Soil CO_2 efflux and production rates as influenced by evapotranspiration in a dry grassland

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Abstract

Aims Our aim was to study the effect of potential biotic drivers, including evapotranspiration (ET) and gross primary production (GPP), on the soil CO_2 production and efflux on the diel time scale.
Methods Eddy covariance, soil respiration and soil CO_2 gradient systems were used to measure the CO_2 and H_2O fluxes in a dry, sandy grassland in Hungary. The contribution of CO_2 production from three soil layers to plot-scale soil respiration was quantified. CO_2 production and efflux residuals after subtracting the effects of the main abiotic and biotic drivers were analysed.
Results Soil CO_2 production showed a strong negative correlation with ET rates with a time lag of 0.5 hours in the two upper layers, whereas less strong, but still significant time-lagged and positive correlations were found between GPP and soil CO_2 production. Our results suggest a rapid negative response of soil CO_2 production rates to transpiration changes, and a delayed positive response to GPP.
Conclusions We found evidence for a combined effect of soil temperature and transpiration that influenced the diel changes in soil CO_2 production. A possible explanation for this pattern could be that a significant part of CO_2 produced in the soil may be transported across soil layers via the xylem.

Keywords diel timescale, evapotranspiration, gross primary production, soil CO_2 production, time series analysis

Introduction

Although evapotranspiration is a key process in ecosystem functioning and has global significance, it was only recently found that it may play a direct and significant role in carbon cycling between the plants and the soil by decreasing root respiration rates (Bekku et al. 2011; Grossiord et al. 2012). Thus, evapotranspiration could have a direct influence on soil CO_2 efflux. Soil CO_2 efflux was typically related to air or soil temperature (T_s), sometimes to soil water content (SWC), and in more recent cases to substrate supply (Lloyd and Taylor 1994; Parkin and Kaspar 2003; Carbone et al. 2008; Kuzyakov and Gavrichkova 2010; Balogh et al. 2011). However, abiotic and biotic factors affecting soil CO_2 efflux are acting on different temporal scales and are interacting with each other (Vargas et al. 2010; Savage et al. 2013). Although the need for a proper mechanistic approach to model the effects of the drivers of soil respiration is obvious (Blagodatsky and Smith 2012), the effect of drivers acting on the diel timescale are still poorly understood. New measurement devices and methods, such as soil CO_2 sensors and automated soil respiration systems, provided new

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insights into soil carbon fluxes (Carbone and Vargas 2008). These methodological advances allowed measurements of soil CO_2 fluxes with a frequency, which is adequate and necessary for the analysis of diel patterns (Martin et al. 2012; Savage et al. 2013).

Previous studies typically focused on the decomposition aspect of soil respiration (F_s) dealing with the effect of T_s and SWC. The effect of T_s on F_s has been extensively studied and used as a basis for soil respiration models in spite of its possible artefacts (Subke and Bahn 2010). The often observed phenomenon of hysteresis in the diel temperature response of soil respiration was usually linked to the different depths of CO_2 production and that of T_s measurements according to a number of studies (Pavelka et al. 2007; Ruehr et al. 2009; Savage et al. 2013; Eler et al. 2013). The hysteresis effect increases the uncertainty of the often applied temperature response of soil or ecosystem respiration, and thus also increases the uncertainties of models and data gap-filling procedures. F_s response to SWC can modify the temperature response, especially in dry ecosystems (Carbone et al. 2008; Lellei-Kovács et al. 2011; Fóti et al. 2014). Recent studies proposed parabolic (Moyano et al. 2013) or log-normal relationships (Balogh et al. 2011) for describing the effect of SWC, developed principally at low and high water contents (Davidson et al. 2012).

Biotic drivers represent the supply-side control in soil respiration models. Biotic drivers that integrate over longer time periods, like biomass, relative growth rate and vegetation indices (Jia and Zhou 2009; Huang and Niu 2012) are useful in describing the phenological changes and physiological state of the vegetation. However, these drivers are not suitable to explain the diel variability of soil respiration. In fact, two additional processes could be relevant on the diel timescale, acting in opposite directions: (1) photosynthesis, and (2) transpiration. Firstly, a time-lagged positive effect of photosynthesis on the respiration of roots and root-associated microbes on the order of hours were found by Mencuccini and Hölttä (2010), who explain this with the increase in easily accessible non-structural hydrocarbon sources for the roots and root-associated organisms. Secondly, it was found that the effect of transpiration could reduce root respiration (Aubrey and Teskey 2009; Bloemen et al. 2013a), and this effect is expected to be immediate (i.e. without hysteretic delay).

Removing the effect of the abiotic drivers from the soil efflux signal has helped to clarify the role of other driving variables (Martin et al. 2012). So far, this has been done by multi-temporal correlation approaches (Vargas et al. 2011), by applying better experimental arrangement and data analysis (Graf et al. 2008), and by the proper vertical partitioning of the soil CO_2 production (Davidson et al., 2006). Since the supply-side control on F_s modifies its response to abiotic drivers, this effect could be detected by using residuals of soil respiration models (Balogh et al. 2011).

To test this, a combined approach was used in this study. We used automated systems: (i) eddy covariance, (ii) soil respiration, and (iii) soil gradient systems to analyse the effect of the different drivers on the soil CO_2 production and efflux. By measuring CO_2 concentration gradients in three soil layers, source attribution to these layers was possible. A correlation analysis was used to find relationships with gross primary production (GPP) and evapotranspiration (ET), both representing biotic drivers that potentially could significantly influence total soil respiration. Our research goal was to investigate whether and to what extent evapotranspiration modifies observed soil CO_2 production and efflux rates in grasslands.

Materials and methods

Site characteristics

The vegetation at the Bugac site (46.69° N, 19.6° E, 114 m above sea level) is a semi-arid sandy grassland dominated by *Festuca pseudovina*, *Carex stenophylla* and *Cynodon dactylon*. Mean annual precipitation of the last ten years (2004-2013) was 575 mm, and the mean annual temperature reached 10.4 °C.The soil is a chernozem type sandy soil with high organic carbon content (Table 1).

The study site is located in the Kiskunság National Park and has been under extensive management (grazing) for the last 20 years. The site was grazed occasionally by cattle from the end of April until the end of November in each year. Grazing pressure was about 0.75 animal ha^{-1} during the study period.

Table 1: Soil characteristics: soil texture, total nitrogen (TN), total organic carbon (TOC), pH, root biomass, organic matter (OM), bulk density (BD) and total porosity (φ). Eight replicates of soil cores of 15 cm diameter were collected from four depths at the end of the vegetation season on 29th September 2011.

depth	Sand (%)	Silt (%)	Clay (%)	TN (%)	TOC (%)	pH (KCl)	Root (kg m^{-3})	OM (%)	BD (g cm^{-3})	ϕ (m^3 m^{-3})
0-10	81.18	10.79	8.03	0.19	5.76	7.22	15.15	9.89	0.998	0.605
10-30	81.11	9.62	9.27	0.11	1.32	7.39	9.27	2.21	1.55	0.408
30-50	83.24	7.51	9.24	0.03	0.64	7.92	3.86	1.04	1.59	0.395
50-80	81.42	10.25	8.32	0.01	0.71	8.15	1.51	1.16	1.66	0.37

Gas exchange measuring systems

The three different gas exchange systems used in this study provided data with different levels of spatial integration; the size of the eddy covariance (EC) flux footprint area was larger by several orders of magnitude than the area covered by the soil respiration system (SRS) or the gradient system. The variables derived from EC flux measurements (Fig. 1, GPP, ET) were considered as biotic drivers of soil CO_2 production rates. Greatest care was taken during the establishment of the experiment to select a part of the EC footprint area with the same average soil characteristics and vegetation composition and cover found in the plots where the SRS and gradient systems were installed. Hence, the GPP and ET estimates obtained in this way can be considered representative also for the small-scale SRS and gradient system measurements.

Data from July 2011 to November 2012 were analysed in this study.

Eddy covariance setup

The EC system at the Bugac site has been measuring the CO_2 and H_2O fluxes continuously since 2002. In dry years this grassland can turn into a net carbon source (Nagy et al. 2007),), but the long-term annual sums of net ecosystem exchange (NEE) is a small net sink, ranging between –171 and +106 g C m^{-2} yr^{-1} (Pintér et al. 2010).

The EC system consists of a CSAT3 sonic anemometer (Campbell Scientific, USA) and a Li-7500 (Licor Inc, USA) open-path infra-red gas analyser (IRGA), both connected to a CR5000 data logger (Campbell Scientific, USA) via an SDM (synchronous device for measurement) interface. Additional measurements used in this study were: air temperature and relative humidity (HMP35AC, Vaisala, Finland), precipitation (ARG 100 rain gauge, Campbell, UK), global radiation (dual pyranometer, Schenk, Austria) incoming and reflected photosynthetically active radiation (SKP215, Campbell, UK), volumetric soil moisture content (CS616, Campbell, UK) and soil temperature (105T, Campbell, UK). These measurements were performed as described in Nagy et al. (2007) and Pintér et al. (2010). Fluxes of sensible and latent heat and CO_2 were processed using an IDL program after Barcza et al. (2003) adopting the CarboEurope IP methodology. For a detailed description of data processing and gap-filling see Nagy et al. (2007) and Farkas et al. (2011).

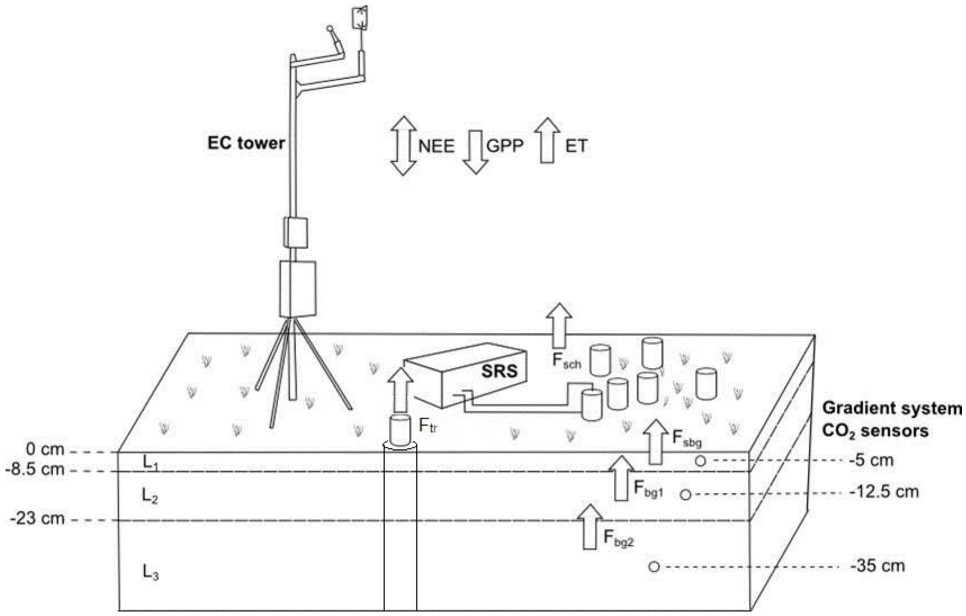

Fig. 1 Experimental setup to measure the different gas fluxes within and over the soil. EC tower: eddy covariance system for measuring net ecosystem exchange of CO_2 (NEE), gross primary production (GPP), evapotranspiration (ET) and climatic variables. SRS: open soil respiration system with 6 chambers for the soil surface CO_2 flux measurements (F_{sch}) and 1 chamber for the trenched plots measurements (F_{tr}). Gradient system: CO_2 sensors inserted into the soil for measuring soil CO_2 concentration and calculating the following fluxes: CO_2 flux at the soil surface (F_{sbg}), below-ground CO_2 flux between layer 2 (L_2) and layer 1 (L_1) (F_{bg1}), below-ground CO_2 flux between layer 3 (L_3) and layer 2 (F_{bg2}).

Soil respiration system

The automated soil respiration system was set up in July 2009. It was upgraded from the 4 chamber to a 10 chamber version in July 2011. The measurement principle is an open dynamic system consisting of an SBA-4 infrared gas analyser (PPSystems, UK), pumps, flow meters (D6F-01A1-110, Omron Co., Japan), electro-magnetic valves, and PVC/metal soil chambers. The chambers were 10.4 cm high with a diameter of 5 cm, covering a soil surface area of approximately 19.6 cm^2. The flow rate through the chambers was 300 ml min^{-1}, which means that the chamber volume is renewed every 40 seconds. The PVC chambers were enclosed in a white metal cylinder with 2 mm airspace in between to stabilize the chamber and to prevent warming by direct radiation. Four vent holes with a total area of 0.95 cm^2 were drilled in the top of the chambers. Vent holes also served to allow precipitation to drip into the chambers. The system causes minor disturbance in the soil structure and the spatial structure of the vegetation. It is applicable without cutting the leaves/shoots of the plants, so it is not disturbing transport processes (phloem and xylem) taking place within the plant stems and roots. It is suitable for continuous, long-term unattended measurements of soil CO_2 efflux and has been used in previous experiments (Nagy et al. 2011). The soil respiration chambers contained no standing aboveground plant material.
After each hour of operation, the system was kept idle for the following hour. Six chambers were used to monitor the total surface CO_2 efflux (F_{sch}) and one chamber for measuring the CO_2 efflux of

trenched plots (F_{tr}). This chamber was moved every 2 weeks among the 4 trenched plots, which were installed in 2010. Plastic tubes were used to exclude roots and root-associated microorganisms in these plots. Soil cores (160 mm diameter, 800 mm deep) were drilled and roots were removed from the soil. The soil was put back into the tubes layer by layer. We started our measurements several months after the installation to avoid artefacts from this disturbance. These plots were only used as a standard for the absence of plant physiological effects.

Data of the six chambers (F_{sch}) were averaged before analysis. As F_{tr} was measured by only one chamber, but at least twice in one measurement cycle (half an hour), these data were also averaged. Individual measurements were eliminated when the residual of an individual data point was outside the range of the mean ± three times the standard deviation of the values in a 21-point moving window centered at this data point.

The system was tested on a calibration tank (CzechGlobe, Brno, Czech Republic) against known fluxes ($F_{sch} = 0.98 \times F_{cal}$, r^2=0.92, n=86) and it was also compared to a LI-6400 system at the study site ($F_{sch} = 0.92 \times F_{LI6400}$, r^2=0.92, n=36).

Gradient method

The soil CO_2 concentration sensors (gradient system) were installed in June 2009. Three GMP343 (Vaisala, Finland) IRGAs were inserted into the soil at depths of 5, 12 and 35 cm, respectively. They were installed in a distance of about 3 m from the eddy station and within 1–2 m from the soil respiration chambers. The sensors were sampled by the CR5000 data logger (also controlling EC measurements) at 10 s intervals and averaged in half-hourly intervals.

The CO_2 fluxes measured by the gradient system were compared to those measured by the soil respiration system. Good agreement was found between the two methods ($F_{sbg} = 0.9334 \times F_{sch}$, r^2=0.61, n=3292).

CO_2 fluxes (F_{sbg}, F_{bg1}, F_{bg2}) were calculated according to Moldrup and Olesen (2000) and Davidson et al. (2006). The water retention curve characteristics in the different layers of the investigated soil were taken from a previous study on the water cycle at the study site (Hagyó 2010). CO_2 productions in the different layers were calculated as the difference between the incoming and outgoing CO_2 fluxes considering the changes of the CO_2 concentrations in the given layer. For a detailed description of the calculations see the Online Resource.

Ancillary measurements

Soil temperatures and volumetric soil water contents were measured at two different depths (5 cm and 30 cm) by the EC system. In order to infer the temperature and soil water content of the intermediate soil layer (L_2), a linear temperature change between the top soil layer (L_1) and the one at 30 cm depth (L_2) was assumed.

Broadband Normalized Difference Vegetation Index (NDVI) values were calculated using the incoming and reflected global and photosynthetically active radiation data according to Wang et al. (2004). Daily maximum radiation was used to calculate the daily NDVI values and running average (1 week window size) of these daily NDVI values were then calculated and used for the analysis.

Soil pH was determined with the KCl method. Soil bulk density was measured using the volumetric core method at 10 cm depth intervals down to 80 cm. Soil texture was determined according to the Hungarian Standard (MSZ-08-0205:1978). Total organic carbon content (TOC) of the samples was determined by sulfochromic oxidation, total nitrogen content (TN) was determined by the Kjeldahl method (Sparks et al. 1996)

Soil respiration models

Three different soil respiration models were used during the data processing to describe the response of the different CO_2 fluxes and CO_2 production rates to the main abiotic and biotic drivers. In the Lloyd-Taylor (1994) model (model 1) soil temperature is the only driving variable

$$F = a \times e^{b \times \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right)} \qquad (1)$$

where F is the soil CO_2 flux (μmol CO_2 m^{-2} s^{-1}), T_s is the soil temperature at 5 cm in Kelvin, *a* and *b* are the model parameters.

Model 2 additionally includes SWC (Balogh et al. 2011):

$$F = a \times e^{b \times \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right) + \left[-0.5 \times \left[\ln \left(\frac{SWC}{c} \right) \right]^2 \right]} \qquad (2)$$

where T_s is the soil temperature at 5 cm in Kelvin, SWC is the volumetric soil water content (%) and *a*, *b* and *c* are the model parameters.

Model 3 extended model 2 by adding NDVI (see Section 2.4) as a driving variable:

$$F = a \times e^{d \times NDVI + b \times \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right) + \left[-0.5 \times \left[\ln \left(\frac{SWC}{c} \right) \right]^2 \right]} \qquad (3)$$

where T_s is the soil temperature at 5 cm in Kelvin, SWC is the volumetric soil water content (%), NDVI is the normalized difference vegetation index and *a*, *b*, *c* and *d* are the model parameters. Nonlinear least-squares fitting was done with Sigmaplot 8.0 (SPSS Inc) and IDL (ITT Visual Solutions, USA).

Time-series analyses of CO_2 productions and fluxes

After calculating the CO_2 production rates in the different soil layers we removed the effect of the drivers by subtracting the output of the above described three models from the CO_2 production rates and analysed the residuals from each model to infer the effects of additional, possibly important drivers. The same analysis was done on the CO_2 efflux rates. The model selection procedure was governed by the dictum to use as low a number of predictors as necessary to still obtain a significant model fit.

The flowchart in Fig. 2 illustrates the main steps of the analysis. In the first step we used lagged cross-correlation to find the time lag with the temperature, as a phase shift between the measured temperature and CO_2 efflux was often detected (Pavelka et al. 2007; Ruehr et al. 2009). As it is proposed that the time lag between the temperature measured in the upper layer of the soil and the CO_2 production could not be longer than a few hours (Ruehr et al. 2009), we used a 0–6 hour time lag window in our analysis. The time lag within this interval with the correlation maximum was chosen for the next step, using zero lag if no positive correlation was found. We used a 5-day moving window approach.

In the second step we fitted the soil respiration models to the measured CO_2 fluxes and CO_2 production rates. Model 1 (Eq. 1) and model 2 (Eq. 2) were used first in 5-day long moving window. The model with higher r^2 was used. The r^2 was calculated as: r^2=1-(residual sum of squares/total sum of squares).

If the fit failed (i.e., either r^2 or the parameters were not significantly different from zero), model 3 was applied with moving window of 10 days, which – if the fit failed again – was increased to 30 days. If the response to the drivers could not be established in the given periods (5, 10, or 30 days), then the parameters of model 3 fitted to the whole dataset were used to calculate the residuals of the fit. The number of cases (days) falling into the different categories are given in the Online Resource.

We assumed that the remaining variance after subtracting the effects of T_s, SWC and NDVI could be attributed to the additional drivers, GPP and ET at the diel timescale. This correlation analysis was performed on the whole dataset.

The residuals were used in the last step (Fig. 2) to calculate the time-lagged correlation between the residuals and ET and between the residuals and GPP within a time-lag window between –8 and 48 hours.

Data processing was done in IDL (ITT Visual Solutions, USA).

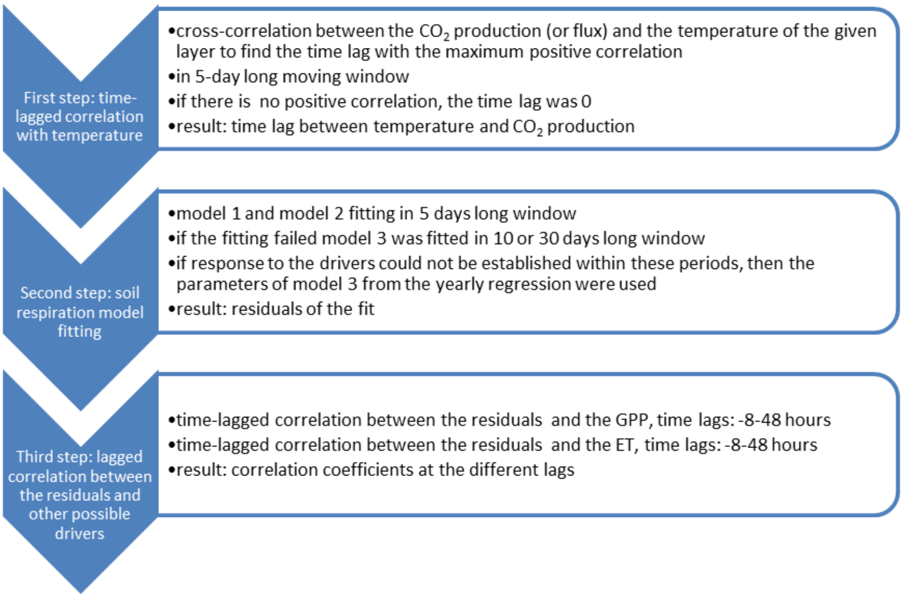

Fig. 2 Flowchart of the data analyses steps.

Results

Meteorological conditions

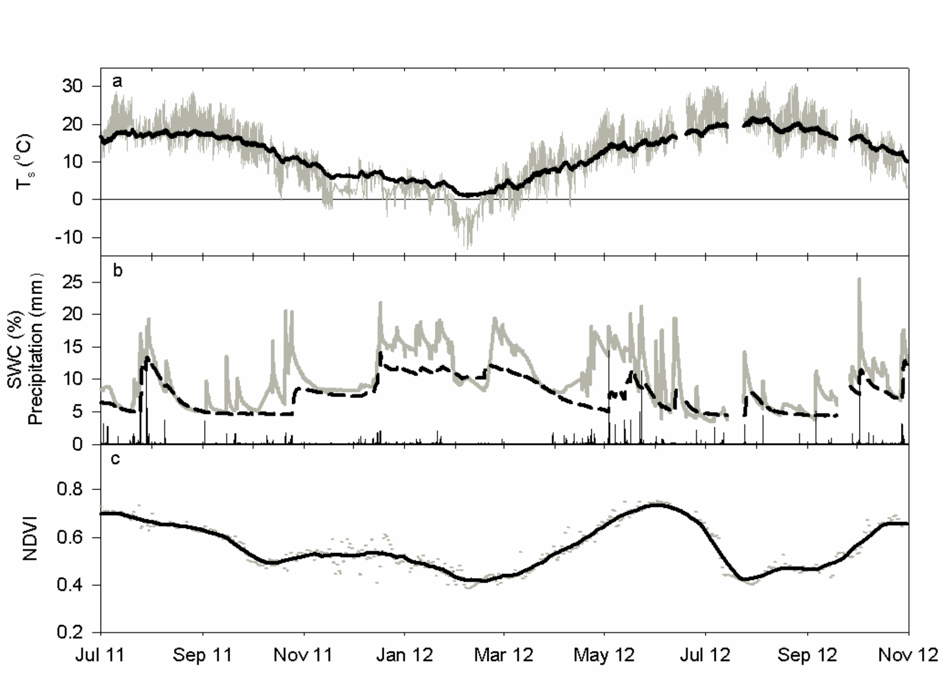

Fig. 3 Half-hourly (a) soil temperature (T_s) at 5 cm (grey line) and at 30 cm depth (black line), (b) precipitation (bars) and volumetric soil water content (SWC) at 5 cm (grey line) and at 30 cm depth (black line) and (c) broadband NDVI values at maximum radiation (grey dots) and their moving average (black line, window size: 10 days) during the study period (1/7/2011–30/10/2012) at the Bugac site.

The study period of 16 months was dry with 520 mm precipitation in total, which is less than the average annual precipitation. The moisture content of the deeper soil layer was usually lower than that of the upper layer (Fig. 3). This phenomenon clearly shows that there was not enough precipitation to replenish the deeper soil layers, even during the winter. The seasonal change of the NDVI was reflected in the seasonal change of NEE and GPP (Fig. 4a, b). The highest NDVI values were observed at the beginning of June 2012, while the lowest occurred during a drought period at the end of July 2012.

Annual course of CO_2 fluxes and production in the soil

Annual courses of CO_2 and H_2O fluxes were determined by the main drivers (Figs. 3 and 4). The effect of the long, dry autumn of 2011 is shown in Fig. 4 as a continuous decrease in all gas exchange rates from the end of August 2011 until the end of the year. Both CO_2 uptake and CO_2 efflux rates were low until the beginning of March 2012. The highest activity was detected in May and June 2012 at time of peak biomass (Fig. 3c). Two active periods could be distinguished in 2012 (Fig. 4b): from April to June and in October. There was an extensive drought period in-between, during which the decrease in respiration activity was less pronounced than that in GPP.
Sudden declines in below-ground fluxes (Fig. 4f, g) were observed several times during the study period. These cases, when flux rates can drop to zero (e.g. F_{bg2}, in May and June 2012), were observed during precipitation events and resulted in large variances in the below-ground CO_2 fluxes within a short period of time.

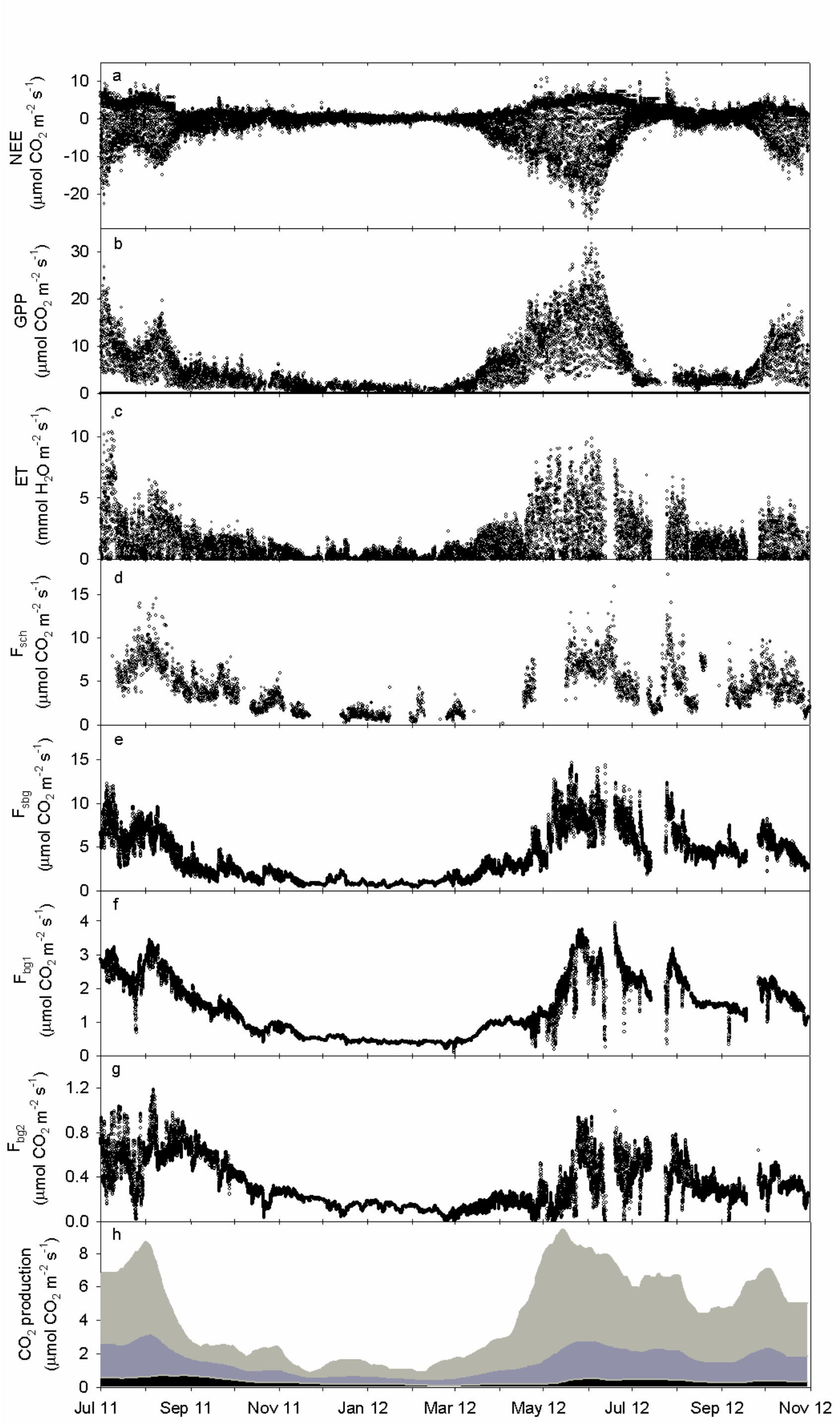

Fig. 4 Seasonal variations of the different half-hourly fluxes as measured by the eddy system (a-c: NEE, GPP, ET), the soil respiration system (d: F_{sch}) and the gradient system (e-g: F_{sbg}, F_{bg1}, F_{bg2}), and (h) mean daily CO_2 production in the different layers during the study period at Bugac (grey: layer 1+2+3, dark grey: layer 2+3, black: layer 3) during the study period (1/7/2011–30/10/2012) at the Bugac site.

The mean daily CO_2 production rates are shown in Fig. 4h. The upper soil layer (L_1) had the highest CO_2 production during the study period, even during winter, and during the drought in autumn 2011. The minimum and maximum contributions of the different layers to the total daily CO_2 production rates were 30–79%, 18–43% and 2–26% with averages 54%, 33% and 13% in L_1, L_2 and L_3, respectively.

Diel courses of gas exchange

CO_2 production was often lower during daytime than during nighttime. In order to investigate this phenomenon, half-hourly averages were selected when NDVI values exceeded 0.68 (Fig. 3c) during the 16 months study period in 2011 and 2012. This selection led to a subset of 58 days. Average diel courses of CO_2 efflux and production rates, ET, GPP and T_s were then computed from the selected data (Fig. 5).

The average CO_2 production within L_1 (the dominant layer) was lower during much of the day than during night-time on the selected days. T_s of the layer, however, followed a different course, peaking during daytime in the late afternoon (Fig. 5a). The average daytime evapotranspiration was high on the selected days (Fig. 5a).

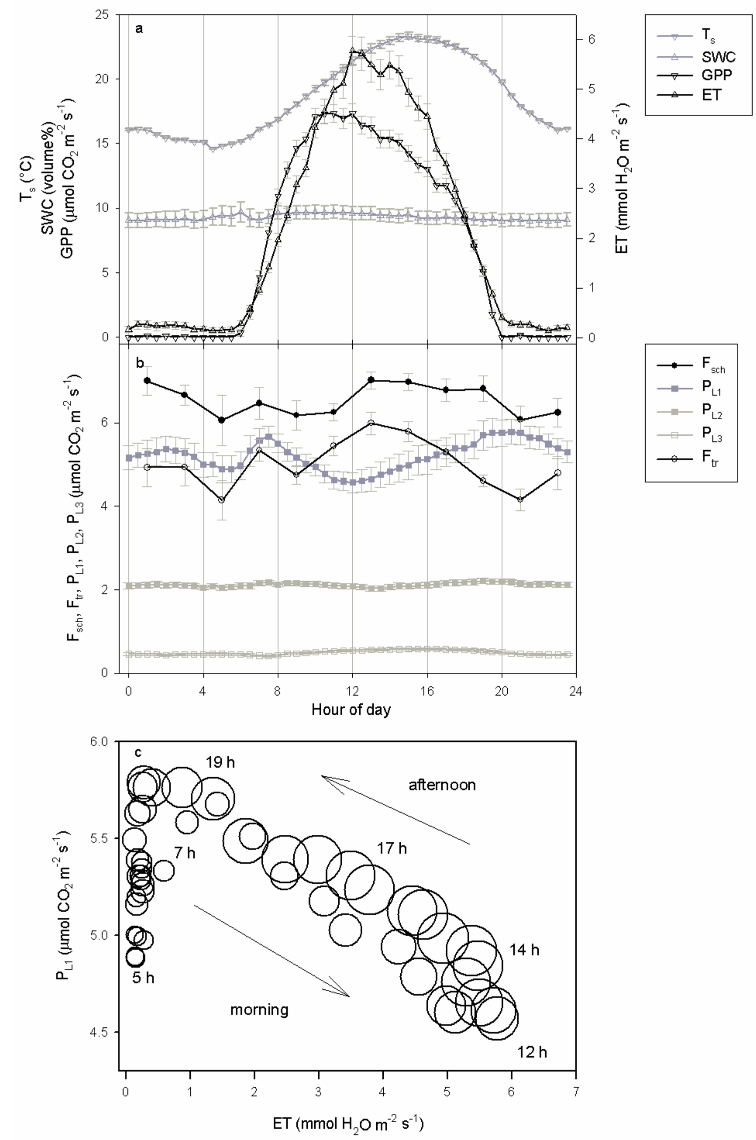

Fig. 5 (a) Average diel courses of soil temperature at 5 cm (T_s), soil moisture at 5 cm (SWC), gross primary production (GPP) and evapotranspiration (ET) in the active period (NDVI≥0.7) in July-August 2011 and in May-June 2012 at the Bugac site. (b) Average diel courses of total soil CO_2 efflux (F_{sch}), CO_2 efflux of trenched plots (F_{tr}) and CO_2 production of the three soil layer (P_{L1}, P_{L2}, P_{L3}) in the same period. (c) Average P_{L1} as a function of average ET in the same period. The size of the circles shows the soil temperature (range: 14.6–23.3 ˚C). Data of 58 days were averaged, with error bars showing the standard error.

Fig. 5b shows the average CO_2 production in the upper layer (P_{L1}) as a function of evapotranspiration (ET), while the circle size shows soil temperature. With increasing soil temperatures during the morning and decreasing ones during the night, a counter clockwise hysteresis of P_{L1} was found. P_{L1} started to decrease after a short rising period (until 7 h) despite the increasing temperature. In parallel with the temperature ET was increasing until midday. P_{L1} started to rise only when ET stopped to increase (from 12 h), peaking when ET was close to zero but T_s was still high (20 h). During the night P_{L1} was decreasing again as well as soil temperature. A positive correlation with soil temperature was found during the night and at midday (12–14 h), leading to the observed hysteresis. The minimum CO_2 production rate was 21% lower than the maximum (4.56 and 5.78 µmol CO_2 m^{-2} s^{-1}, respectively), although the maximum was measured at the lower soil temperature (21.3 and 18.7 ˚C).

Time lag between transpiration, C uptake, environmental conditions and respiration losses

Summary of model results and residual analysis

In the case of F_{sch} the Lloyd-Taylor model (model 1, r^2=0.43) gave lower goodness-of-fit value than the model including the log-normal soil moisture response (model 2, r^2=0.56). The incorporation of NDVI into the soil respiration model improved r^2 further by 13% (model 3, r^2=0.689) (Table 2).

Table 2: r^2 values, number of data points (N), coefficients after fitting model 1, 2, 3 (Eq. 1–3) to half-hourly average soil surface CO_2 fluxes (F_{sch}, F_{tr}), below-ground fluxes (F_{bgs}, F_{bg1}, F_{bg2}) and CO_2 production rates (P_{L1}, P_{L2}, P_{L3}) of the full study period. Statistical significance levels of the coefficients and model fitting were P<0.0001 in all cases.

		r^2	N	a	b	c	d
Model 1 $F = a\times e^{b\times\left(\frac{1}{56.02}-\frac{1}{T_s-227.13}\right)}$	**F_{sch}**	**0.431**	3590	2.53	161.55	-	-
	F_{tr}	0.5	3349	1.89	194.96	-	-
	F_{sbg}	0.54	22032	2.21	246.6	-	-
	F_{bg1}	0.68	22032	0.99	236.2	-	-
	F_{bg2}	0.19	22020	0.15	242.01	-	-
	P_{L1}	0.38	21807	0.76	273.4	-	-
	P_{L2}	0.67	21999	0.72	262.9	-	-
	P_{L3}	0.35	21954	0.17	281.07	-	-
Model 2 $F = a\times e^{b\times\left(\frac{1}{56.02}-\frac{1}{T_s-227.13}\right)+\left[-0.5\times\left[\ln\left(\frac{SWC}{c}\right)\right]^2\right]}$	**F_{sch}**	**0.555**	3544	2.99	208.05	12.43	-
	F_{tr}	0.479	3349	2.17	195.76	13.08	-
	F_{sbg}	0.58	22032	2.62	308.1	14.34	-
	F_{bg1}	0.7	22032	1.08	233.3	8.03	-
	F_{bg2}	0.49	22020	0.303	189.19	6.08	-
	P_{L1}	0.48	21807	1.85	418.39	31.7	-
	P_{L2}	0.69	21999	0.79	297.9	10.74	-
	P_{L3}	0.505	21954	0.26	279.16	7.8	-
Model 3 $F = a\times e^{d\times NDVI+b\times\left(\frac{1}{56.02}-\frac{1}{T_s-227.13}\right)+\left[-0.5\times\left[\ln\left(\frac{SWC}{c}\right)\right]^2\right]}$	**F_{sch}**	**0.689**	3544	0.58	177.65	11.85	2.93
	F_{tr}	0.555	3349	0.53	169.57	12.76	2.5
	F_{sbg}	0.665	22032	0.383	231.23	12.33	3.42
	F_{bg1}	0.812	22032	0.258	181.46	6.95	2.66
	F_{bg2}	0.58	22030	0.083	268.17	6.31	1.98
	P_{L1}	0.495	21184	0.38	216.67	14.79	3.12
	P_{L2}	0.751	21185	0.224	234.25	9.69	2.48
	P_{L3}	0.58	21184	0.085	315.07	7.54	1.84

The average soil CO_2 efflux measured at the surface (F_{sch}) showed no correlation with average ET nor with the average soil temperature in the active period when NDVI values exceeded 0.68, even when a time lag of up to 5 hours was considered, while fluxes from the vegetation removal treatment (F_{tr}) showed best correlation with temperature at 0 hours time lag (data not shown). We however had expected that the effect of ET on P_{L1} should also be found in the surface soil CO_2 efflux, therefore we asked the question whether this effect can be seen in the residuals. We used model 3 to remove the effect of the main abiotic drivers from the whole dataset. For F_{sch} residuals a significant negative correlation was found with ET during the active periods, selected by high NDVI values (≥ 0.68). Contrastingly, no correlation was found between F_{tr} residuals and ET for the same period.

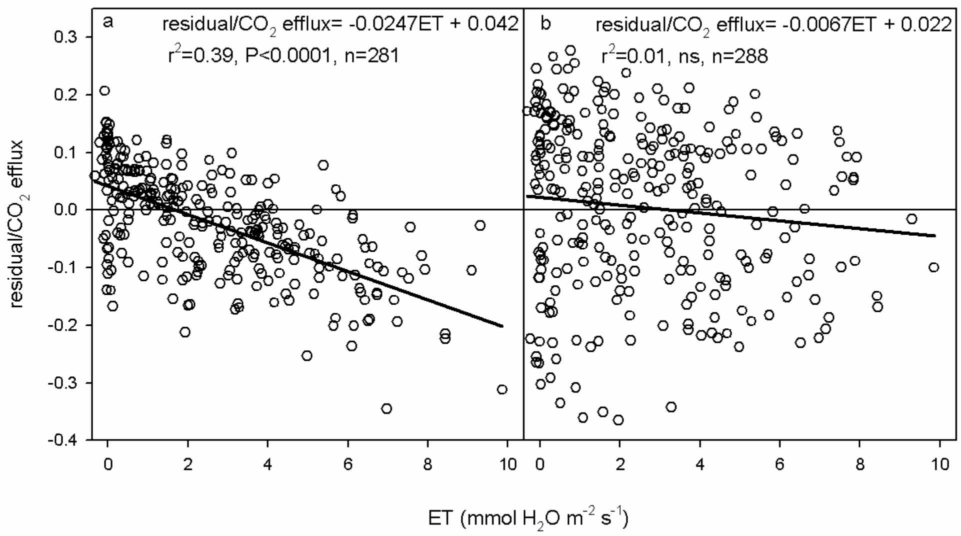

Fig. 6 Standardized residuals of (a) surface CO_2 efflux (F_{sch}) and (b) trenched plots without roots (F_{tr}) as a function of ET values in the active periods with NDVI ≥0.68. The linear regressions are shown (solid line).

To quantify the effect of ET on soil respiration rates, standardized flux residuals were plotted as a function of ET. At low ET values, F_{sch} was 5% higher than predicted by the model. At high ET rates, the measured F_{sch} was significantly lower than predicted (–10 to –20% at ET > 6 mmol H_2O m^{-2} s^{-1}). Overall, the difference between the standardized residuals at low and high evapotranspiration rates was about 0.2, which means a 20% difference compared to the measured CO_2 effluxes (Fig. 6a).

Results of time-series analyses

Correlations between F_{sch}, P_{L1-3} and abiotic (T_s, SWC) and biotic drivers (ET, GPP) were further analysed with time-series analyses of the whole dataset in order to reveal the detailed diel and seasonal correlations.

Time lagged correlations between F_{sch}, P_{L1-3} and T_s were calculated in the first step of our analyses (cf. Fig. 2) using moving windows of 5 days length. No consistent time lag was found between the two variables. In the case of F_{sch} the correlation coefficient was statistically significant in 158 out of the 345 cases (days), with a zero lag being the most frequent time lag (92 cases or 58% of these cases). Cases with significant correlations were uniformly distributed over the study period with no seasonal preference (data not shown).

Time lagged correlation was further analysed both with ET and GPP for the full study period. Residuals were calculated after subtracting the main effects of soil temperature, soil water content and NDVI (Fig. 2) from F_{sch} and P_{L1-3} rates. These residuals were then correlated with ET and GPP. As the time lags of the significant correlations were not normally distributed, we calculated the mode of the time lags for F_{sch} and the CO_2 production in the different layers.
Strong negative correlations between the residuals and ET were found mostly between –2 and 5 hours time lag in the upper two layers, but with longer time lags in the third layer (Online Resource Fig. 2 b-d). Approximately 12–16 hours after the negative correlation peak there was a positive correlation in all cases. The annual course of the significant correlations shows that the time lag of the negative correlations slightly changes during the year (Online Resource Fig. 2). There was no clear diel pattern during winter. The modes of time lags of the significant negative correlations for F_{sch}, P_{L1}, P_{L2} and P_{L3}, respectively were at 1.5, 0.5, 0.5, 4.5 hours.
In the case of the GPP we assumed that the positive correlation maximum represents the connection between GPP and CO_2 production. Positive significant correlations could be found during the whole study period, but the correlation coefficient was lower than that with ET (Online Resource Fig. 2 e–h). The modes of the time lags of the significant positive correlations for F_{sch}, P_{L1}, P_{L2} and P_{L3}, respectively were at 15, 11, 18, 20 hours.

Discussion

Annual course of CO_2 fluxes and production in the soil

The seasonal courses of the CO_2 fluxes followed the changes of the main environmental drivers, as temperature (as well as incoming radiation) and the amount of soil water available to plants. There were differences between the two autumns studied: the second half of 2011 was very dry, the soil CO_2 production rates in autumn 2012 were two times the rates observed in autumn 2011 (Fig. 4). Significant rain events affected the belowground CO_2 fluxes negatively, especially the below-ground fluxes (Fig. 4). The observed decline (even down to zero) in these fluxes was mainly caused by the indirect effect of precipitation: the increasing CO_2 concentration due to the enhanced respiratory activity on excess moisture in the upper soil layers decreased, or even reversed the normal CO_2 gradient within the soil (Nagy et al. 2011).
The distribution of the CO_2 production rates along the three soil layers corresponded well with our expectations. It was expected that the upper layer would be the most significant in contributing to total CO_2 efflux (Davidson et al., 2006; Verma and Kelleners, 2012), since it contains the majority of active roots and associated microbial communities (Subke and Bahn 2010) as well as the majority of the fresh SOM.. In spite of the highly variable water supply, the upper layer was the main contributor to the total CO_2 efflux even under drought conditions (Fig. 4).

Diel courses of gas exchange

CO_2 production rates were often found to be higher during the night than during daytime (Fig. 5a) in the active periods. Several factors that could be the reason for this phenomenon were considered. Since highest CO_2 concentrations up to 1400 ppm at 10 cm above ground level are found during nights with no wind, or low wind velocity, the question is whether these high concentrations in the air are actually rather a result of CO_2 advection from surrounding areas which would then be erroneously interpreted as higher apparent productivity in the soil. If this were the case, then we would expect an apparently positive correlation between calculated soil CO_2 production (as a direct function of measured CO_2 concentration in the soil), and soil temperature, based on the fact that soils tend to cool less under calm and low wind speed conditions, and consequently temperature stays highest in these periods. Our data, however, show the opposite: a significantly negative correlation between P_{L1} and CO_2 concentration at 10 cm during nights of the active period. This finding also excludes the potential interpretation that soil temperatures remain warmer during calm nights (which would result in increased P_{L1}) than during more turbulent nights.

Alternatively, the increase of both autotrophic and heterotrophic respiration due to water redistribution from deeper layers to the dry surface soil layer (Carbone et al. 2008; Ruehr et al. 2009), could explain the higher nighttime production. However, the water content of the upper layers showed no significant changes during the day (0.7 % on average during the selected period with NDVI ≥ 0.68) as would be required to maintain this hypothesis. Another explanation could be increased water availability during the night and especially in the early morning when the surface water content can be increased by dew formation. But this phenomenon possibly only affects the uppermost layer (litter and the surface of the soil) and is unlikely to influence deeper layers.

From this we conclude that it may not be the increase in respiration at night that needs further attention, but the decrease in respiration during the day. It was recently found that transpiration can modify the apparent autotrophic CO_2 production by the transport of CO_2 in the xylem of trees (Grossiord et al. 2012; Bloemen et al. 2013a; Bloemen et al. 2013b). Therefore, the transpiration should be considered as a factor potentially affecting apparent soil CO_2 production, not only in trees, but also in grasses, herbs and forbes. CO_2 produced in the soil that equilibrates with the CO_2 in the xylem stream in the roots bypasses the conventional soil chamber measurements, and thus we can hypothesize that a negative correlation with a short time lag should be found between respiration processes and ET. Our measurements are in agreement with this hypothesis: a negative correlation was found between P_{L1} and ET. P_{L1} was correlated with soil temperature at night and during midday (12–14h) when ET was almost constant. Contrastingly, during times with little temporal changes in T_s but relevant changes in ET (e.g. during the afternoon, 14–19 h) a negative correlation between P_{L1} and ET led to the hysteresis loop seen in Figure 5c. These two factors seemed to govern the changes in P_{L1} during the entire day. The short rising period of P_{L1} in the early morning could be attributed to the temperature changes, but when ET became significantly higher (more than 1 mmol H_2O m^{-2} s^{-1}) P_{L1} started falling. Another turning point was with decreasing ET during late afternoon: P_{L1} was rising to its maximum after ET started to decline, despite the decreasing temperature. Our results show that P_{L1} was lowered by about 20% due to the effect of transpiration. No correlation was found between F_{sch} and T_s, nor ET. However, F_{tr} was positively correlated with both T_s and ET. This difference indirectly shows the significance of living roots in the soils and their potential to modify soil CO_2 efflux via transpiration.

Time lag between evapotranspiration, C uptake, environmental conditions and respiration losses

Summary of model results and residual analysis

The Lloyd-Taylor soil respiration model extended by a log-normal function of soil moisture and by an exponential function of NDVI was able to properly describe the response of soil respiration to these drivers at our site. The log-normal shape of soil moisture-respiration response was proposed before (Balogh et al. 2011; Moyano et al. 2013). It originated from the Michaelis-Menten kinetics of the response of respiration to substrate and oxygen availability (Davidson et al. 2012). The incorporation of NDVI into the soil respiration model improved the explanatory power of the model similarly to the findings of Huang and Niu (2012). As the reflectance and greenness of the surface change with the phenological changes of the vegetation, photosynthesis-related vegetation indices can be used to estimate the effect of CO_2 uptake on respiration (Huang et al. 2012), or even the ratio of root-derived CO_2 in ecosystem respiration (Wang et al. 2010), so it can be incorporated into soil respiration models (Huang and Niu 2012).

After subtracting the effect of the main drivers by fitting model 3 we found a significant negative correlation between the residuals of the soil respiration rates and ET when NDVI was high. The difference between soil respiration at low and at high transpiration rates could reach as much as 20% as compared to the measured rates. Similar results were obtained when only the CO_2 production of the upper layer was considered (Fig. 5). The effect is not so high as it was found for trees (Aubrey and Teskey 2009), but still it was significant, hence it should be considered in soil CO_2 production models. This suggests that calculations and modelling based on daytime measurements in the active periods could significantly underestimate the real CO_2 production of the soil.

Results of time-series analyses

Contrary to the findings of other studies (Davidson et al. 2006b; Vargas et al. 2010), there was no consistent time lag between soil temperature and soil CO_2 efflux, neither at higher, nor at lower soil water contents (data not shown). The most frequent time lag with significant correlation between soil temperature and soil CO_2 efflux (F_{sch}) was 0 hours and the average lag time of significant correlations was 1.15 hours. These time lags are in good agreement with the CO_2 production rates, which can be explained by the upper layer (0-8 cm) being the main contributor to the total CO_2 efflux with the calculated diffusion rates.

Several studies (e.g. Moyano et al. 2007; Kuzyakov and Gavrichkova 2010; Hopkins et al. 2013) proposed CO_2 uptake (GPP) as a driver of soil (root) respiration, while others (e.g. Aubrey and Teskey 2009; Bloemen et al. 2013a) stated that the transpiration has a major effect on the diel variability of soil CO_2 efflux. The daily courses of transpiration and GPP are very similar due to the stomatal co-regulation of both processes (Hetherington and Woodward 2003). Therefore, it could be difficult to separate the two effects. In this study, we found similar time-lagged correlations of CO_2 production with ET and GPP, but the correlations were stronger in the case of ET during the whole study period.

The effect of CO_2 uptake can be significant according to girdling studies (Högberg et al. 2001; Jones et al. 2009), but it can be assumed that its effect on the diel variability can be less pronounced due to the longer turnover time of soluble carbohydrates compared to diel changes (Högberg et al. 2008). Moreover, starch accumulation during the day ensures the continuous carbohydrate export from leaves to non-photosynthetic tissues at night, avoiding large fluctuations on diel scale (Lu et al. 2005; Mencuccini and Hölttä 2010).

But the effect of ET is expected to be instantly: root water uptake should keep pace with transpiration (Aston and Lawlor 1979), especially in herbaceous plants where the role of capacitance is probably minor as compared to trees (Högberg and Read 2006). In this study, a shorter time lag was found in the response to ET (0.5 hour time lag in the upper soil layers) compared to a longer one with GPP (11–18 hours in the upper soil layers). The latter corresponds well with an average a time lag of 12.5 hours between CO_2 uptake and soil respiration found by different studies in grasslands, while this time lag increased to 22 hours if only field studies were considered (Kuzyakov and Gavrichkova 2010).

Further, the time lags of the peak correlation changed during the study period. Longer time lags for ET and GPP were obtained in the most active periods for all layers. This can be explained by the fact that transport routes of carbon and water get longer as the shoot and the root systems become longer in the course of the season (Mencuccini and Hölttä 2010). The same effect could be important in deeper layers: the longer the route within the plant, the longer the time lags between the physiological processes.

Implications for soil and ecosystem respiration measurements

According to our results, soil CO_2 production could be decreased by 20% due to the effect of evapotranspiration (Fig. 7) in the active periods. Since manual soil respiration measurements are usually made during daytime due to practical reasons, response functions to environmental drivers derived from these measurements could underestimate the all-day CO_2 efflux. Given the amount of CO_2 emitted through the soil to the atmosphere is lower during daytime due to the xylem-transported CO_2, but does it have any effect on the calculations of ecosystem respiration (R_{eco})? Daytime R_{eco} estimations are usually based on the temperature response observed at night (Reichstein et al. 2005), thus when the soil CO_2 efflux to the atmosphere has shown to be higher at our site. However we should consider that the transpiration stream does not affect the amount of CO_2 produced under the surface, our results only suggest that the transport route could be different at daytime and nighttime. Therefore it can be assumed that this phenomenon has no influence on GPP estimations in grasslands. Bloemen et al. (2013b) found that most of the xylem-transported CO_2 was respired to the atmosphere through stem and branch efflux in trees. However, the important difference between herbaceous plants and trees in this respect is that the transport route is shorter and that the xylem sap CO_2 transport happens in the vicinity of the photosynthetic tissues. Therefore the re-fixation of the xylem-transported CO_2 is more likely in herbaceous plants.
Our results showed a nice example how the different gas fluxes are tightly coupled in the soil-vegetation-atmosphere system. Soil respiration models considering this phenomenon could be able to explain a large part of diel variation and improve the goodness of annual sum estimations and GPP partitions.

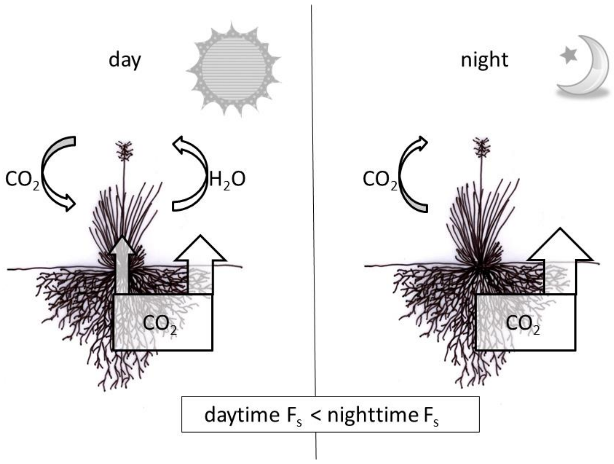

Fig. 7 The difference between daytime and nighttime soil respiration processes in grasslands: a significant part of the CO_2 produced in the soil could be transported via transpiration stream and assimilated in the plant during daytime.

Conclusions

Three automated techniques of CO_2 gas exchange measurements were used to quantify the effects of principal biotic and abiotic factors on soil CO_2 production on different (from diel to annual) timescales. We found that besides temperature and soil moisture, transpiration was controlling the diel course of the CO_2 production. After subtracting the effects of the main abiotic drivers we found strong negative correlations between evapotranspiration and soil CO_2 production rates, and less strong, but still significant positive correlations between gross CO_2 uptake and soil CO_2 production. Since our results suggest that the daytime CO_2 production measurements in grasslands could be underestimated due to the CO_2 transport in the xylem, our findings strongly suggest that the effect of transpiration should be considered both in soil respiration models and in field measurement protocols.

Our results provide further evidence of a potential hidden CO_2 transport within the plants, which is not measured by traditional CO_2 gas exchange techniques. Estimations of soil CO_2 production and GPP would hence benefit from explicit consideration of this phenomenon.

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