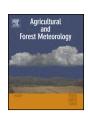
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Differential responses of soil respiration to soil warming and experimental throughfall reduction in a transitional oak forest in central China



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ABSTRACT

Examining responses of soil respiration to climate change is crucial for understanding future terrestrial carbon (C) cycling. However, the interaction between climate warming and precipitation reduction on soil respiration has not been well documented. This study aimed to determine the impacts of soil warming and throughfall reduction on soil respiration and its components (heterotrophic respiration and autotrophic respiration).

A field manipulation experiment with soil warming and throughfall reduction was conducted in an oak natural forest ($Quercus\ aliena$) at a transitional climatic zone in central China during the growing seasons (May–November) in 2011 and 2012. Soil temperature was elevated by 1.23–1.66 °C relative to the ambient environment by using infrared heaters, and throughfall was reduced by 50% through roof interception.

There were significant interactive effects of soil warming and throughfall reduction on soil respiration and autotrophic respiration in both 2011 and 2012. Soil warming substantially elevated soil respiration by 32.0–46.3% and autotrophic respiration by 57.8–63.2% without throughfall reduction, respectively, but suppressed both of them with throughfall reduction. Throughfall reduction increased soil respiration by 16.2–37.2% and autotrophic respiration by 62.9–97.7% under ambient temperature, whereas decreased them by 13.7–29.2% and 22.6–51.9% under soil warming. Heterotrophic respiration was significantly increased by soil warming while showed little effect by throughfall reduction or its interactions with soil warming. The offset of the positive warming effect on soil respiration under throughfall reduction may be attributed mainly to the changes in soil microbial biomass and fine root biomass induced by throughfall reduction.

Our observations suggest that either climate warming or precipitation reduction may increase soil CO_2 emission, but this stimulation in oak forests will be largely counteracted if climate warming accompanies with simultaneous precipitation reduction at the climatic transitional zone.

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1. Introduction

Increasing global temperature and changing precipitation regime associated with global climate change is expected to exacerbate and engender regional drought events, especially in mid-latitude and subtropical dry regions (IPCC, 2013), which will

most likely alter the structure and function of forest ecosystems, and consequently affect terrestrial carbon (C) cycling (Rustad et al., 2001; Lin et al., 2011; Wu et al., 2011; Xia et al., 2014). Most field evidence suggests that climate warming generally stimulates plant growth and ecosystems C flux (e.g. NPP, ecosystem photosynthesis, and ecosystem respiration), whereas decreased precipitation shows the opposite effects (Wu et al., 2011; Zhou et al., 2013).

Soil respiration is the second-largest terrestrial C flux in the global C cycle (Bond-Lamberty and Thomson, 2010), and therefore, any potential change in the rate of soil respiration induced by biotic

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(Högberg et al., 2001, 2008; Caquet et al., 2012) or abiotic factors (Flanagan and Johnson, 2005; Flanagan et al., 2013) will have strong impact on the global C cycling and subsequently climate change (Davidson and Janssens, 2006; Phillips et al., 2012). Therefore, a deep insight into soil respiration would enhance our ability to predict terrestrial C fluxes and C sink potential under future climate change.

Soil respiration is strongly influenced by soil temperature and water availability (Verhoef et al., 1996), and these two environmental factors are closely related to climate warming and changing precipitation patterns (Rustad et al., 2001; Zhou et al., 2006; Schindlbacher et al., 2012). Numerous studies have examined the responses of soil respiration to soil warming and precipitation reduction in forest ecosystems (Sotta et al., 2007; Xu et al., 2009). A meta-analyses showed that experimental warming significantly increased soil respiration in forest ecosystems (Rustad et al., 2001; Wu et al., 2011), as a result of increased decomposition of soil organic C (SOC). However, soil respiration was suppressed by experimental warming in a semi-arid Pannonian sand forest-steppe ecosystem (Lellei-Kovács et al., 2008). The differential responses of soil respiration to rising temperature could be attributed to interactions with other environmental factors, such as soil water availability (Wang et al., 2014). Throughfall reduction was reported to reduce soil respiration in a temperate mixed beech-spruce forest (Nikolova et al., 2009) and in a tropical terra firme forest (Sotta et al., 2007), whereas elevate soil respiration in the wet tropical rain forest (Cleveland et al., 2010). Wu et al. (2011) found that decreased precipitation, regardless of vegetation types, could reduce soil respiration by 12%. These contradictory results have been attributed to the difference in soil texture, plant root, and soil microbial activities (Sotta et al., 2007). Even though individual effects of increasing temperature and reduced precipitation on soil respiration have been widely studied, it remains unclear how soil respiration responds to the concurrent changes in temperature and precipitation, and whether they interacted with each other to affect soil respiration.

One of the key challenges to evaluate the role of soil respiration in global C cycling is that soil respiration is a combined flux comprised of autotrophic respiration of roots and associated rhizosphere community, and heterotrophic respiration from the decomposition process of SOC (Kuzyakov, 2002; Jassal and Black, 2006; Hinko-Najera et al., 2015; Song et al., 2015). Autotrophic respiration is strongly affected by the allocation of recently assimilated photosynthates to belowground and root activity (Högberg et al., 2001; Shi et al., 2011), whereas heterotrophic respiration is dependent on the microbe activity and substrate availability, such as C input from litterfall, root turnover, and soil C content (Hanson et al., 2000; Hinko-Najera et al., 2015). The two components represent different ecological and biological processes and respond differently to changes in environment drivers, including temperature and water (Boone et al., 1998; Scott-Denton et al., 2006; Schindlbacher et al., 2009; Wang et al., 2014), and thus, have profound implications on the soil C storage (Boone et al., 1998; Luan et al., 2011a). For example, respiration from bulk soil was higher than that from planted soils under soil warming (Hartley et al., 2007). However, the two respiration components displayed similar levels of elevation under warming treatment in a mature Norway spruce forest (Schindlbacher et al., 2009). In a temperate broadleaved evergreen eucalypt forest, throughfall reduction strongly suppressed autotrophic respiration, but had no effect on heterotrophic respiration (Hinko-Najera et al., 2015). Therefore, without partitioning and quantifying soil respiration components, soil total respiration measurements alone provide little insight into terrestrial C cycling and are insufficient to evaluate its response to future climate change (Kuzyakov, 2002; Wang et al., 2014).

Forests dominated by oak species (Quercus spp.) are the largest forest biome in area and in vegetation C storage among all forest types in China, which covers a total area of 15.5×10^6 ha (15.2%) of all forests; Fang et al., 1996) and storing 835.94 Tg vegetation C (22.4% of all forests; Wang et al., 2001). Therefore, oak forests play an important role in controlling ecosystem C cycling and regional climate changes in China, and have been reported to be strong C sinks in terrestrial ecosystems (Fang et al., 2001). Previous studies in oak forest ecosystems have found that the rising temperature can stimulate soil respiration (Luan et al., 2014), whereas experimental drought can reduce aboveground biomass (Ogaya et al., 2003) and soil respiration (Asensio et al., 2007). In addition, oaks are dominantly associated with ectomycorrhizal, which can produce extracellular enzymes to degrade soil organic matter (Phillips et al., 2013), and thus exert influence on the response of soil respiration to climate change. Whether these C sinks will persist or become sources under climate change is uncertain and may depend largely on the responses of soil respiration to climate change (Deng et al.,

We conducted a field manipulation experiment by soil warming and throughfall reduction in a temperate oak natural forest from 2010 to 2012, in order to examine the responses of soil respiration to climate warming and changing precipitation pattern. The study site was located at a transitional climatic zone from northern subtropical to warm-temperate climate in central China, because the transitional climatic zone was illustrated to be more susceptible to changing climate than the other regions (Mahlstein et al., 2013). Previous study in this area indicates that the seasonal variability of soil respiration is dependent on soil temperature but independent of soil moisture as a result of the relative sufficient rainfall (Luan et al., 2011a). Soil warming can reduce soil moisture through stimulating evapotranspiration, leading to elevated root production (Majdi and Öhrvik, 2008) and soil microbial activity (Schindlbacher et al., 2012). Thus, we first hypothesized that soil warming should increase soil respiration by elevating both heterotrophic and autotrophic respiration. Given that throughfall reduction can partially decrease throughfall and improve soil aeration condition, and probably increase plant root and soil microbial activity (Liu et al., 2014), our second hypothesis is that throughfall reduction also elevate soil respiration through enhancing both heterotrophic and autotrophic respiration. However, a combination of throughfall reduction and soil warming may aggravate soil water deficits and suppress plant and soil microbial metabolism. Therefore, our third hypothesis is that soil respiration under the combined treatment should be lower than that under any single factor.

2. Materials and methods

2.1. Site description

The study site is located at the Baotianman Nature Reserve (111°47′–112°04′E, 33°20′–33°36′N), Henan Province, central China. The mean annual temperature is 15.1°C, with monthly air temperatures ranging from 1.5°C in January to 27.8°C in July (at 1400 m a.s.l.). The mean annual precipitation is approximately 894 mm with 60% of rainfall falling in summer season (from June to August). Upland soils are dominated by Haplic luvisol soils (Luan et al., 2011a). The typical forest in this area is the warm-temperate forest composed of temperate deciduous broadleaf trees as well as some subtropical tree species due to its transitional location in the northern transitional subtropical to warm-temperate climate.

The experiment was carried out in an oak natural forest (58 years old), dominated by *Quercus aliena* var. *acuteserrata*, which accounts for 66% of the overstory. Other non-dominant tree species

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