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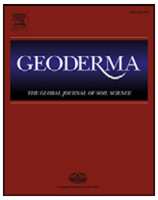

Strong pulse effects of precipitation events on soil microbial respiration in temperate forests

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ABSTRACT

Precipitation is a critical factor triggering soil biogeochemical processes in arid and semi-arid regions. In this study, we selected soils from two temperate forests—a mature natural forest and a degraded secondary forest—in a semi-arid region. We investigated the pulse effects of simulated precipitation (to reach 55% soil water-holding capacity) on the soil microbial respiration rate (R_S). We performed high-intensity measurements (at 5-min intervals for 48 h) to determine the maximum value of R_S ($R_{S\text{-max}}$), the time to reach $R_{S\text{-max}}$ ($T_{R_{S\text{-max}}}$), and the duration of the pulse effect (from the start to the end of ½$R_{S\text{-max}}$). The responses of R_S to simulated precipitation were rapid and strong. $R_{S\text{-max}}$ was significantly higher in degraded secondary forest (18.69 μg C g soil^{-1} h^{-1}) than in mature natural forest (7.94 μg C g soil^{-1} h^{-1}). In contrast, the duration of the pulse effect and $T_{R_{S\text{-max}}}$ were significantly lower in degraded secondary forest than in mature natural forest. Furthermore, the accumulative microbial respiration per gram of soil ($A_{R_{S\text{-soil}}}$) did not differ significantly between degraded secondary forest and mature natural forest, but the accumulative microbial respiration per gram of soil organic C ($A_{R_{S\text{-soc}}}$) was significantly higher in degraded secondary forest than in mature natural forest. Soil microbial biomass, soil nutrient, and litter nitrogen content were strongly correlated with the duration of the pulse effect and $T_{R_{S\text{-max}}}$. Soil physical structure, pH, and litter nitrogen content were strongly correlated with $R_{S\text{-max}}$ and $A_{R_{S\text{-soc}}}$. Our results indicate that the responses of soil microbial respiration to simulated precipitation are rapid and strong and that microbial respiration rate per gram C can be used to precisely determine the precipitation pulse of different soil samples as well as the effects of changing precipitation patterns on soil C content under various scenarios of global climate change.

1. Introduction

Precipitation events trigger a cascade of biogeochemical transformations in soils, thereby leading to a hierarchy of soil moisture pulse events and corresponding ecological responses (Schwinning and Sala, 2004a). The pulse effects of precipitation can result in rapid release of nutrients (within minutes or hours) by soil microorganisms (Cui and Caldwell, 1997); moreover, at longer time scales (years), they may influence the responses of primary producers and consumers (Ostfeld and Keesing, 2000). The phenomena that rewetting of dry soils results in a pulse of carbon (C) and nitrogen (N) mineralization have been termed the Birch effect (Birch, 1958). The soil microbial respiration rate (R_S) has been shown to vary according to the frequency and intensity of precipitation (Schwinning and Sala, 2004a; Kim et al., 2012). In general, the pulse effects of precipitation depend on: the following factors (1) the previous status of soil water content; (2) the precipitation intensity; and (3) precipitation frequency. In addition, soil type and quality, vegetation, and duration of precipitation have been reported to modify the pulse effect (Schwinning et al., 2004b).

Some studies have reported that simulated precipitation (or rewetting) can enhance R_S relative to soil under drought conditions (Davidson et al., 2000; Fierer and Schimel, 2003). This pulse effect can increase cumulative CO_2 release by more than three-fold relative to soils with a stable moisture regime (Miller et al., 2005). Furthermore, intra-seasonal precipitation patterns—such as precipitation intensity, frequency, and time—can influence the biological processes in soils, especially in water-limited ecosystems (Schwinning et al., 2003). Small precipitation events may facilitate the respiration of biological crust C, whereas large precipitation events may primarily promote the respiration of microbial C (Cable and Huxman, 2004; Schwinning and Sala, 2004a).

Arid and semi-arid ecosystems are particularly sensitive to precipitation, because important resources (e.g., water and nutrients) are discontinuously available for long periods under discrete precipitation events. While the pulse effects of precipitation events on R_S are known to be important for soil nutrient cycles and soil organic matter (SOM) turnover in semi-arid and arid regions, these effects have not yet been well elucidated (Huxman et al., 2004; Kim et al., 2012; Sala and Lauenroth, 1982; Sponseller, 2007). Iovieno and Baath (2008) have found that the responses of R_S to precipitation events are rapid, and R_S can return to background levels within a short time (e.g., 1 h). However, most studies

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have been conducted at relatively long measurement intervals, such as hours (Butterly et al., 2010; Rudaz et al., 1991; Sponseller, 2007), days, or weeks (Chowdhury et al., 2011; Wu and Brookes, 2005). Owing to the lack of measurements at the scale of seconds or minutes, the pulse effects of precipitation on R_S remain less understood.

Various explanations have been proposed for the observed pulse effects of precipitation. Some researchers have suggested that the availability of physically protected SOM to microbes is enhanced after precipitation because of changes in the soil structure (Göransson et al., 2013; Iovieno and Baath, 2008). Jones and Murphy (2007) reported that with substrate addition, activation of soil microbes occurred almost instantaneously (within <60 s), and that the average time to half-maximum CO_2 production was 10–14 min, which demonstrated the important effect of substrate indirectly. Another alternative explanation is a rapid increase in soil microbial biomass after precipitation (Evans and Wallenstein, 2012; Lundquist et al., 1999; Manzoni et al., 2014; Meisner et al., 2013). Fierer and Schimel (2003) labeled soils with 14C-glucose and showed that the pulse of CO_2 emission was generated from the mineralization of microbial biomass C. Butterly et al. (2009) demonstrated that the intensity of R_S after simulated precipitation was highest in the treatment with the largest and most active biomass via substrate addition. Collectively, these findings suggest that soils with more microbes and available substrate have stronger pulse effects and produce larger quantities of CO_2.

In this study, we conducted incubation experiments using forest soils from two temperate forests—a mature natural forest and a degraded secondary forest—in a semi-arid temperate region. We performed high-intensity measurements (272 times for 48 h) to investigate the pulse effects of simulated precipitation on R_S. Our specific objectives for the present study were as follows: (1) to investigate the dynamics of pulse effects on R_S in response to precipitation events; (2) to examine the differences of pulse effects (e.g., reactive intensity and durability) between mature natural forest and degraded secondary forest soils; and (3) to investigate how microbial biomass and vegetable type contribute to the observed pulse effects in these different temperate forest soils.

2. Materials and methods

2.1. Site description

The experimental plots used in the study were located west of Beijing at an average elevation of 1330 m (Hou et al., 2006). This region has a temperate continental monsoon climate and the mean annual temperature and precipitation are 11 °C and 639 mm, respectively. The regional soils are classified as Lixisols, according to the classification of world reference base for soil resources (Phillips and Marion, 2007).

We collected soils from two temperate forests—a mature natural forest and a degraded secondary forest. The mature natural forest was located at 39° 57′ N, 115° 25′ E, and the dominant tree species were *Quercus wutaishanica*, *Betula platyphylla*, and *Larix principis-rupprechtii*. The contents of soil organic carbon (SOC) and total N (TN) were 4.01% and 0.30%, respectively. The soil particle size distribution was 78% sand, 21% silt, and 1% clay (He et al., 2009). The degraded secondary forest was located at 39° 58′ N, 115° 26′ E, and the dominant plant species were secondary shrubs such as *Corylus mandshurica*, *Abelia biflora*, and *Fraxinus rhynchophylla*. The contents of SOC and TN were 3.46% and 0.26%, respectively. The particle size distribution was approximately 25% sand, 69% silt, and 6% clay (He et al., 2009). Additional details regarding the two forests are shown in Table 1.

2.2. Field sampling

Soil sampling was conducted during September 2014. Four experimental plots (30 m × 40 m) were established in each forest. Soil samples

Table 1
General soil properties of experimental plots.

Forest type	Community properties			Soil biochemistry properties									Soil physical properties		
	Dominant species	Litter C content (%)	Litter N content (%)	SOC[a] (%)	TN (%)	PLFA (nmol g^{-1})	Bacteria (nmol g^{-1})	Fungi (nmol g^{-1})	Actinomycete (nmol g^{-1})	pH	ORP (mv)	COND (s m^{-1})	Sand (%)	Silt (%)	Clay (%)
Natural forest	*Quercus wutaishanica*, *Betula platyphylla*, *Larix principis-rupprechtii*	45.60[b] (0.01)	0.96 (0.01)	4.01 (0.41)	0.30 (0.03)	13.47 (1.87)	5.39 (1.36)	2.38 (0.52)	0.34 (0.05)	6.90 (0.47)	194 (24.81)	253.83 (74.85)	78.49 (24.45)	20.51 (23.15)	1 (1.33)
Secondary forest	*Corylus mandshurica*, *Abelia biflora*, *Fraxinus rhynchophylla*	40.49 (0.05)	1.42 (0.01)	3.46 (0.07)	0.26 (0.01)	9.08 (1.09)	3.98 (0.60)	0.94 (0.37)	0.24 (0.03)	7.44 (0.00)	119 (0.00)	250.20 (0.00)	25.22 (11.92)	68.79 (10.81)	5.98 (1.49)
P		0.04	0.04	0.04	0.14	0.02	0.70	0.04	0.21	0.21	0.04	0.21	0.04	0.21	0.04

[a] SOC, soil organic carbon; TN, soil total nitrogen; PLFA, phospholipid fatty acid; ORP, oxidation–reduction potential; COND, conductivity.
[b] Data are presented as mean ± standard deviation in parentheses ($n = 4$).