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Rhizospheric, mycorrhizal and heterotrophic respiration in dry grasslands

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ABSTRACT

The main objective of the present study was to determine the contributions of autotrophic and heterotrophic components to the total soil CO_2 efflux over three years with high-frequency data acquisition by means of automated measurements. Soil CO_2 efflux was measured continuously by using an automated open system of 10 soil respiration chambers in a sandy grassland in Hungary. Mesh-collar technique was applied to separate the components of the total respiration. Data were collected (1) in root-exclusion (Exr), (2) in root- and mycorrhiza exclusion (Exrm) and (3) in control plots (Exc, roots and mycorrhiza included). We fitted three different models to describe the dependence of total soil CO_2 efflux measured on the Exc (Rs), CO_2 efflux measured on Exr (R_{TR}) and CO_2 efflux measured on Exrm (R_{TRM}) on abiotic and biotic drivers. The best fitted model (based on AIC) was later on used in a simulation process.

The contribution by rhizospheric respiration (simulated, R_{rhizo*}) was 36 ± 21%, the contribution by mycorrhizal respiration (simulated, R_{myc*}) to the total soil respiration was 9 ± 9% while the contribution by heterotrophic respiration (simulated, R_{het*}) was 55 ± 21% on average. Measured mycorrhizal respiration (R_M) responded to GPP with a time lag of 0–2 days in active period. Drought affected the autotrophic component of soil respiration the most intensively: raise of soil water content resulted in increase of R_S by 175% while R_{TR} and R_{TRM} increased by 127% and 93%, respectively.

The results highlight the fact that it would be useful to establish and apply separate models for each component.

1. Introduction

Soil respiration is usually divided into heterotrophic and autotrophic components [1–6]. These were often investigated during short-term (half to one year or even for a shorter time) experiments studying trees [7–11]. Investigating the contributions made by the different soil respiration (R_S) components to the total soil CO_2 efflux changes over a period of time and studying the course of the components and their drivers over a longer time period may contribute to our better understanding of the processes involved.

In terms of soil microbiota the mycorrhizal fungi are considered to be one of the key components of sustainable soil-plant systems especially in arid ecosystems [12]. Plants provide the fungi with fixed carbon, accounting for up to 20% of the total carbon fixation by the plant [13,14]. Mycorrhizal respiration is considered autotrophic [15], representing an important pathway of carbon flux in the soil. Besides the mycorrhizal respiration, roots and other root-associated microbes (rhizospheric component) contribute to R_a as well. The other major part of the total soil CO_2 efflux is the heterotrophic respiration, which is the result of the decomposition of soil organic matter (SOM) and litter [16]. In forests the estimated ratios of the autotrophic respiration vary between 50 and 60% [17] but this value can range from 10% to 90% seasonally [10,18]. In temperate grasslands the contribution of the autotrophic component to the total soil respiration amounted to about 40% on annual scale [19].

Controversial results were reported about the responses of the

Abbreviations: ASRS, automated soil respiration system; BD, bulk density; EC, eddy covariance; Exc, control (no exclusion) treatment; Exr, root-exclusion treatment; Exrm, root- and mycorrhiza exclusion treatment; GPP, gross primary production; NDVI, normalized difference vegetation index; R_S, total soil respiration; R_{TR}, measured CO_2 efflux of the root-exclusion treatment; R_{TRM}, measured CO_2 efflux of the root-and mycorrhiza exclusion treatment; R_{het*}, simulated CO_2 efflux of the root-and mycorrhiza exclusion treatment; $R_{(het+myc)*}$, simulated CO_2 efflux of the root-exclusion treatment; SOM, soil organic matter; SWC, soil water content; SWC_n, normalized SWC; T_s, soil temperature; TOC, total soil organic carbon; TN, total soil nitrogen

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Table 1
Soil characteristics: soil texture (Sand, Silt, Clay), total nitrogen (TN), total organic carbon (TOC), pH, root biomass, bulk density (BD). Four replicates of soil cores of 15 cm diameter were collected from four depths at the end of the vegetation season on the 26th September 2011.

depth (cm)	Sand (%)	Silt (%)	Clay (%)	TN (%)	TOC (%)	pH (KCl)	Root (kg m^{-3})	BD (g cm^{-3})
0–10	81.18	10.79	8.03	0.19	3.04	7.22	15.15	0.998
10–30	81.11	9.62	9.27	0.11	1.79	7.39	9.27	1.55
30–50	83.24	7.51	9.24	0.03	0.47	7.92	3.86	1.59
50–80	81.42	10.25	8.32	0.01	0.19	8.15	1.51	1.66

different soil respiration components to the main environmental factors. Some studies indicated that heterotrophic and autotrophic components showed no differences in their temperature sensitivity [7,20,21], whereas other authors observed significant differences [2,22–24]. Soil moisture is another important environmental driver of soil CO_2 efflux [25]. Heterotrophic respiration responds primarily to temperature and soil moisture, while mycorrhizal respiration responds more readily to PAR in an indirect way in grasslands under sheep grazing [19]. Drought events generate carbon loss from the soil and decrease net primary production [26,27]. Several studies reported the significant effects of drought on the soil respiration components [28,29], although the observations were again controversial. Some authors found that the heterotrophic component of soil CO_2 efflux was more sensitive to the drought stress events than the autotrophic component [30–32], while other studies suggested that the drought stress period mostly decreased the rates of root- and mycorrhizal respiration compared to the heterotrophic component originating from microbial respiration [33–35]. The reason for these contradictory findings could be the functional differences of the study sites and vegetation types [36].

In addition to the abiotic drivers biotic factors are also relevant [37,38], since biotic effects can modify the response to the abiotic ones [17]. Moreover, biotic factors can strongly influence soil CO_2 efflux at different time scales (both diel and seasonal scales) [39,40], therefore their effect should be considered in the long-term estimations. However, the effect of the biotic drivers needs clarification since the different components have different responses. Two different types of response were given by autotrophic components and heterotrophic components to the changes in gross primary production (GPP) and temperature in croplands [5], where autotrophic components was mainly independent of temperature and driven by GPP, while heterotrophic components responded mainly to temperature.

Recent methodological advances in automated soil respiration measurement systems allowed high frequency measurements to be taken [5], providing insights into the variations of soil CO_2 efflux at different time scales [41]. Continuous monitoring provides huge quantities of data, which help to better understand the responses of the components to biotic and abiotic factors. The estimation of the CO_2 efflux components could also be further refined by simultaneous manipulation studies. Several methods were adopted to separate the components of total soil respiration. The trenching and girdling methods based on the idea of interrupting the phloem transport from the leaves to the roots were adopted in forests [15]. The clipping and shading methods were applied mainly in grasslands and shrub communities [37]. Partitioning the soil CO_2 efflux by isotopic methods [3] can have large uncertainties due to the complexity of substrates [42]. The use of membrane mesh-collar technique [2,6,43] could also supply useful data for detailed studies in this field. The advantages and disadvantages of the different methods were reviewed in detail by Refs. [18] and [44], highlighting the drawbacks of the partitioning methods e.g. the changing soil water content in the treatments [2,17,44,45]. If there are significant changes in the environmental factors due to the experimental techniques, they should be taken into account because the changes in soil water content can strongly modify the total soil respiration [46,47].

The aims of the present study were:

1) to estimate the contributions of rhizospheric, mycorrhizal and heterotrophic components to the total soil CO_2 efflux in a dry sandy grassland, based on *in situ* use of membrane mesh-collar technique, combined with high temporal resolution automated chamber-based measurements in a 3-year period,
2) to analyze the response of the soil respiration components to the main environmental factors such as soil temperature (T_s), soil water content (SWC) and to biotic variables as normalized difference vegetation index (NDVI) and gross primary production (GPP).

2. Materials and methods

2.1. Site description

The study was performed from August 2010 to May 2014 in the semi-arid sandy grassland at the Kiskunság National Park in Hungary, at Bugac site (location 46.69 N, 19.6 E, 114 m a. s. l.). The soil type is chernozem with high total organic carbon (TOC) and total nitrogen (TN) contents (Table 1). The CO_2 and H_2O fluxes have been continuously measured by the eddy covariance system at the Bugac site since 2002. The average annual temperature was 10.4 °C and the mean annual precipitation was 575 mm (2004–2013). The site was used as a pasture with extensive grazing by Hungarian grey cattle in the last 20 years. Stocking density was 0.23–0.58 animal ha^{-1} between 2004 and 2012. The vegetation is dominated by *Festuca pseudovina*, *Carex stenophylla*, *Cynodon dactylon, Poa spp.* [48].

2.2. Partitioning method and experimental setup

In September 2010, three treatments were established for the experiment (Fig. 1). Ten soil cores (80 cm long and 15 cm inner diameter) were excavated, sieved and then root-free soil was re-packed layer by layer into (1) 5 repetitions of vertically placed PVC tubes giving the root- and mycorrhiza exclusion treatment (Exrm), (2) 5 repetitions of vertically placed PVC tubes with windows of micro-pore inox meshes (40 μm pore size) for the root-exclusion treatment (Exr), while (3) control plots (undisturbed soil and vegetation, Exc) were also selected. Inox mesh was used to exclude roots, but let the mycorrhiza filaments grow into the tubes. The tubes were placed at a distance of 5 m from the eddy covariance tower in the southern direction, while the control plots were selected in the vicinity of the tubes (within a distance of 2 m). The distance between the centers of the tubes was 50 cm.

Grass litter was present at the topsoil of the control plots, while in case of Exr and Exrm treatments we did not add litter to the topsoil of the PVC tubes, therefore litter in these treatments originated from the surrounding vegetation. Seedlings from the PVC tubes were regularly removed.

2.3. Soil and mycorrhiza analysis

Soil samples were collected from four depths (0–10 cm, 10–30 cm, 30–50 cm and 50–80 cm) in 2-2 replicates from the root-excluded and root- and mycorrhiza excluded soil cores at the beginning of the study. Soil characteristics are shown in Table 1.