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Autotrophic and heterotrophic soil respiration responds asymmetrically to drought in a subtropical forest in the Southeast China

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ABSTRACT

Both increasing frequency of drought and drought duration are expected for many terrestrial ecosystems under on-going climate change. However, our understanding of the drought effect on soil respiration (R_s), which comprises the second largest carbon (C) flux of the global C cycle, remains limited. To explore the effects of reduced precipitation on R_s and its components, we conducted an experiment of throughfall rainfall exclusion during two consecutive growing seasons in a subtropical forest in the Southeast China. Following throughfall exclusion R_s declined rapidly, and did not recover until three to four months following rewetting, in both 2014 and 2015. During the experiment, throughfall exclusion significantly reduced autotrophic soil respiration (R_a); however, heterotrophic soil respiration (R_h) was unaffected, resulting in a reduced contribution (R_a/R_s) from 33 ± 1% for the control to 16 ± 3% under throughfall exclusion. Experimental drought significantly reduced soil microbial C and fine root biomass, and subsequent to rewetting, soil microbial C recovered quickly, but fine root biomass relapsed slowly. Our results suggested that prolonged drought decreases R_s through modifications in soil microbial activities and fine root metabolic capacity, which are induced by reduced soil water availability. Moreover, our results imply that drought-induced reductions in R_s originate primarily from R_a . Our results highlight the need to account for asymmetric responses to drought between R_a and R_h when predicting the reaction of the ecosystem C balance in response to future drought events.

1. Introduction

Soil respiration (R_s) constitutes the second-largest terrestrial carbon (C) flux (Bond-Lamberty and Thomson, 2010), releasing approximately 58 Pg CO₂ annually from terrestrial ecosystems, which is 10-fold that of anthropogenic combustion emissions (Hanson et al., 2000; Schlesinger and Andrews, 2000). Therefore, even subtle changes in R_s can have a significant impact on the global C cycle. Both soil temperature and soil moisture are critical environmental determinants for R_s (Laganière et al., 2012; Lellei-Kovács et al., 2016). Previous studies have indicated that global warming accelerates R_s (Lu et al., 2013; Noh et al., 2015; Xu et al., 2015). However, the impacts of extreme droughts, whose intensity and frequency are anticipated to increase during the 21st century (IPCC, 2013), on R_s remain uncertain. Previous precipitation manipulation experiments have revealed that the effects of reduced precipitation on R_s are highly variable, and their effects tend to be contingent on soil moisture conditions (Borken et al., 2006; Sotta et al., 2007; Cleveland et al., 2010; Doughty et al., 2015). In addition, the responses of R_s to drought may differ between growing and non-growing seasons (Suseela and Dukes, 2013; Zhang et al., 2015).

Soil moisture directly influences R_s through physiological processes (Manzoni et al., 2012; Schindlbacher et al., 2012; Li et al., 2013), and indirectly by diffusion of oxygen through the substrate (Cleveland et al., 2010; Van Straaten et al., 2011). Predicting the response of R_s to altered soil water availability is inherently difficult, as R_s includes both heterotrophic (R_h) and autotrophic (R_a) components (Kuzyakov, 2006; Hinko-Najera et al., 2015). The R_h depends on microbial activity and substrate availability (Scott-Denton et al., 2006; Hinko-Najera et al., 2015), while R_a is regulated by the allocation of recently assimilated C (Hanson et al., 2000; Kuzyakov, 2010; Doughty et al., 2015). Recent studies have revealed that R_a and R_h respond differently under drought conditions (Borken et al., 2006; Sanaullah et al., 2012; Kopittke et al.,

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| Table 1 | 1 |
|---------|---|
|---------|---|

| Soil properties of different soil layer i | n the evergreen broad | lleaved forest (mean ± | \pm s.e.m., $n = 3$) |
|---|-----------------------|------------------------|-------------------------|
|---|-----------------------|------------------------|-------------------------|

| Soil depth (cm) Bul | Bulk density (g•cm ⁻³) | SOC | TN | MBC (mg•kg ⁻¹) | рН (H ₂ O) | Soil texture (%) ^a | | |
|---------------------|------------------------------------|----------------------|---------------|-------------------------------|--------------------------|-------------------------------|------|------|
| | | (g•kg ⁻) | (g•kg -) | | | Sand | Silt | Clay |
| 0–10 | 1.06 ± 0.02 | 55.4 ± 0.8 | 3.2 ± 0.1 | 665.0 ± 34.0 | 4.5 ± 0.1 | 68.8 | 20.0 | 11.2 |
| 10-20 | 1.10 ± 0.02 | 32.9 ± 1.7 | 2.0 ± 0.2 | 377.3 ± 14.1 | 4.8 ± 0.1 | 63.2 | 25.8 | 11.0 |
| 20-40 | 1.18 ± 0.01 | 19.6 ± 0.8 | 1.3 ± 0.1 | 161.6 ± 14.3 | 4.9 ± 0.2 | 59.4 | 16.7 | 23.9 |
| 40–60 | $1.27~\pm~0.02$ | $12.6~\pm~1.1$ | $0.8~\pm~0.1$ | 168.1 ± 19.1 | 5.1 ± 0.1 | - | - | - |

^a Bu et al. (2012).

2014); however, it remains unclear whether R_a or R_h is more sensitive to droughts.

In addition, how R_s and its components respond to subsequent rewetting also remains uncertain. Rewetting induced R_s bursts, referred to as the "Birch effect" (Birch, 1958), have been observed in a temperate forest soil (Borken et al., 2006). However, these R_s bursts appear to be intimately dependent on soil properties, vegetation type, and the length and intensity of the drying-wetting cycle (Muhr et al., 2011; Manzoni et al., 2012; Hagedorn and Joos, 2014). These findings indicate that different magnitudes and directions of R_s in response to rewetting occur, making predictions of soil C balances under increasing drought conditions rather difficult (Hagedorn and Joos, 2014).

The subtropical region of China is characterized as an extensive C reserve with high rates of C fluxes that are sustained by abundant light, heat, and water resources (Yu et al., 2014). Due to low atmospheric conditions that are controlled by a West Pacific Subtropical High-Pressure System, in combination with a prevailing descending airflow, this region is often impacted by high temperatures and severe drought stress during the summer (Mi et al., 2009). Moreover, this region is expected to experience an increasing probability of drought intensity and frequency in the 21st century (Dai, 2011). More frequent or prolonged droughts can significantly reduce soil water availability, and in turn, could strongly impact C cycles, plant productivity, and biodiversity (Wessel et al., 2004; Beier et al., 2012).

Here, we employed a rainfall throughfall exclusion (TFE) experiment to simulate the effects of growing season drought on R_s in an evergreen broadleaved forest in subtropical China. Our goal was to determine the impacts of reduced soil water availability on R_s . Our drought experiment included two periods, one in the summer of 2014, and the other in the spring of 2015. We hypothesized that water reduction would decrease R_s , and the reduced R_s might primarily result from R_h , as low soil water availability limits R_h more than R_a components (Borken et al., 2006). We expected a rapid increase in R_s with rewetting following a spring drought due to abundant summer rainfall, but a slow R_s recovery following a summer drought due to limited autumn rainfall. We quantified soil temperature, soil moisture, soil microbial biomass C (MBC), and fine root biomass (FRB) to better understand the links between the changes in R_s and its components that were induced by droughts.

2. Materials and methods

2.1. Site description

Our study was conducted in the Wuyi Mountain National Nature Reserve (27°33′-27°54′N, 117°27′-117°51′E), with an area of 56,527 ha, which is located in the Southeast China. The typical forest in this region is evergreen broadleaved forest (Yu et al., 2014). The climate is midsubtropics with a mean annual temperature of 15.2 °C and mean annual precipitation of 2764 mm from 2006 to 2016. Approximately 70% of the precipitation fell in the growing season, from March to August (data from a meteorological station that was 500 m away from the site).

The experiment was conducted within a 15 ha evergreen broadleaved forest (tree ages ranged from 60 to 70 years) at an altitude ranging from 620 m to 674 m a.s.l., and slopes ranging from 30° to 32°. This area was dominated by *Castanopsis eyrie* Tutch, *Cyclobalanopsis myrsinifolia* Oersted and *Castanopsis carlesii* Hay, accounting for 78% of the overstory stand basal area. Based on the measurements of three plots (30 m × 30 m for each), the mean of tree height and diameter at breast height were 11.6 ± 1.6 m and 15.5 ± 2.3 cm, respectively. The stand had 90% of tree canopy cover, 1656 trees ha⁻¹ of stem density, and 30.9 m² ha⁻¹ of basal area. The shrub layer vegetation consisted primarily of *Rapanea neriifolia, Engelhardia fenzelii* and *Indocalamus tessellates*. The bulk density, organic C, and total nitrogen concentration of the soil in the 0–10 cm mineral soil layer were 1.06 ± 0.02 g cm⁻³, 55.4 ± 0.8 g kg⁻¹, and 3.2 ± 0.1 g kg⁻¹, respectively. Soil properties in other soil layers are presented in Table 1. The litter layer thickness ranged from 1 to 3 cm, and the annual litterfall was 3.8 ± 0.2 t ha⁻¹ yr⁻¹ between 2003 and 2012.

2.2. Experimental design

In the winter of 2013, three experimental plots $(30 \text{ m} \times 30 \text{ m})$ were randomly established within the 15 ha evergreen broadleaved forest with similar topography. These plots were approximately 200 m apart. For each of the three plots, four $3 \text{ m} \times 3 \text{ m}$ subplots were established with 10 m buffer zones between them. No tree trunks existed in any control and treatment subplots. Two of the four subplots received throughfall exclusion (TFE) treatment, whereas the other two served as the control treatment. Trenches were dug, and all roots were cut off in one of the TFE subplots and one of the control subplots to estimate the autotrophic and heterotrophic components of soil respiration (Schindlbacher et al., 2009; Noh et al., 2015). To minimize the transient response caused by decomposition of dead roots, the trenching treatment was conducted six months before soil efflux measurements began in the trenched subplots (Noh et al., 2017). Trenches were dug in an area of $1 \text{ m} \times 1 \text{ m}$, and were excavated to a depth of 60 cm (below which few roots existed) (Bu et al., 2012), or to bedrock, when the soil depth was < 60 cm. After lining the trench with a double-layer polyethylene film, the soil was backfilled. The aboveground components of the understory vegetation in the trenched subplots were carefully removed with minimal soil disturbance, and were kept free of any vegetation by repeated manual removal throughout the entire study period. The perimeter of the drought treatment subplots was also trenched to a depth of 30 cm and lined with double-layer polyethylene film to prevent surface run-off and lateral water movement into the subplots.

We installed portable rain shelters $(3 \text{ m} \times 3 \text{ m})$ that were covered with transparent polyethylene film, and framed using tunnel-shaped galvanized aluminum tube supports with roughly 2.0 m in height. The rain shelters were covered between June 13th and September 12th, 2014, and between March 15th and June 27th, 2015. Throughfall that accumulated on the roofs during both TFE treatment periods was drained into gutters over a distance of about 20 m before it flowed into the ground external to the plots. The sidewalls of the rain shelters were left open, which facilitated air flow to minimize the difference in temperature and humidity between their interiors and exteriors (Sherman et al., 2012). The polyethylene films were removed on Download English Version:

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