Soil Biology & Biochemistry 112 (2017) 90–99

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Soil carbon loss regulated by drought intensity and available substrate: A meta-analysis

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ARTICLE INFO

Article history:
Received 22 November 2016
Received in revised form
5 April 2017
Accepted 13 April 2017
Available online 12 May 2017

Keywords:
Dry-rewetting cycles
F:B ratio
Metabolic quotient
Microbial community
Soil respiration
Soil organic matter

ABSTRACT

Drought is one of the most important climate change factors, but its effects on ecosystems are little understood. While known to influence soil carbon (C) cycling, it remains unresolved if altered rainfall patterns induced by climate change will stimulate positive feedbacks of CO_2 into the atmosphere. Using a meta-analysis frame-work including 1495 observations from 60 studies encompassing a variety of ecosystems and soil types, we investigated drought effects on respiration rates, cumulative respiration during drying-rewetting cycles, metabolic quotient (qCO_2), dissolved organic C (DOC), microbial biomass and fungi to bacteria (F:B) ratios from laboratory and field experiments. We show that C-rich soils (>2% organic carbon) increase CO_2 release into the atmosphere after intense droughts, but that C-poor soils show a net decline in C losses. We explain this self-reinforcing mechanism of climate change in C-rich soils by: (i) high substrate availability that magnify bursts of CO_2 release after drought events and (ii) a shift in microbial community with increased loss of C per unit of biomass. These findings shed light on important responses of soil CO_2 emissions to drought, which could either offset or facilitate positive feedbacks to global warming. Our results should be considered in global climate models, as even small changes in soil CO_2 emission have large repercussions for global warming.

1. Introduction

Large areas of the world will experience more intense droughts in the near future, with extended dry periods alternated by heavy precipitation events (Dai, 2011, 2013; IPCC, 2013). While soil holds the majority of carbon (C) in most terrestrial ecosystems (Schmidt et al., 2011), drought can cause intense C losses from soil and turn entire ecosystems into C sources, resulting in a large positive feedback to global warming (Frank et al., 2015; Novick et al., 2015; Hoover and Rogers, 2016). Precipitation distribution is expected to be a key factor determining C losses from ecosystems with acute and extreme droughts causing larger losses of C from ecosystems compared to chronic droughts (Frank et al., 2015; Hoover and Rogers, 2016). Much of these losses originate from soil, where extreme droughts intensify temporal fluctuations in soil moisture, significantly affecting microbial decomposition of organic matter and consequential release of CO_2 into the atmosphere (Nielsen and Ball, 2015). The response of soil C to intense drying-rewetting cycles has been recognized since the pioneering work of Birch (1958), who showed that rewetting of soil after a drought period with little or no rain can result in large pulses of CO_2 release into the atmosphere. These pulses can be so large that the total loss of soil C through microbial respiration during entire drying-rewetting cycles are larger compared to soils that are constantly moist (Borken and Matzner, 2009).

Despite a large scientific effort, clear patterns of drought effects on soil C dynamics have not emerged, possibly due to different experimental manipulations and soil characteristics that can modulate the response of C cycling. The number of wet and dry days, the drought intensity and the number of drying-rewetting cycles are all factors known to control the magnitude of C loss through microbial respiration during drying-rewetting cycles (Borken and Matzner, 2009). However, other factors, including C availability and microbial community composition also play an important role (Borken and Matzner, 2009; Zhou et al., 2016). Soil

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http://dx.doi.org/10.1016/j.soilbio.2017.04.020
0038-0717/

microbial respiration is largely governed by concentrations of soil organic C (SOC) and dissolved organic C (DOC) (Wang et al., 2003), while the microbial community composition has potential to modulate the allocation of C between different soil pools and the atmosphere (Schmidt et al., 2011; Schimel and Schaeffer, 2012). Indeed, fungal to bacteria (F:B) ratios have been used to improve biogeochemical modeling of ecosystem C dynamics in response to environmental changes (Waring et al., 2013), as fungi and bacteria are ecologically and physiologically different, support different soil food-chains (de Vries et al., 2006) and differ in their C use efficiency (Sakamoto and Oba, 1994). Because both fungi and bacteria are sensitive to soil moisture (Manzoni et al., 2012), understanding how drought intensity and substrate availability could modulate drought-induced soil C release and allocation to microbial biomass will be important to reduce uncertainty of model predictions (Bardgett et al., 2008).

The aims of this study are to quantify effects of drought on soil C cycling and to identify predictors of response to drought intensity and duration. We used meta-analysis to evaluate respiration, qCO_2, DOC and microbial community composition in response to drought duration, number of dry-rewetting cycles, drought intensity, SOC content and soil texture. None of the previous reviews of drought effect on C cycling (Borken and Matzner, 2009; Wu et al., 2011; Manzoni et al., 2012) have quantitatively investigated the effects of drying and rewetting phases separately to explain drought intensity and duration effects and provide possible mechanisms. We differentiated between responses in field and laboratory studies, where laboratory studies included soil incubation and greenhouse experiments without plants (see materials and methods). Furthermore we examined possible links between responses in respiration and microbial community composition and size. We used a new meta-analytical approach with a random effect model accounting for the non-independence of multiple observations extracted from the same study (Curtis and Queenborough, 2012).

2. Methods

2.1. Data acquisition and selection

We collected data from published articles exploring at least one of the following variables in response to drought manipulation: microbial biomass carbon (MBC), soil respiration, metabolic quotient (qCO_2), cumulative respiration, dissolved organic carbon (DOC) and F:B ratio (or individual values for both fungi and bacteria). We searched for articles in Web of Science, Google Scholar and Scopus, using the search terms “dry-rewetting”, “drying-rewetting”, “drought”, “microbial”, “soil” (and a combination of them). We also searched for articles that were cited in the publications we found. A number of criteria had to be fulfilled to be included in the meta-analysis: experiments had to have a control treatment with an ambient regime of precipitation (for field experiments) or with moisture kept constant (for pot and soil laboratory incubation experiments); a drought treatment with reduced or total exclusion of precipitation in field experiments, no water addition during the dry period in pot and soil laboratory incubation experiments and with a rewetting phase (where soil moisture was brought to the control), or a drought treatment with consistently lower soil moisture than the control (*i.e.*, without dry-rewetting cycles; Fig. 1); at least one of the variables investigated had to be reported in both control and drought treatment; the treatment and control started with the same soil type and plant species, and were conducted under equal spatial and temporal scales.

The variables investigated were each measured at different time points (Fig. 1). Observations were separated into drying and rewetting phases for laboratory incubations that had one or more

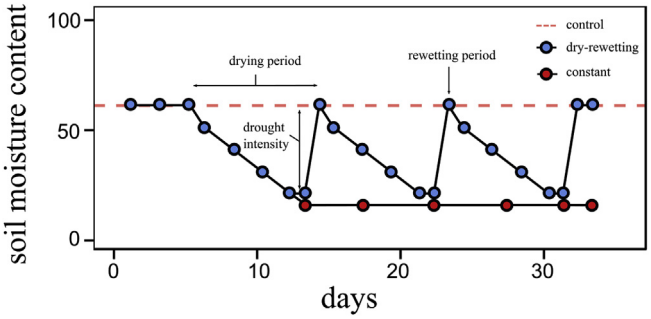

Fig. 1. General illustration of selection criteria (presence of control and treatment) and drought characteristics (dry and rewet periods and drought intensity) of retrieved studies, showing soil moisture content against experiment length (days). Points represent time of measurement for both dry-rewetting and constant drought treatments. Length of rewetted and dry phases was variable between studies.

rewetting events. In field experiments all observations were considered as part of the drying phase, since rewetting through precipitation occurred both in control and drought treatments. Because MBC and F:B ratio can each be measured with different techniques, which may be difficult to compare, we decided to use data from a single technique for each response variable. For microbial biomass the most common technique in our data set was the fumigation-extraction technique (259 observations from 31 studies; Vance et al., 1987) while F:B ratios were predominantly based on the phospholipid fatty acid (PLFA) analysis in soil (87 observations from 16 studies; Frostegård et al., 2011).

Following these criteria, a total of 60 studies were included, providing 629 paired observations (control *vs* treatment) of respiration, 162 for cumulative respiration, 259 for microbial biomass, 200 for DOC and 87 for F:B ratio (including 83 specific for fungi and 77 specific for bacteria). Mean, number of replicates and standard deviation of the response variables were calculated or extracted for all treatments and controls, whereby different treatments (e.g., soil type, fertilizer application) were considered as separate experiments (Gurevitch and Hedges, 1999). Figure data were extracted using Plot digitizer software (Huwaldt, 2013) to convert data-points to numerical values.

When values of qCO_2 were not reported, the ratio was estimated when respiration and MBC measurements were both reported (100 observation pairs in 13 studies). In those cases, standard deviations for control and drought treatments were derived with Taylor expansion (Stuart and Ord, 1994):

$$\widehat{\sigma}_{total} = \sqrt{\frac{\mu_R^2}{\mu_{MBC}^2}\left[\frac{\sigma_R^2}{\mu_R^2} - 2\frac{Cov(R,\ MBC)}{\mu_R\ \mu_{MBC}} + \frac{\sigma_{MBC}^2}{\mu_{MBC}^2}\right]}$$

where μ indicates mean and σ^2 and Cov the variance and covariance of respiration (R) and microbial biomass C (MBC), respectively. As studies did not report covariance or raw data, the covariance term was approximated based on reported mean values of MBC and R, and their variance (where available). A cross-study covariance estimate, $\overline{Cov}(R,\ MBC)$, was derived from all reported mean values, R_i and MBC_i, reported in the dataset, and the ratio of overall covariance to the pooled variance of R_i and MBC_i was calculated. Study-specific covariance estimates, reflecting levels of variation in each study, were then obtained by multiplying this ratio with, the pooled variance of R and MBC in each study.

For each observation we recorded informative data about soil and drought characteristics as well as other experimental settings, to be included as categorical and continuous explanatory moderators in the meta-analysis. For the soil characteristics we collected