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Autotrophic component of soil respiration is repressed by drought more than the heterotrophic one in a dry grassland

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Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Summer droughts projected to increase in Central Europe due to climate change strongly influence the carbon cycle of ecosystems. Persistent respiration activities during drought periods are responsible for a significant carbon loss, which may turn the ecosystem from sink to source of carbon. There are still gaps in our knowledge regarding the characteristic changes taking place in the respiration of the different components of the ecosystem respiration in response to drought events.

Here, we combined a physical separation of soil respiration components with continuous measurements of soil CO₂ efflux and its isotopic (¹³C) signal at a dry grassland site in Hungary. The physical separation of soil respiration components was achieved by the use of inox meshes and tubes inserted into the soil. The root-excluded and root- and mycorrhiza-excluded treatments served to measure the isotopic signal of the rhizospheric, mycorrhizal fungi and heterotrophic components, respectively.

In the dry grassland investigated in this study the three components of the soil CO₂ efflux decreased at different rates under drought conditions. During drought the contribution made by the heterotrophic components was the highest. Rhizospheric component was the most sensitive to soil drying with its relative contribution to the total soil respiration dropping from 71 ± 4% (non-stressed) to 36 ± 12% under drought conditions. According to our results, the heterotrophic component of soil respiration is the major contributor to the respiration activities during drought events.

1 Introduction

Grassland ecosystems strongly respond to drought events via substantial reduction of primary production (Hoover et al., 2014; Nagy et al., 2007; Parton et al., 2012; Reichstein et al., 2013). In contrast, below-ground respiration is not as strongly affected (van der Molen et al., 2011; Yang and Zhou, 2013), but tends to be reduced as well under drought (Balogh et al., 2011; Suseela and Dukes, 2013). According to climate change

BGD

12, 16885–16911, 2015

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



it has been under extensive management (grazing) for the last 20 years. Ten-year mean annual precipitation (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 (Balogh et al., 2014).

2.2 Spatial separation of soil CO₂ efflux components

In 2010, ten soil cores (160 mm in diameter and 800 mm in depth) were excavated, the roots have been removed and the root-free soil was packed layer by layer into PVC tubes. Five tubes were used to exclude both roots and mycorrhiza. Walls of another 5 tubes were partially removed and replaced by inox meshes (40 μm pore size) to exclude roots, while ensuring that the mycorrhiza filaments can grow into the tubes (Moyano et al., 2007). These root-free and root- and mycorrhiza-free soil cores were settled at a distance of 10 m from the eddy covariance tower to the south direction. The distance between the soil cores/tubes was 50 cm.

Soil CO₂ efflux and its isotopic signal were measured in plots of:

- undisturbed soil: total soil respiration, R_{soil} ,
- without roots and arbuscular mycorrhizal fungi = heterotrophic component only, R_{rme} ,
- root-excluded soil = without roots, but with arbuscular mycorrhizal fungi, R_{re} .

2.3 Gas exchange measuring systems

Three different gas exchange systems were used in this study: eddy-covariance system (EC), automated soil respiration measuring system (SRS) was connected to an isotopic CO₂ analyser (CRDS-technique). The size of the EC flux footprint area was larger by several orders of magnitude than the area covered by the SRS. 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 as found in

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the plots where the SRS was installed. Hence, the NEE and ET estimates obtained in this way can be considered representative also for the small-scale SRS and isotope measurements.

Data from 15 May 2013 to 12 November 2013 (182 days) were analysed in this study.

2.3.1 Eddy covariance setup

The EC system at the Bugac site has been measuring the CO₂ and H₂O fluxes continuously since 2002. In dry years this grassland can turn into a net carbon source (Nagy et al., 2007), but the longer-term annual sums of net ecosystem exchange (NEE) show it to be a net sink, ranging from -171 to +106 gC m⁻² yr⁻¹ (Pintér et al., 2010) with a -100 gC m⁻² yr⁻¹ average.

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 (105 T, 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 CO₂ 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).

2.3.2 Soil respiration system

The 10 chamber automated soil respiration system was set up in July 2011. The system is an open dynamic one, consisting of an SBA-4 infrared gas analyser (PPSys-

BGD

12, 16885–16911, 2015

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



the CRDS giving a sequence of reference and analysis (soil CO₂ efflux as sampled from the chamber) air for 3–3 min in one hour of operation.

2.4 Data processing and modelling

Data processing and statistical analysis were done in R (R Core Team, 2014). Before calculating daily averages of $\delta^{13}\text{C}$ values, a filtering method was applied to each dataset. Out of each 180 s long measurement on a certain chamber, the first 70 s (to measure a steady state signal) and the last 20 s were cut and the remaining values were used for further calculations. As reference and chamber air were measured sequentially, reference values during chamber measurements were estimated by linear interpolation between the neighbouring reference sequences.

After the interpolation, $\delta^{13}\text{C}$ values of the soil CO₂ efflux were calculated using the isotopic mass balance approach in each plot:

$$\delta^{13}\text{C}_R = \frac{\delta^{13}\text{C}_{\text{out}} \times c_{\text{out}} - \delta^{13}\text{C}_{\text{in}} \times c_{\text{in}}}{c_{\text{out}} - c_{\text{in}}} \quad (1)$$

where $\delta^{13}\text{C}_{\text{out}}$ and $\delta^{13}\text{C}_{\text{in}}$ are the isotopic signature of the outgoing and incoming air of the chamber and c_{out} and c_{in} are the CO₂ concentration of the outgoing and incoming air of the chamber, respectively.

$$\delta^{13}\text{C} = \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \quad (2)$$

and R stands for the $^{13}\text{C}:^{12}\text{C}$ isotope ratio of the sample and the international VPDB standard (0.011182), respectively.

Individual measurements were filtered out by using a moving-window procedure if the investigated value (at the window center) was outside the range of the mean \pm median absolute deviation of the values in a 10 days moving window. This filtering

BGD

12, 16885–16911, 2015

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



procedure left an overall data availability of 68–70%. Daily averages were calculated using the remaining data.

To determine the isotopic signature of the ecosystem respiration (R_{eco}), Keeling plots were constructed by plotting the night-time $\delta^{13}\text{C}$ values measured 10 cm over the surface against the inverse of the CO_2 concentration. The extrapolated y-intercept of the linear regression was used as $\delta^{13}\text{C}_{\text{Reco}}$ values.

Total soil CO_2 efflux was separated isotopically into its components. Two-source mixing models were used to estimate the fraction (a) of the rhizospheric (root and rhizospheric microbes) and mycorrhizospheric (root, rhizospheric microbes and mycorrhizal fungi) components (Moyano et al., 2009), based on the measured fractions:

$$\delta^{13}\text{C}_{\text{Rsoil}} = a \times \delta^{13}\text{C}_{\text{Rrhizo}} + (1 - a) \times \delta^{13}\text{C}_{\text{Rre}} \quad (3)$$

$$\delta^{13}\text{C}_{\text{Rsoil}} = b \times \delta^{13}\text{C}_{\text{Rmycrhiz}} + (1 - b) \times \delta^{13}\text{C}_{\text{Rrme}} \quad (4)$$

where $\delta^{13}\text{C}_{\text{Rsoil}}$ is the $\delta^{13}\text{C}$ of the total soil CO_2 efflux, $\delta^{13}\text{C}_{\text{Rre}}$ is the $\delta^{13}\text{C}$ of the root-excluded soil, $\delta^{13}\text{C}_{\text{Rrme}}$ is the $\delta^{13}\text{C}$ of the root- and mycorrhiza-excluded soil (heterotrophic respiration), a is the fraction of the rhizospheric component and b is the fraction of the mycorrhizospheric component to the total soil efflux. $\delta^{13}\text{C}_{\text{Rrhizo}}$ value was estimated by plotting $\delta^{13}\text{C}_{\text{Rsoil}}$ values against the $R_{\text{re}}/R_{\text{soil}}$ ratio. Since $R_{\text{re}}/R_{\text{soil}}$ and $R_{\text{rme}}/R_{\text{soil}}$ is hypothetically zero when only rhizospheric respiration is present, y-intercept of the linear correlation was assumed as $\delta^{13}\text{C}_{\text{Rrhizo}}$. $\delta^{13}\text{C}_{\text{Rmyc}}$ was estimated by plotting $\delta^{13}\text{C}_{\text{Rre}}$ values against the $R_{\text{re}}/R_{\text{rme}}$ fraction (Table 1).

Rhizospheric, mycorrhizal and heterotrophic respirations (R_{rhizo} , R_{myc} , R_{het}) were calculated by multiplying the estimated daily contributions to total respiration with the total soil respiration (R_{soil}). Cross-correlation was calculated between daily minimum half-hourly NEE (NEE_{min}) and daily component respirations (R_{rhizo} , R_{myc} , R_{het}).

BGD

12, 16885–16911, 2015

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2.5 Microbial investigations

Soil samples for the microbial investigations were taken after the gas exchange measurements in May 2014 to avoid the disturbance of the measurements by the soil sampling. Sampling date was chosen considering the maximum of the carbon sequestration capacity of the investigated grassland (Nagy et al., 2007). 5–5 samples were taken from 5 soil layers (0–10, 10–20, 20–30, 30–40 and 40–50 cm) in each plot.

Determination of AM fungal hyphal length in the soil was based on the methods of Bååth and Söderström (1979) using separation by wet-sieving and centrifugation. The separated fungal hyphae were stained using agar solution (0.75 %) containing trypan blue (0.05 %) then dried for 24 h at 70 °C. The hyphal length was measured in the dried agar film by the intersection method (Tennant, 1975) under a binocular microscope.

The fluorescein diacetate (FDA) hydrolysis assay was used to estimate the total microbial activity in soil samples and expressed as mg fluorescein released kg⁻¹ dry soil (Adam and Duncan, 2001).

2.6 Uncertainty assessment

Isotopic signal of soil respired CO₂ has been studied extensively but several uncertainties related to the different methods have been revealed. Steady-state methods were found to provide more robust estimates than static chambers but still charged with biases (e.g. diffusive fractionation, Nickerson and Risk, 2009). Open systems have the advantage of unattended automatic measurement collecting large amount of data but are less sensitive to small isotopic differences (Midwood and Millard, 2011).

In our study $\delta^{13}\text{C}_{\text{Reco}}$ estimates were independent of chamber related biases, using night-time $\delta^{13}\text{CO}_2$ and CO₂ concentration data of the free air over the surface for the calculation (Keeling-plot approach). This approach gave similar results to the chamber-based measurements, providing also partial verification of the latter ones. Moreover, isotopic measurements were independent on soil CO₂ efflux measurements, since IRGA and CRDS systems took different air samples from the same soil chambers.

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Isotopic data together with CO₂ efflux rates were collected during 1980 measurement cycles on 182 days in order to have robust estimates of isotopic signals.

A C4 grass (*Cynodon dactylon*) was also present in the study site potentially modifying the $\delta^{13}\text{C}$ of the respired CO₂. Its cover was about 10% in the pasture (Koncz et al., 2014), but it was less frequent (i.e. less than 5%) in the experimental area. Calculated uncertainties of the relative contributions of each components (rhizospheric, mycorrhizal fungi and heterotrophic) contain the uncertainty due to a possible 5% contribution by the C4 grass.

Error propagation was done by parametric bootstrapping using the boot library in R (Canty and Ripley, 2014). The advantage of the bootstrapping method over the other methods to estimate uncertainty of a result of a complicated statistical equation is that it allows to estimate confidence intervals even with non-Gaussian distributed data and with complicated interactions that may not necessarily follow a Gaussian distribution. In practise, all components in an equation are perturbed by a random deviation from their initial value and the results are collected for thousands of runs (in our case we used 5000 sets of random deviations), and the standard error of the mean is derived from the statistical distribution of the outcomes of all simulation runs (Davison and Hinkley, 1997; Wilks, 2006).

3 Results

3.1 Microbial biomass and activity

Hyphal length per g soil was significantly lower in the upper layers of root- and mycorrhiza-excluded soil compared to the undisturbed soil, but it was significantly higher in root-excluded plots at 10–20 cm depth. Hyphal length of the root-excluded soil was similar to undisturbed soil in the other soil layers. Fluorescein values were significantly lower in all soil layers of the root- and mycorrhiza-excluded plots compared

BGD

12, 16885–16911, 2015

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



to the undisturbed soil. Fluorescein values of the root-excluded plots were also lower than in undisturbed soil, but this difference was not significant (Fig. 1).

3.2 $\delta^{13}\text{C}$ of the respiration components

Figure 2 shows the measured and estimated $\delta^{13}\text{C}$ values of the different soil CO_2 efflux components. $\delta^{13}\text{C}_{R_{\text{rme}}}$ was the highest, while $\delta^{13}\text{C}_{R_{\text{eco}}}$ was the lowest, suggesting that rhizospheric respiration was the most substantially depleted, while heterotrophic respiration was the least depleted in ^{13}C . Mean of $\delta^{13}\text{C}_{R_{\text{eco}}}$, $\delta^{13}\text{C}_{R_{\text{soil}}}$, $\delta^{13}\text{C}_{R_{\text{re}}}$ and $\delta^{13}\text{C}_{R_{\text{rme}}}$ were -27.9 ± 0.5 , -26.8 ± 1.3 , -26.4 ± 1.8 and $-25.7 \pm 2\%$ (mean \pm SE), respectively. The estimated isotopic signal of the respiration of mycorrhizospheric, rhizospheric and mycorrhizal fungi components were -28.6 ± 1.5 , -28.9 ± 1.8 and $-27.2 \pm 2.3\%$ (estimate \pm SE), respectively (Fig. 2).

3.3 Meteorological conditions, NEE, ET, soil CO_2 efflux, $\delta^{13}\text{C}$ of CO_2 efflux

The end of May and the beginning of June was the most productive period in the year due to good water availability, the lowest NEE (strongest carbon sink activity) and highest evapotranspiration (ET) values were measured in this period (Fig. 3a). It rained only a few times from the end of June to 19 August (total precip: 10 mm) and the accompanying high temperature resulted in drought. Daily minimum NEE was around zero at the end of July and in August. Rain events after the drought period had significant effects on soil CO_2 effluxes (Fig. 3c). There was a second active period in autumn following rains, but CO_2 uptake and ET were lower than in May or June.

R_{soil} was the highest among the soil CO_2 effluxes, while R_{rme} was the lowest, the average CO_2 effluxes in the whole study period were 5.0 ± 2.1 , 3.8 ± 1.6 and $2.6 \pm 1.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (mean \pm SD) in R_{soil} , R_{re} and R_{rme} , respectively. R_{re} was sometimes higher than R_{soil} , especially shortly after rain events.

Isotopic signature of R_{eco} was the lowest in May and June, increased in July and August and decreased again in October and November. $\delta^{13}\text{C}_{R_{\text{eco}}}$ showed clear re-

BGD

12, 16885–16911, 2015

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



sponses to precipitation pulses: sudden declines were observed during the rain events. Chamber-based $\delta^{13}\text{C}_{\text{Rsoil}}$ showed similar changes during the study period. $\delta^{13}\text{C}_{\text{Rrme}}$ and $\delta^{13}\text{C}_{\text{Rre}}$ showed large scatter during the whole study period with no clear trends to be detected. Difference between $\delta^{13}\text{C}_{\text{Rsoil}}$ and $\delta^{13}\text{C}_{\text{Rrme}}$ was largest in the active period and smallest under drought conditions.

According to the NEE, SWC values and isotopic signals we distinguished 5 periods within the study period: an active period from 15 May to 20 June, a drying (stress development) period from 21 June to 22 July, a drought period from 23 July to 19 August, a wetting (stress release) period from 20 August to 16 September and a re-greening (recovery) period from 17 September to the end of the study period (11 November) (Fig. 3).

3.4 Ratio of the different components in total soil respiration during the vegetation period

Two end-member mixing models (Eqs. 3 and 4) were used to estimate the relative contributions of rhizospheric, mycorrhizal fungi and heterotrophic components to total soil respiration during the study period. The autotrophic component (mycorrhizospheric component) of soil respiration showed significant decrease during the drying and drought periods. During the active period estimated rhizospheric contribution was lower than mycorrhizospheric and this difference was attributed to the mycorrhizal fungi component (Fig. 4). Average contribution (mean \pm SE) made by the rhizospheric component decreased by 50 % as a response to drought from $71 \pm 4\%$ in the active period to $36 \pm 12\%$ during the drought period (Fig. 4). Relative mycorrhizal contribution was the highest ($23 \pm 14\%$; mean \pm SE) during the drought period. The estimated (relative) rhizospheric contribution increased after the rain events, even after a small amount of precipitation (e.g. at the end of July). The estimated contribution by the heterotrophic component increased from about 20 to 60 % (data not shown) at some point during the drying period, when no precipitation occurred.

Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



positive correlation with $\delta^{13}\text{C}_{\text{Rsoil}}$ (the regression was used to estimate $\delta^{13}\text{C}_{\text{Rrhizo}}$), so $\delta^{13}\text{C}_{\text{Rsoil}}$ was high if the ratio of heterotrophic CO_2 efflux to the total soil CO_2 efflux was found to be high. Moreover, $R_{\text{rme}}/R_{\text{soil}}$ ratios were the highest on the driest days, supporting the estimated decline of the autotrophic component.

According to these studies and to our results we can assume that the different vegetation types can respond differently to drought: woodlands can increase the autotrophic ratio, while grasslands can decrease it (Casals et al., 2011; Gomez-Casanovas et al., 2012; Risk et al., 2012). Since plants with different rooting habits have different water availability during dry periods (van der Molen et al., 2011), this could explain the differences in the response to drought by the different ecosystems.

4.2 Measured and estimated isotopic signals of the soil respiration components

Measured and calculated $\delta^{13}\text{C}$ values of the different respiration components showed similar differences to the ones reviewed by Bowling et al. (2008). $\delta^{13}\text{C}_{\text{Reco}}$ (containing also the signal from above ground green biomass) was the most depleted, while $\delta^{13}\text{C}_{\text{Rrme}}$ was the least depleted. $\delta^{13}\text{C}$ of the root- and mycorrhiza-excluded respiration was similar to SOM $\delta^{13}\text{C}$ measured in a previous study (Denef et al., 2013): -25 and -26‰ in the topsoil layers (without the litter layer). CO_2 effluxes from mycorrhizal fungi were expected to be more enriched in ^{13}C relative to the total soil respiration (about $+3\text{‰}$, Bowling et al., 2008). Estimated $\delta^{13}\text{C}$ of mycorrhizal fungi component was $-27.24 \pm 2.3\text{‰}$ (estimate \pm SE), which is 1.7‰ higher than the rhizospheric component ($-28.9 \pm 1.8\text{‰}$; estimate \pm SE).

4.3 Microbial investigations

High hyphal density was maintained in R_{re} plots and lower, but still significant microbial activities (SOM decomposition) were detected in R_{rme} plots, therefore the measured $\delta^{13}\text{C}$ values showed the sources of the root-free ($\delta^{13}\text{C}_{\text{Rre}}$) and root- and mycorrhiza-

tial productivity is generally linked to soil carbon content, a pronounced decrease in soil organic matter due to the enhanced activity of the heterotrophic component under drought may directly affect the long term productivity of grasslands.

Author contributions. J. Balogh, M. Papp, K. Pintér and Z. Nagy conceived and designed the experiment, M. Papp, K. Pintér and K. Posta performed the experiment, J. Balogh analyzed the data and wrote the paper, but all co-authors contributed to writing.

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Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Autotrophic component of soil respiration is repressed

J. Balogh et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Table 1.** Measured and estimated CO₂ effluxes and isotopic signals in this study.

	CO ₂ efflux	Isotopic signals
measured	$R_{\text{eco}}, R_{\text{soil}}, R_{\text{re}}, R_{\text{rme}}$	$\delta^{13}\text{C}_{\text{Reco}}, \delta^{13}\text{C}_{\text{Rsoil}}, \delta^{13}\text{C}_{\text{Rre}}, \delta^{13}\text{C}_{\text{Rrme}}$
estimated	$R_{\text{rhizo}}, R_{\text{myc}}, R_{\text{het}}$	$\delta^{13}\text{C}_{\text{Rmycrhiz}}, \delta^{13}\text{C}_{\text{Rrhizo}}, \delta^{13}\text{C}_{\text{Rmyc}}$

Autotrophic component of soil respiration is repressed

J. Balogh et al.

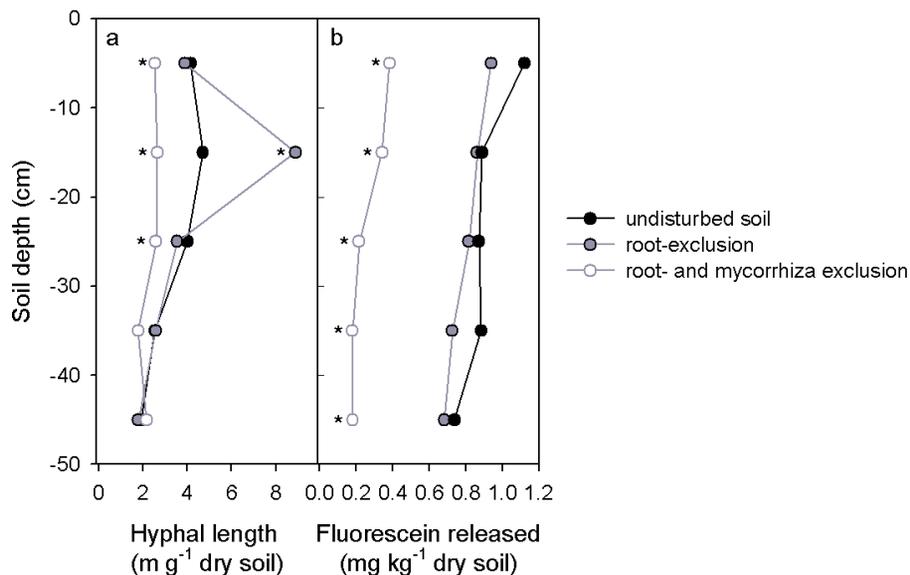


Figure 1. (a) Mean hyphal length (mg^{-1} dry soil) and (b) mean microbial activity expressed as fluorescein released (mg kg^{-1} dry soil) in the undisturbed soil, root-exclusion and root- and mycorrhiza-exclusion in different soil depths. Asterisks denote significant differences from undisturbed soil.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[⏪](#)
[⏩](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


Autotrophic component of soil respiration is repressed

J. Balogh et al.

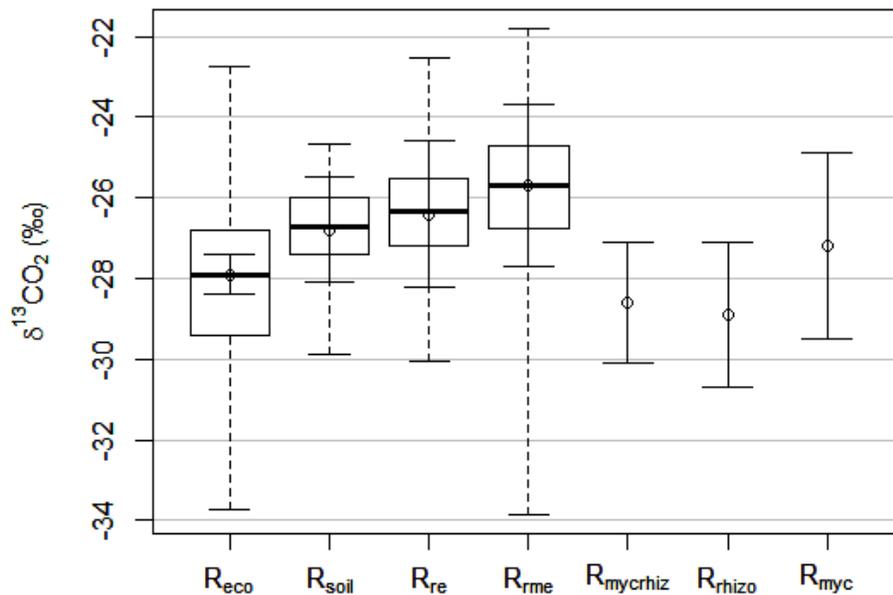


Figure 2. Measured (R_{eco} , R_{soil} , R_{re} , R_{rme}) and estimated ($R_{mycrhiz}$, R_{rhizo} , R_{myc}) $\delta^{13}C$ values of the respiration components. Horizontal lines in boxes show medians and dashed whiskers show data extremes. Open circles and solid whiskers show means \pm propagated standard errors.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Autotrophic component of soil respiration is repressed

J. Balogh et al.

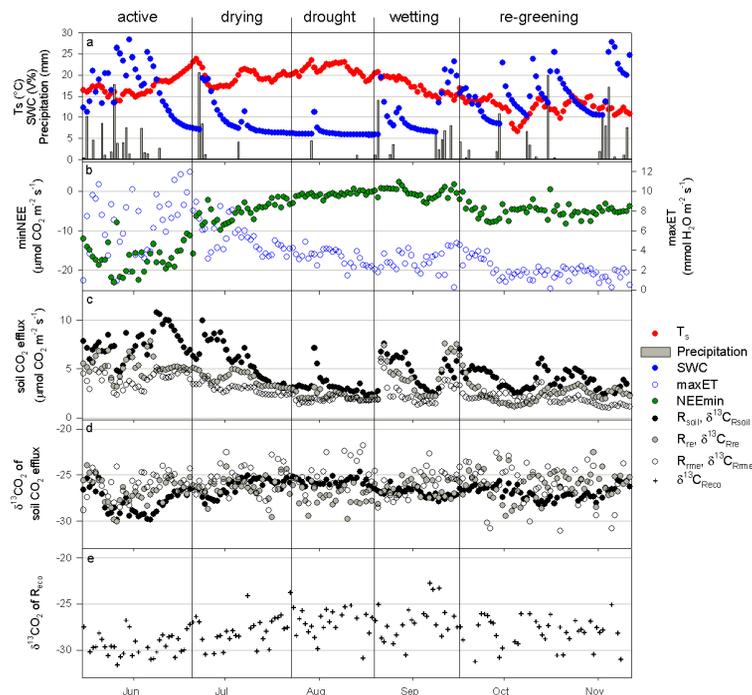


Figure 3. (a) Daily averages of soil temperature (T_s), soil water content (SWC) at 5 cm depth and daily sum of precipitation, (b) daily minimum half-hourly NEE and maximum half-hourly ET, (c) daily averages of CO_2 efflux in undisturbed soil (R_{soil}), root-excluded soil (R_{re}) and root- and mycorrhizal fungi-excluded soil (R_{rme}), (d) daily averages of $\delta^{13}\text{C}$ of soil CO_2 efflux in undisturbed soil ($\delta^{13}\text{C}_{R_{\text{soil}}}$), root-excluded soil ($\delta^{13}\text{C}_{R_{\text{re}}}$) and root- and mycorrhizal fungi-excluded soil ($\delta^{13}\text{C}_{R_{\text{rme}}}$) and (e) daily averages of $\delta^{13}\text{C}$ of ecosystem respiration ($\delta^{13}\text{C}_{R_{\text{eco}}}$) during the study period in 2013, at Bugac site.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Autotrophic component of soil respiration is repressed

J. Balogh et al.

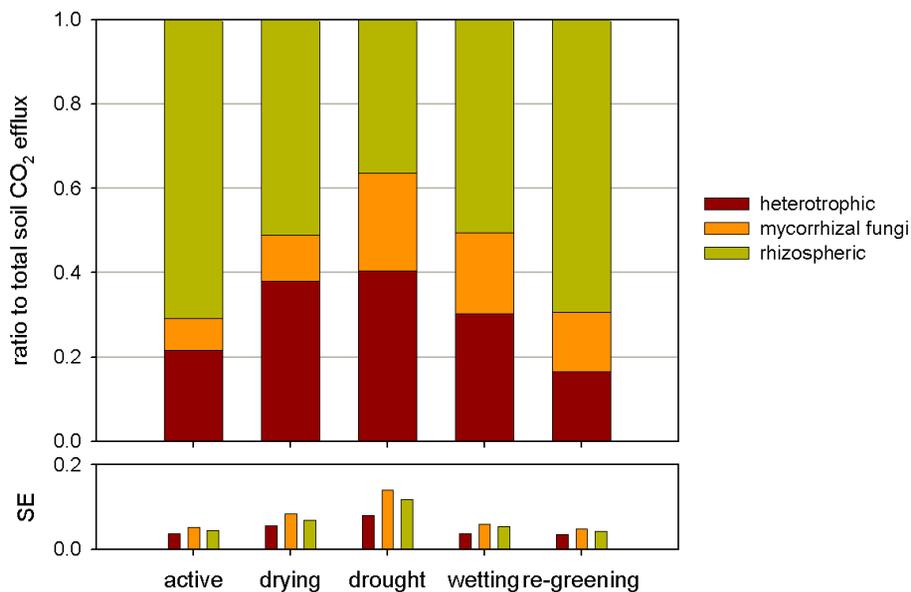


Figure 4. Relative contributions made by rhizospheric, mycorrhizal fungi and heterotrophic components to the total soil respiration in the different parts of the vegetation period (15 May 2013–12 November 2013) at Bugac site. Propagated uncertainties of each estimate are shown in the lower panel.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

