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Components of soil respiration

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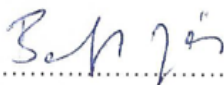
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BACKGROUND AND OBJECTIVES

Recently grasslands are receiving more and more attention in both international and domestic scientific life due to their spread and their ability to sequester or emit carbon dioxide (CO_2). Soil respiration (R_s, CO_2 emitted from soil) is one of the largest components of the carbon turnover of ecosystems, so it is also crucial in defining the CO_2 balance of systems. Soil respiration means a continuous, variable flow of CO_2 from the soil to the atmosphere, which can be separated into different components. Soil respiration is usually divided into heterotrophic and autotrophic components. 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 addition to the abiotic drivers biotic factors are also relevant, since biotic effects can modify the response to the abiotic ones. Moreover, biotic factors can strongly influence soil CO_2 efflux at different time scales (both diel and seasonal scales), 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. Recent methodological advances in automated soil respiration measurement systems allowed high frequency measurements to be taken, providing insights into the variations of soil CO_2 efflux at different time scales. Continuous monitoring provides huge quantities of data, which help to better understand the responses of the components to biotic and abiotic factors.

Soil CO_2 emissions can be measured in several ways. The most common techniques are the dynamic gas exchange chambers and gradient systems. One of the disadvantages of commercially available chamber systems is that they are very expensive to obtain. On the other hand, due to the relatively large size of the gas exchange chambers (internal diameter 10 cm or more, eg. LI-8100, EGM-4) they are difficult to use in closed grasslands, and the above-ground parts of the vegetation have to be cut regularly so their respiration activity should not interfere with the sequestration of CO_2 streams from the soil. An additional difficulty may be the issue of operational safety, since in the case of closed system devices, the closing and opening of the chambers is ensured by moving parts. Failure of these in field conditions (eg. an obstacle to the movement of the cover) may result in an unnoticed incorrect measurement.

The automated soil respiration system (ASRS) that works reliably in the field and can perform measurements in grasslands with the least possible disturbance was required. The reliability and measurement accuracy of newly developed system were tested by calibration under laboratory conditions and by measurement under field conditions.

The objectives of the study

1. Development of an automated soil respiration system (ASRS), which works reliably even in field conditions, and the use of which can be implemented in grasslands with the least possible disturbance.

2. Examining the relationships between soil respiration components and major abiotic environmental factors such as soil temperature (T_s), soil moisture content (SWC), and biotic variables such as "normalized difference vegetation index" (NDVI) and gross primary production (GPP).

3. Clarification of the temporal relationship between carbon allocation and soil respiration, determination of its extent.

4. Estimation of the ratio of rhizospheric, mycorrhizal and heterotrophic components within total soil respiration on dry, sandy grassland based on a 3-year in situ measurement cycle with an automated open-chamber soil respiration measurement system.

MATERIALS AND METHODS

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°41'28" N, 19°36'42" E, 114 m a. s. l.). The soil type of the 550 ha pasture is chernozem with high total organic carbon (TOC) and total nitrogen (TN) contents. 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. There are more than 80 different plant species in the area. The vegetation is dominated by *Festuca pseudovina*, *Carex stenophylla*, *Cynodon dactylon, Poa spp.* The micrometeorological measurements and occasional soil respiration measurements have been began at the Bugac site since 2002.

Partitioning method

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. Caps with holes were placed at the bottom of the PVC pipes for water permeability. Inox mesh was used to exclude roots, but let the mycorrhiza filaments grow into the tubes.

Instruments used for measurements

Using the eddy-covariance method, it is possible to measure the Net Ecosystem Exchange (NEE). The *eddy covariance (EC) system* consisted 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: 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).

The developed *ASRS open dynamic system* consist of an SBA-5 infrared gas analyser (PPSystems, UK), pumps (MP, P), flow meters (D6F-01A1-110, Omron Co., Japan), electro-magnetic valves, and 10 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 cm2. The PVC chambers were enclosed in a white metal cylinder with 2 mm airspace in between to prevent the chambers from warming up by direct radiation. Four vent holes with a total area of 0.95 cm^2 were drilled

in the top of the chambers. Soil moisture sensors and soil temperature sensors (5TM, Decagon Devices) were also attached to the system.

The *LICOR-6400 infrared gas analyzer* and its associated soil respiration measurement chamber were used for our occasional soil respiration measurements during field testing, which were performed every two weeks starting in 2011. Measurement of soil temperature (T_s, ° C) (performed simultaneously with soil respiration in the upper 5 cm layer of soil) was implemented between 2011-2012 with a hand-held digital thermometer, and from 2013 with a thermometer connected to the soil respiration analyzer (001 MHP ICSS 316G, Omega Engineering Ltd., UK). To measure the soil moisture content in volume percent (SWC,%) (which was performed in the upper 5 cm layer of the soil at the same time as the soil respiration measurement) between 2011-2012, an ML2 reflectometer (ML2, Delta-T Devices Co., Cambridge, UK), then, from 2013, a Field Scout soil moisture meter (Field Scout TDR 300, time domain reflectometry, Spectrum Technologies, IL-USA) was used.

In addition to the study of soil characteristics (soil texture, TN, TOC, root biomass, ph, bulk density), the microbial activity of soil samples was also analyzed, which included fluorescein diacetate (FDA) hydrolysis and hypha length analysis. Our field measurements related to the study of the effect of biomass cutting on soil respiration were also performed in Bugac, in an area closed from grazing.

Data analyses and calculation of soil respiration components

We used four models to describe the dependence of total soil respiration and the components on abiotic and biotic drivers. The used soil respiration models were as follows:

1. Lloyd-Taylor model (Model 1):

$$Resp = R_{10} * e^{\left[E_0 * \left(\frac{1}{56,02} - \frac{1}{T_s - 227,13}\right)\right]} \tag{1}$$

where *Resp* is the soil respiration. Two parameters (R_{10} and E_0) were fitted. R_{10} is the respiration rate at 10 °C ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$), E_0 is the parameter related to the activation energy in Kelvin degrees, T_s is the soil temperature at 5 cm (in K).

2. Lloyd-Taylor model including soil water content (SWC) response (Model 2):

$$Resp = R_{10} * e^{\left[E_0 * \left(\frac{1}{56,02} - \frac{1}{T_s - 227,13}\right)\right] + \left[-0,5 * \left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]} \tag{2}$$

where SWC_{opt} is the optimal soil water content for soil respiration (in %). Three parameters (R_{10}, E_0 and SWC_{opt}) were fitted.

3. Model 3 including normalized difference vegetation index (NDVI).

Broadband Normalized Difference Vegetation Index (NDVI) values were calculated using the incoming and reflected global and photosynthetically active radiation data.
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.

$$Resp = R_{10} * e^{d*NDVI+E_0*\left[\left(\frac{1}{56,02}-\frac{1}{T_s-227,13}\right)\right]+\left[-0,5*\left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]} \tag{3}$$

where d is an additional model parameter. Four parameters (R_{10}, E_0, SWC_{opt} and d) were fitted.

4. Model 4 for describing SWC response:

$$Resp = R_{opt} * e^{\left[-0,5*\left[\ln\left(\frac{SWC}{SWC_{opt}}\right)\right]^2\right]} \tag{4}$$

Respiration values measured in the same way (excavated soil, sieved, backfilled into different PVC pipes in order of soil layers) (root-excluded = R_{TR} and root and mycorrhiza-excluded treatments = R_{TRM}) allow mycorrhizal respiration to be determined. The R_M was calculated as follows:

$$R_M = R_{TR}-R_{TRM} \tag{5}$$

It is known that main shortcoming of the mesh-exclusion technique is the disturbance of soil structure and aggregates. As a correction for the resulting shortcoming, the CO_2 emission values of the treatments were estimated, and in order to eliminate the differences in the soil moisture values, the SWC values were raised to the same scale, we normalized according to the following equation:

$$SWC_n = \frac{SWC_{mean}}{SWC_{max}} \tag{6}$$

where SWC_n is the normalized hourly value for a treatment, SWC_{mean} is the hourly average value of the measured soil water content in Exc, Exr and Exrm, respectively, while SWC_{max} is the maximum value measured also in the given treatment.

Prior to estimating the hourly respiration values of the components, a moving window (5, 10, 30 days, 1, and 3 years) model fitting was performed to select the appropriate model parameters. The estimation was necessary due to the change in soil moisture content in the treatments due to partitioning. Estimates for Exr treatment (root-excluded treatment) correspond to heterotrophic and mycorrhizal respiration ($R_{(het+myc)*}$), while estimates for Exrm (root and mycorrhiza-excluded) treatment represent heterotrophic respiration (R_{het*}).

The contribution by the different soil respiration components to R_s was calculated from the estimated values of the Exr ($R_{(het+myc)*}$) and of the Exrm (R_{het*}) and from the measured data of Exc (R_s) according to the following equations. The difference between the estimated root-excluded and root- and mycorrhiza-excluded respiration was used to estimate the rate of estimated mycorrhizal respiration (R_{myc*}):

$$R_{myc*} = R_{(het+myc)*} - R_{het*} \tag{7}$$

The estimated rhizospheric respiration (R_{rhizo*}) value was determined as the difference between the measured total soil respiration value and the estimated root-exclusion treatment respiration value based on the following equation:

$$R_{rhizo*} = R_s - R_{(het+myc)*} \tag{8}$$

Data processing, calculations and model fits were done in R program.

RESULTS

ASRS calibration

The CO_2 emission measured by the automated soil respiration measuring system (ASRS) we developed and the CO_2 emission of the calibration tank showed a close correlation, thus proving the accuracy of the ASRS measurements. During field testing, our data recorded by the ASRS were compared with the results of a system commonly used to measure R_s (LI-6400). The results also support the reliability of the developed system.

Model fitting

Fitted parametersof the three models show that Model (3) (eq. 3), where soil temperature, soil water content and vegetation index (NDVI) acted as independent variables was superior to the other two Model. The results of Model 4 fitting (eq. 4) demonstrated that the soil respiration components have different SWC sensitivity.

Effects of photosynthetic activity and carbon allocation on mycorrhizal respiration

The relationship between mycorrhizal respiration (R_M) and photosynthetic activity (GPP) was also examined with different time lags, by months, and except for three months a significant correlation was found. The highest correlation coefficient occurred in March, and the most common time lag was found to be zero days.

Proportion of estimated soil respiration components

The contribution by R_{het*} to the total soil respiration during the 3-year study period averaged 55±21%. The ratio of R_{myc*} to the total soil respiration averaged 9±9% and the proportion of Rrhizo* averaged 36±21%. The average contributions of R_{het*} and R_{rhizo*} components to the total soil CO2 efflux were 52±19% and 39±20% in the growing (active) period, and 70±25% and 21±21% in the dormant period, respectively. The R_{myc*} seemed to be more stable with average contribution of 9±9% in the growing and in the dormant period, as well.

Daily variability of soil respiration components

The daily variability of soil respiration is significantly influenced by temperature, soil moisture, and carbon allocation. Based on our results, we can conclude that the respiration intensities of different treatments vary from phenological phase, but it is also clear that the respiration intensity of R_{TRM} treatment is less affected by the change in SWC. In order to explain the standard deviations of the annual course, we also examined the daily variability of the individual components - the degree of deviation from the daily mean - in the different phenological phases. Our results highlight the effect of photosynthesis on soil respiration through substrate supply and highlight the importance of temporality between them.

NEW SCIENTIFIC RESULTS

The new scientific results of the doctoral thesis can be summarized in the following points:

1. We have demonstrated that the newly developed automated soil respiration system is reliable and suitable for continuous recording of soil respiration, thus studying the daily and annual variability of soil respiration.

2. After model fitting, we found that among the models we used, in addition to abiotic factors (soil temperature, soil moisture), the model including the biotic independent variable (vegetation index, NDVI) shows the strongest correlation with soil respiration, which refers the sensitivity of the autotrophic component to CO_2 uptake.

3. We showed the different drought sensitivity of the different components by analyzing the soil moisture content and the daily average respiration values. We found that the heterotrophic respiration component is less sensitive to soil drying.

4. We examined the relationship between daily GPP amount and daily mean R_M and found that there was a significant relationship between photosynthetic activity and mycorrhizal respiration.

5. Based on our measurements, we estimated the proportion of rhizospheric, mycorrhizal and heterotrophic components within total soil respiration, and found that the proportion of autorthophic and heterotrophic components differs on dry sandy grass during the active and dormant periods.

6. In addition to the annual variability, we determined the daily dynamics of CO_2 emissions of each component and found that soil respiration is primarily associated with carbon uptake (assimilate transport) within one day.

CONCLUSIONS AND SUGGESTIONS

Comparison of calibration and soil respiration measuring instruments

The advantage of the newly developed soil respiration system is that its small diameter chambers (d = 5 cm) can be used in grasslands with the least possible disturbance, thus minimizing the disturbance of the soil as well as the roots close to the soil surface. Measurements on the calibration tank confirmed the reliable operation of the instrument, so no further correction of the measurements was required.

In contrast to campaign-like measurement occasions, continuous data collection makes it possible to analyze and explore the causes of daily and annual variability in soil respiration. We recommend the use of devices similar to the automated, open-system soil respiration measuring instrument we have developed for soil respiration studies.

Method / process of partitioning

The technique used to separate the different respiration components proved to be successful, which is supported by the results of mycorrhizal sampling. One potential problem with the root exclusion method is that the SWC is generally higher in the treatments compared to the control, which can be explained by the lack of transpiration. In our study, SWC values were significantly higher in the Exr and Exrm treatments compared to the values measured on the Exc spots.

During data processing, we recommend taking these differences into account, which can be achieved by normalizing the SWC values and estimating the CO_2 emissions of the components.

Effects of abiotic and biotic environmental factors

There was a weaker relationship between the heterotrophic component and soil drying, so we can conclude that the autotrophic component is more sensitive to drought. We found similar results in our partitioning study based on isotope technique. In addition to abiotic factors, the effect of biotic factors also needs to be considered.

This is evidenced by the use of Model 3, which includes NDVI as an independent variable, compared to goodness of fit compared to fittings containing only abiotic factors, thereby highlighting the sensitivity of the autotrophic component to CO_2 uptake.

In our work, we used correlation analysis to analyze the time lag between photosynthetic activity and mycorrhizal respiration, as a result of which we found a significant correlation. The most common time lag was zero days. The time elapsed between GPP and R_M in active periods (0–2 days) suggests a rapid translocation of photosynthetic products.

Based on our results, we recommend the use of models that include both abiotic (soil temperature, soil moisture) and biotic (vegetation index) variables to estimate soil respiration.

Proportion and variability of soil CO_2 emissions from different components

We showed that the average contribution of the heterotrophic component to the total soil respiration was 55% and the average contribution of the autorophic component to the total soil respiration was 45% during the study period and that there was a difference during the dormant and growth periods.

In addition to the seasonal changes of the components by phenological phase, it is important to mention the daily dynamics of changes in soil respiration. Based on the zero day time lag between GPP and CO_2 emissions in the active period, a strong dependence of soil respiration on photosynthesis can be established with effect within one day.

The knowledge about the carbon turnover of ecosystems, specification of input parameters of model simulations, consideration of different proportions and dynamics of different components are important aspects, therefore we recommend the study of soil respiration components of other ecosystems (eg. agro-ecosystems).

PUBLICATIONS RELATED TO THE TOPIC OF THE THESIS

Publications in scientific journals:

1. Marianna Papp, Szilvia Fóti, Zoltán Nagy, Krisztina Pintér, Katalin Posta, Sándor Fekete, Zsolt Csintalan, János Balogh (2018): Rhizospheric, mycorrhizal and heterotrophic respiration in dry grasslands. EUROPEAN JOURNAL OF SOIL BIOLOGY 85: pp. 43-52.

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Co-authored article related to the topic:

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