



Contrasting responses of heterotrophic and root-dependent respiration to soil warming in a subtropical plantation



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ABSTRACT

The most advanced global land models remain highly uncertain in their predictions of the magnitude and direction of the effects of global warming on soil respiration. To better understand how soil respiration responds to warming, we conducted a three-year soil warming experiment in a subtropical *Castanopsis hystrix* plantation. Soil respiration (R_s) is considered the sum of root-dependent respiration (R_{rd}) and heterotrophic respiration (R_h). We estimated root-dependent respiration using the difference in soil respiration between trenched (100 cm deep) and non-trenched plots. Our results showed that soil moisture was significantly higher in the trenched than non-trenched subplots in the second year, but not in the third year. Soil warming increased R_h and suppressed R_{rd} . The responses of R_h and R_{rd} to soil warming varied with the seasons, being greater in the dry-cool than in the wet-warm season. The elevated R_h levels may have resulted from the increased soil temperature and decreased soil moisture due to warming. The decline in soil total nitrogen (STN) content attributed to soil warming decreased arbuscular mycorrhizal fungi (AMF) biomass, which led to the reduced R_{rd} . The decreased R_{rd} and increased R_h appear to have offset each other, resulting in unaltered R_s levels under the warming treatment. Our study shows that mycorrhizal colonization can have similar effects on soil carbon as it does abiotic environmental factors such as temperature and moisture, and affects R_s dynamics.

1. Introduction

Climate change is expected to increase global surface temperatures by 1.5–2 °C at the end of the 21st century (IPCC, 2013). Elevated soil temperatures and reduced soil moisture induced by global warming could strongly impact terrestrial carbon (C) cycles, including soil respiration (R_s), the source of the largest efflux of carbon dioxide (CO_2) from terrestrial ecosystems to the atmosphere (Luo, 2007). R_s is comprised of autotrophic (root and associated rhizosphere respiration; R_a) and heterotrophic (decomposition of organic matter in soil; R_h) components (Hanson et al., 2000; Kuzyakov, 2006) that may respond similarly (Schindlbacher et al., 2009) or differently (Gomez-Casanovas et al., 2012; Zhou et al., 2007) to climate change. Therefore, a better understanding of the responses of R_a and R_h to soil warming would be crucial to improving model predictions of the climate-carbon feedback.

Experiments on R_s and its components' responses to warming have

been conducted in a variety of forests (Matias et al., 2011; Melillo et al., 2011; Melillo et al., 2002; Noh et al., 2016; Schindlbacher et al., 2012; Schindlbacher et al., 2009). Meta-analyses of warming experiments in temperate zones have indicated that R_s , R_h , and R_a are positively correlated with soil temperature (Lu et al., 2013; Wang et al., 2014). However, at lower latitudes, where ecosystems presumably operate closer to or already at their temperature optima, it is unknown whether a similar response would occur. The predicted results of climate change include an increase in temperature and changes in seasonal precipitation patterns in most tropical and subtropical land regions (IPCC, 2007; Zhou et al., 2011a). Some studies have highlighted the potential vulnerability of subtropical forest structures under these projected climate changes (Zhou et al., 2013). Recent studies have shown the effects of simulated warming on tree photosynthesis, soil microbial communities, and enzyme activities through translocation experiments along an altitudinal gradient in subtropical forests (Fang et al., 2016; Li et al.,

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2016). Nevertheless, information on the direct responses of below-ground C fluxes, including R_s and its components, to warming remains limited.

Despite recent advances in understanding the roles of rhizosymbionts and exudation on soil C dynamics, including R_s , the relative contributions of biological and physical controls of soil CO_2 efflux remain limited. The increased soil temperature and decreased soil moisture induced by warming may affect the amount and activity of plant roots and soil microorganisms. Particularly, recent studies have shown that roots and their associated microbial communities play a critical role in soil organic carbon (SOC) decomposition and stabilization (Averill et al., 2014). Root growth and root biomass in mineral soil could be significantly stimulated (Andresen et al., 2010) or inhibited (Zhou et al., 2011b) under warming conditions. Recent studies have reported both positive (Gavito et al., 2003), and negative (Staddon et al., 2003) effects of warming on the growth of arbuscular mycorrhizal fungi (AMF). The causes of these different responses remain unknown, especially as they can be either direct or mediated by vegetation (Staddon et al., 2003). Soil microbial biomass and community composition have been found to show highly variable responses to elevated temperatures (Andresen et al., 2009; Schindlbacher et al., 2011). AMF, which form associations with the roots of ~80% of land plant species and represent the dominant mycorrhizal type in many tropical forests, could also affect the rate of SOC sequestration (Camenzind et al., 2014). The carbohydrates exuded by AMF hyphae can also stimulate the activity of decomposers and further facilitate the decomposition of complex organic materials in soils (Cheng et al., 2012; Hodge et al., 2001; Phillips et al., 2012).

There is a growing recognition that planted forests can reduce logging pressure on natural forests, contribute to sequestering atmospheric CO_2 , and restore degraded lands (Kelty, 2006). Because tree species composition and stand structure in plantations are not as complicated as those in natural forests, the plantation is a good model system to investigate how experimental warming can affect soil C fluxes, tree root dynamics, and their interactions. Therefore, we designed a manipulation experiment to quantify the effects of soil warming on the heterotrophic and root-associated components of R_s in a subtropical plantation forest composed of *Castanopsis hystrix*. The specific objectives were to address: (i) How R_s and its source components respond to soil warming in a subtropical plantation? (ii) If the impacts of soil warming on R_s and its components vary seasonally? (iii) If the effects of soil warming on R_s and its components are mediated by tree roots and soil microbes?

2. Materials and methods

2.1. Site location

Soil warming manipulation experiments were carried out in a *C. hystrix*-dominated plantation with few understory species in Guangxi Youyiguan Forest Ecosystem Research Station at the Experimental Center for Tropical Forestry, Chinese Academy of Forestry (22°05'N, 106°86'E), on the outskirts of Pingxiang City, Guangxi Zhuang Autonomous Region, a subtropical region of China. The region is characterized by a typical subtropical monsoon climate, with an annual average precipitation of 1300 mm, of which nearly 80% falls in the wet-warm season (April–September) and 20% in the dry-cool season (October–March). The mean annual temperature is 22.3 °C. Over the last 60 years, this region has undergone an increase in air temperature of 0.12 °C per decade (measured 1953–2014; Fig. 1). The elevation of the *C. hystrix* plantation is 550 m. The *C. hystrix* plantation was established in 1983 after the clear-cutting of a *Cunninghamia lanceolata* plantation. The diameter of trees at breast height, total tree height, and stem density of the *C. hystrix* plantation in 2012, at the beginning of this experiment, averaged 25.7 cm, 18.3 m, and 333 trees ha^{-1} , respectively. The loamy-textured soil at the study site was formed from a

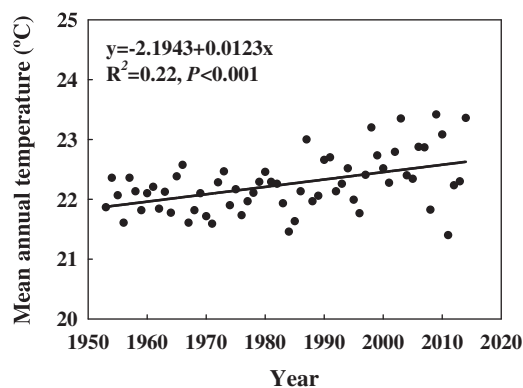


Fig. 1. Trends in annual ambient temperature from 1954 to 2014 at Longzhou County's weather station (30 km away from the study site).

granitic parent geological material and was classified as a Ferrosol in the Chinese system of soil classification, equivalent to an Oxisol in the USDA Soil Taxonomy (USDA, 1996). The basic ecological monitoring study complied fully with the “Observation Methodology for Long-term Forest Ecosystem Research” of National Standards of the People's Republic of China (GB/T 33027-2016).

2.2. Experimental design

We conducted a soil warming experiment in the *C. hystrix* plantation using ambient soil temperature as the control and applying a nearly 2 °C temperature increase as the treatment. Six pairs of 4 × 3 m plots were randomly established on the site over a 30 × 70 m area, each pair containing a plot that was subject to warming and a control temperature plot that was not subject to warming. Each warming plot was heated using an infrared heater (Kalgo Electronics Inc., Bethlehem, PA, USA) that was suspended 2 m above the centerline and parallel to the 3-m-edge line of the plot (Wan et al., 2002). A ‘dummy’ heater with the same shape and size as the infrared heater was suspended 2 m above the middle of each control temperature plot to simulate the shading effects of the infrared heater in the warming plots. To measure R_s and its source components, each plot was further divided into two 2 × 3 m subplots, one of which was randomly assigned to be trenched while the other remained non-trenched. The trenches were dug 1 m deep to minimize the influence of roots entering the subplots. In a previous study, most of the root biomass of 7 dominant tree species (including a *Castanopsis* species) in a subtropical forest was distributed in the upper soil layer (0–50 cm) (Hao and Peng, 2009). Therefore, the 100 cm trench was deep enough to exclude most living roots in the present study. The sides of the trenches were covered with thick plastic, and then the trenches were backfilled. R_h was measured in trenched subplots, while R_s was measured in non-trenched subplots. We defined R_{rd} instead of R_a by subtracting R_h from R_s . R_{rd} comprises R_a and respiration resulting from SOM decomposition dependent on roots. Thus, R_{rd} can more accurately describe the differences between two plots. Experimental warming treatments began in January 2012 and lasted for three years.

During the experimental period, continuous temperature and soil volumetric moisture data were acquired from a depth of 5 cm at the center of each subplot then logged at 60 min intervals, using an HL20 Environmental Monitoring System (Harvesting Science and Technology Co., Ltd, Beijing, China). The potential evapotranspiration (PET) was estimated using the Thornthwaite equation (Pereira and Pruitt, 2004).

2.3. Sampling and measurements

Two polyvinyl chloride (PVC) collars (19.6 cm inner diameter, 8 cm height) were inserted to a depth of 3 cm in each of the 24 subplots. The

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