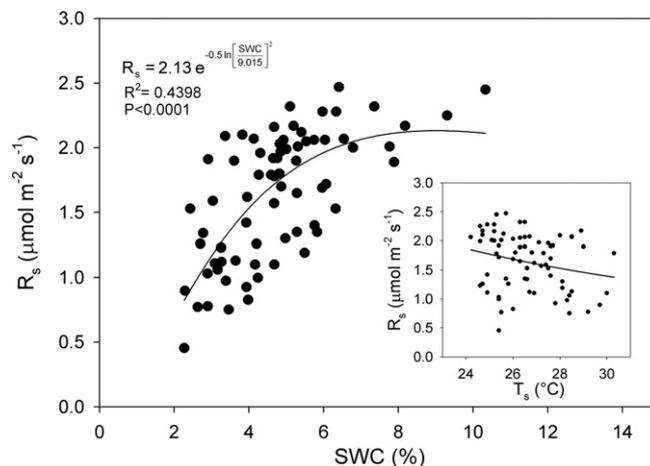


Fig. 1. Dependence of soil respiration on soil volumetric water content as measured in the upper 6 cm of the soil. Inset: R_s as a function of T_s during this experiment. No significant correlation was found between R_s and T_s in the narrow T_s range and time. R_s , SWC and T_s were measured along a perimeter of a 15 m long circle transect within 1.5 h in August 2007 at the Bugac site. Individual data are presented.

respiration data set (see above). The residuals from this fitting procedure (R_{s_res}) were then correlated to gap-filled net ecosystem exchange (NEE) data using the lagged correlation technique. For this purpose, complete diurnal courses of R_s data are needed, including the important night time measurements. Only negative NEE (CO_2 uptake) data set was compared to the residuals. The aim was to find the time lag when correlation between NEE and R_{s_res}

showed maximum (in absolute terms). The effect of NEE on R_{s_res} was then incorporated into Eq. (2) to give Eq. (4) as:

$$R_s = R_{10} e^{\left[E_0 \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right) \right]} \left[-0.5 \left[\ln \left(\frac{SWC}{SWC_{opt}} \right) \right]^2 \right] + a NEE_{lag} + b \quad (4)$$

where NEE_{lag} is the time-lagged NEE ($\mu\text{mol m}^{-2} \text{s}^{-1}$), a is the slope, b is the intercept of the R_{s_res} vs. NEE linear regression.

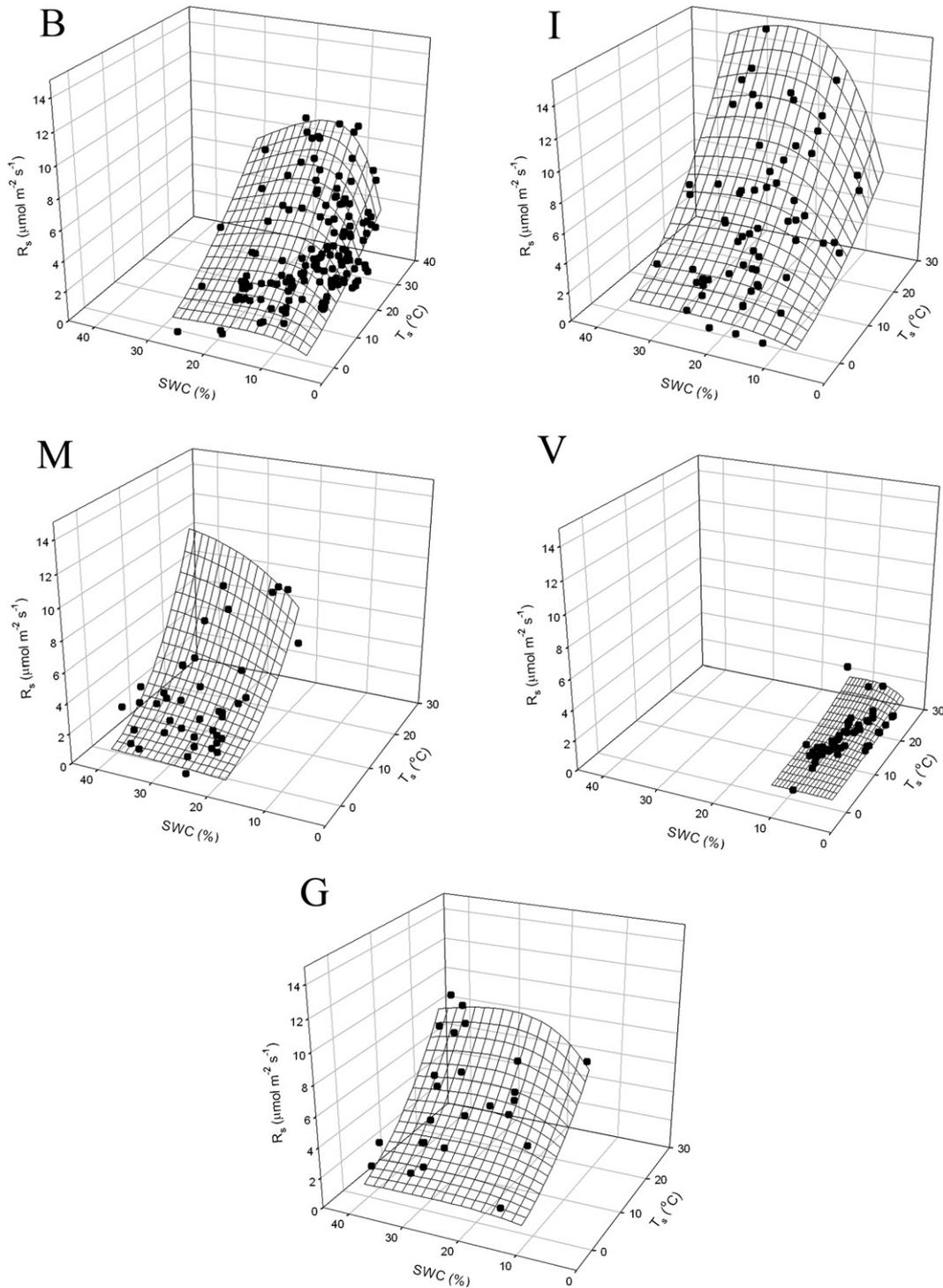


Fig. 2. Dependence of soil respiration on soil temperature (at 5 cm soil depth) and soil water content (0–6 cm) at the different sites: sand grassland (B), loess grassland (I), mountain pasture (M), open sandy grassland (V), oak forest (G). Data points are averages of 3–5 spatial replications. Values of the fitted coefficients and statistical significances are shown in Table 2.

Curve and surface fitting procedures were performed with fitting statistics calculated using Sigmaplot 8.0 (SPSS Inc). Data processing of lagged correlation was made by software written in IDL (ITT Visual Solutions, USA).

3. Results

3.1. General site and soil properties

The general characteristics of the sites and soils are summarized in Table 1, showing a relatively wide range in clay and organic carbon contents as encountered by the different soil types. The climate of the sites is relatively similar considering mean annual temperatures and annual precipitation sums (Table 1).

The soil types at the four Festuca grasslands are different, two of them (B and I) are chernozem soils with high TOC and TN contents, one of them (V) is arenosol and the last one (M) is a vertisol with the lowest TOC content. Soil clay contents at V and I sites are lower than the average (Table 1), while it is the highest out of the investigated soils at site M (Table 1). The brown forest soil of the site G is characterized by the second highest clay content and medium TOC values (Table 1). These data are valid for the upper 10 cm soil layer at the investigated sites. Highest CO₂ sink capacities during favorable conditions (no water shortage) were shown by the loess grassland (site I), followed by the sandy grassland site (B), the mountain clay soil grassland site (M) and the open sand grassland (V). The relatively wide range of clay contents and total soil organic carbon contents made possible to investigate the effects of these variables on parameters of the different models.

3.2. Effect of abiotic drivers on R_s

Significant direct effect of SWC on R_s was shown (Fig. 1) during a short term (1.5 h) measurement along a 15 m long transect at the Bugac site on 2nd August 2007. T_s was between 25 and 30 °C during the measurements and SWC values were between 2 and 8% by volume. This spatial heterogeneity of SWC provided the SWC range (Fig. 1). While the relationship between R_s and T_s was not significant there was highly significant relationship between R_s and SWC.

The seasonal R_s–SWC relation is expected to follow an optimum curve (e.g. Byrne et al., 2005), and can be described together with the R_s response to temperature by a response plane as fitted by Eq. (2) (Fig. 2). The fitted parameters (R₁₀, E₀ and SWC_{opt}) were statistically significant in all cases (Table 2). SWC_{opt} values ranged from 10.8 (loamy sand, site V) to 50% by volume (silty clay loam, site M), E₀ from 215 (site B) to 374 K (site M) and R₁₀ from 0.35 (site V) to 4.5 (site I) μmol CO₂ m⁻² s⁻¹. Similar R₁₀ and E₀ values have been reported in a study covering data from several grasslands (Bahn et al., 2008). Higher than optimal SWC values were experienced in only a few cases during the soil respiration measurements, a fact explained by the aridity prevailing in the region.

Ranges of the fitted parameters proved to be wide enough to investigate their relation to soil clay and soil total organic carbon (TOC) contents. Soil clay content showed significant linear correlation with SWC_{opt} (Fig. 3a), while E₀ was significantly negatively correlated to TOC (Fig. 3b). R₁₀ did not correlate to any of the investigated parameters.

3.3. The relationship between NEE and R_s

R_s showed a late afternoon or evening maximum, lagging behind T_s by several hours. Minimum values of soil respiration were observed at dawn or early morning. Looking at the lagged correlations between NEE and diurnal courses of R_s data at Bugac (data from 2006 to 2007), two (negative) correlation peaks were found

(Fig. 4, solid line, indicated by arrows), one of them at 3 h lag (R = 0.794, N = 28, P < 0.0001) and another one at 13.5 h lag (R = 0.728, N = 28, P < 0.0001). Fitting Eq. (2) to the same R_s data set (Fig. 2, Table 2) gave residuals (R_{s,res}), that were also correlated to NEE (Fig. 4) using the same lagged correlation technique as for R_s data above (Fig. 4 dashed line). The maximum found between NEE and R_s at 13.5 h lag persisted also between NEE and R_{s,res} while the one at 3 h lag disappeared, suggesting that this latter effect was probably manifested through the covariates (T_s and SWC) to NEE. Correlation was significant when considering the lag between 10 and 16 h (Fig. 4). Introducing the correlation between NEE and R_{s,res} at 13.5 h lag into Eq. (2) led to Eq. (4). It is to be noted that while the slope of the relationship was statistically significant, the intercept was not indicating an uncertainty factor. This uncertainty however, can be considered as low.

3.4. Modeling soil respiration in the sandy pasture

R_s was simulated at the site B using three models with soil temperature as a single driving variable (Eq. (1)), with T_s and SWC as driving variables (Eq. (2)) and by incorporating the lagged correlation between NEE and R_{s,res} after applying Eq. (2) (as shown in Eq. (4)).

Simulated and measured R_s showed the greatest discrepancy from the 1:1 line (Fig. 5) when using Eq. (1) (Table 3). Closer agreement was found between measured and modeled R_s based on Eq. (2), when T_s and SWC data were used together as predictor variables. While the coefficient of determination was not improved further by including the lagged correlation between NEE and R_{s,res} (Eq. (4)), the agreement between modeled and measured data was better in terms of slope closer to unity (Table 3, Fig. 5). At the same time the value of the intercept of the same relation was not statistically significant but small in magnitude.

4. Discussion

4.1. Response of soil respiration to soil temperature and soil water content

Time series of soil respiration data from five locations of strongly differing soil types were analyzed in order to describe empirical relations suitable for modeling applications. Seasonal trends of the ecosystem respiration vs. temperature have already been shown (Reichstein et al., 2005) with a general distinction between active and inactive periods. Simultaneous dependence of R_s on SWC and T_s was however less frequently formulated explicitly (Davidson et al., 1998; Jia et al., 2007; Brown et al., 2009; Wu et al., 2010), in spite of its practical value in modeling studies.

In this study we verified the direct effect of soil water content on R_s as found in other studies, too (Li et al., 2008; Wu et al., 2010). The significance of the R_s–SWC relationship within such a narrow spatial and temporal frame shows that variation in soil water

Table 2

R² values, number of data points (N), coefficients: R₁₀ (μmol CO₂ m⁻² s⁻¹), E₀ (K), SWC_{opt} (vol%) and statistical significance levels (***P < 0.0001, **P < 0.001) of coefficients after fitting Eq. (2) to R_s data of the five different soils.

Site	$R_s = R_{10} e^{\left[\frac{E_0}{56.02} \left(\frac{1}{T_s - 227.13} \right) \right] - 0.5 \left[\ln \left(\frac{SWC}{SWC_{opt}} \right) \right]^2}$				
	R ²	N	R ₁₀	E ₀	SWC _{opt}
Sand pasture (B)	0.47***	161	3.469***	215.223***	14.187***
Loess grassland (I)	0.724***	70	4.557***	272.887***	25.348***
Mountain pasture (M)	0.803***	40	3.87***	374.95***	50**
Open grassland (V)	0.488***	53	0.351***	361.994***	10.823***
Oak forest (G)	0.679***	25	4.27***	287.02***	27.33***

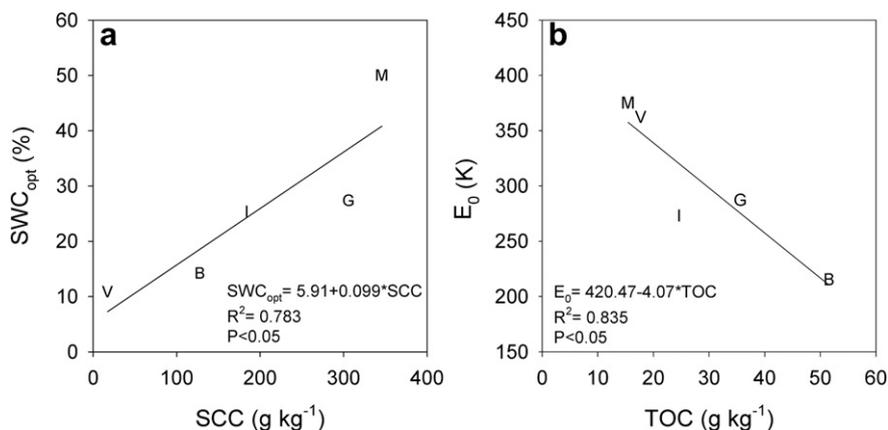


Fig. 3. Dependence of soil water content value optimal for R_s (SWC_{opt}) on soil clay content (SCC) in the upper 10 cm soil layer (a), and dependence of the factor related to activation energy (E₀) on soil total organic carbon content in the upper 10 cm soil layer (b). Parameters (SWC_{opt} and E₀) are derived after fitting Eq. (2).

content should be considered at these scales (hours and meters, respectively), when modeling R_s in water limited ecosystems.

It is to be emphasized that data on Fig. 2 include both the seasonal and interannual variability, given the measurement temporal resolution. Consequently, the fitted relationships are temporally integrative and include the effect of root mass changes, as well as photosynthetic supply through the year. The response surface of R_s (to T_s and SWC) is dominated by the natural distribution of T_s and SWC values during an annual cycle. Therefore, T_s–SWC regions (Fig. 2) are probably well representing the sites during the growing season, less so during wintertime, contain smaller amount of information on rainy days and only a few information for frozen soils. While the former constraint can be one of the characteristics of the site, the latter is a limitation arising for technical reasons. In addition to the above integrated responses by R_s to T_s and SWC, we demonstrated a direct link between R_s and SWC on relatively small spatial scales.

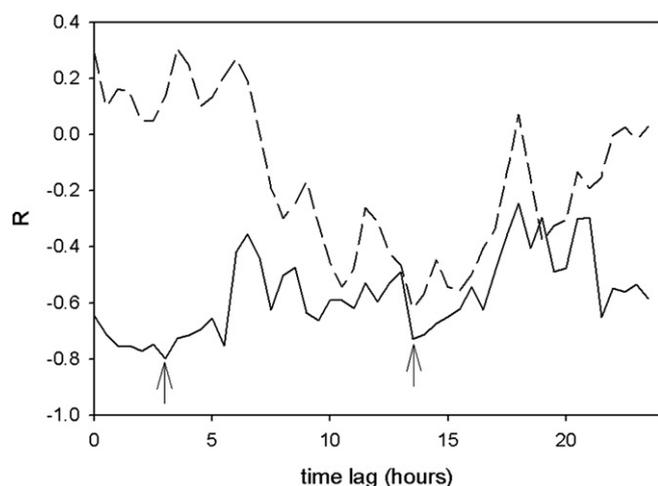


Fig. 4. Correlation coefficient (R) between R_s and NEE (solid line) and R_s and NEE (dashed line) as function of increasing time lag as based on 7 data sets of diurnal R_s and NEE courses during the growing seasons in 2006 and 2007 at the Bugac sandy grassland site. Lagged correlations with (solid lines) and without (dashed line) the effect of covariates (T_s and SWC) were plotted. The two peaks of maximum correlations - at 3 h and 13.5 h in the first case (NEE–R_s relation) - are indicated by arrows, while only one peak (at 13.5 h lag) persisted when investigating the correlation between NEE and the residuals (R_s–res). At maximum (absolute) correlation the relationship between R_s–res and NEE is statistically significant (R = –0.618, N = 28, P < 0.0005, R_s–res = –0.3155 × NEE_{lag} – 0.5403). Negative NEE means CO₂ uptake by the vegetation, thus the correlation between NEE and R (and R_s–res) is also negative.

The high clay content of heavy soils as opposed to the low clay content of sandy soils were coupled to a wide range of TOC and TN contents. The wide range of soil clay contents made it possible to show the quasi linear relation between soil clay content and soil water content optimal for R_s. This is also expected theoretically from the fact that pore size distribution will be pushed toward smaller pore sizes with higher clay contents and these smaller diameter pores will hold the water with more negative water potential. The net result is that plant available soil water content range will be at higher values in soils of higher clay fraction (Thornley and Johnson, 1990; Pintér et al., 2008).

The significant negative correlation between E₀ and TOC may be explained by the availability of labile C substrates. Larger amounts of fresh carbon supply, while serving as substrate for respiration, may inhibit decomposition of plant residues (de Graaff et al., 2010). Thus, SOM decomposition, and therefore R_s, is largely determined by current photosynthesis. Further, it has been observed that greater proportion of C was lost from the labile carbon pool than from the whole soil during an incubation study (Plante et al., 2010). From these reports it seems that, while temperature sensitivity of recalcitrant carbon may be greater than that of the other fractions (Knorr et al., 2005; Xu et al., 2010; Craine et al., 2010), fresh and labile carbon supplies may govern the bulk soil respiration. Labile C

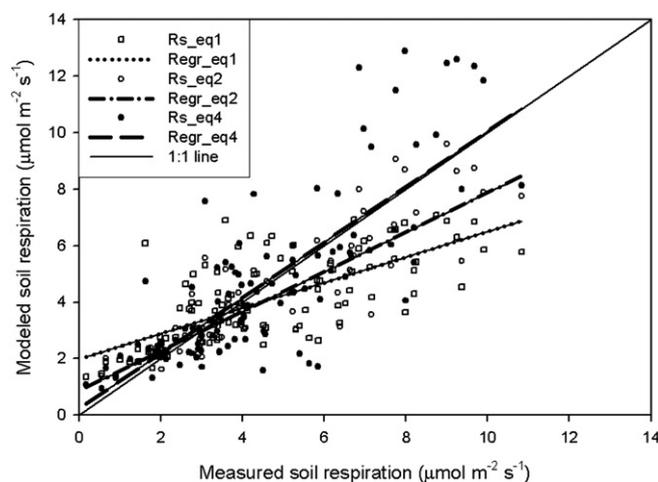


Fig. 5. Modeled vs. measured R_s data at the Bugac site in the period 2004–2008. Modeled data are based on Eq. (1), Eq. (2) and Eq. (4), respectively. Linear regression statistics for the different models are shown in Table 3.

Table 3
Fitted coefficients (R_{10} in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, E_0 in K, SWC_{opt} in vol%, and a , b) from the three models and the coefficients of the linear regressions of measured vs. simulated (by using the three models of Eq. (1), Eq. (2) and Eq. (3)) soil respiration data. Statistical significance levels (*** $P < 0.0001$, ** $P < 0.001$, ^{ns} non significant) of coefficients are shown.

Measured vs. simulated R_s	Fitted coefficients from models 1., 2. and 3.								
	R^2	N	Slope	Intercept	R_{10}	E_0	SWC_{opt}	a	b
Eq. (1)	0.495	104	0.45***	1.98***	2.979***	176.66***	–	–	–
Eq. (2)	0.667	104	0.7***	0.87**	3.469***	215.22***	14.187***	–	–
Eq. (4)	0.644	104	0.98***	0.23 ^{ns}	3.469***	215.22***	14.187***	–0.316**	–0.54 ^{ns}

has also been reported as a better predictor of bulk soil respiration than recalcitrant C (Hernandez and Hobbie, 2010).

In the light of the above, the negative relation between E_0 and TOC found in the present study may be viewed as an example of R_s being governed by easily degradable substrates of lower temperature sensitivity rather than by the recalcitrant pool. The net result, therefore, may be that, while temperature sensitivity of old carbon is greater than that of the labile carbon, temperature sensitivity of the whole system correlates negatively to TOC. This fact is also supported by the findings of Bader and Cheng (2007), that the temperature response of the bulk soil respiration is mediated by the fresh carbon supply, in other words, by the current photosynthetic capacity.

4.2. Response of soil respiration to CO_2 uptake

A short time lag (3 h) between R_s and NEE seemed to be a fast response of respiration rates of roots and root-associated microbes to photosynthesis, but it could also be a result of the two processes being driven by the same climatic variables. The relationship between R_{s_res} after fitting Eq. (2) and NEE showed a diurnal course with a maximum correlation at 10–16 h lag. A similar time lag 7–12 h was found by Tang et al. (2005). Both the short (3 h) and the longer (~12 h) lags were reported in a review (Kuzyakov and Gavrichkova, 2010). The above results from the present study suggest the R_s –NEE correlation peak at the shorter (3 h) lag was probably a manifestation of the lags of root zone T_s and SWC behind irradiance and air temperature (NEE covariates), while the R_{s_res} –NEE correlation at half a day (10–16 h) lags probably reflects the lag caused by combined effects of transport, substrate supply and diffusion to the surface. These results should also be accounted for when using only daytime measurements of R_s for calculating annual fluxes (Li et al., 2008).

Residuals from fitting R_s data to abiotic drivers are strongly determined by the daytime photosynthetic activity. The strength of this relationship is shown by the -0.3 slope of R_{s_res} vs. NEE_{lag} . Assuming NEE of -8 – $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ the contribution unexplained by the abiotic drivers is about -2.4 – $3 \mu\text{mol m}^{-2} \text{ s}^{-1}$. This contribution is substantial yet unaccounted by many of models using only the abiotic drivers.

The R_{s_res} –NEE relationship was successfully incorporated into a soil respiration model. There is a strong request to couple the effects of abiotic and biotic drivers of soil respiration, especially in eddy-covariance studies for the accurate estimation of components of ecosystem respiration. This model integrates a variable measured by EC system, couples the results of eddy and chamber methods and can be used for partitioning NEE.

5. Conclusions

Efforts in modeling soil respiration may become more successful if the most important drivers are considered together. Our general soil respiration model based on abiotic drivers (T_s , SWC) was successfully applied to different soil types. Model parameters showed significant relationships with soil clay content and TOC. As

these data are available for most of the soils, their incorporation into soil respiration models is proposed.

The role of the biotic driver (photosynthetic supply) has been found to be more significant than expected. While the above results are based on seasonal data of integrative character, prediction of instantaneous R_s rates has been demonstrated to be more efficient by using the link between lagged half-hourly NEE and R_s residuals (i.e. after fitting R_s on T_s and SWC data). This link can be utilized to improve soil respiration models in an additive way considering the time-lagged effect of NEE after applying the dependence of R_s on SWC and T_s . Half-hourly net ecosystem CO_2 exchange data are available at all eddy-covariance sites, therefore better estimations of carbon balance components could be easily obtained by using our approach. In this way, the daily variability of soil respiration caused by the current carbon uptake could be also incorporated in respiration models. Models of soil respiration can be greatly improved by using soil moisture and temperature in parallel as predictor variables, which can be complemented with the effect of the lagged instantaneous CO_2 uptake.

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