



Precipitation affects soil microbial and extracellular enzymatic responses to warming



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ABSTRACT

Soil microbial communities and extracellular enzymes have important roles in many terrestrial ecosystem processes and are influenced by climate change drivers. In the present study, the individual and/or interactive effects of climate change drivers on soil microbial communities and extracellular enzyme activities were measured in experimental field plots planted with *Pinus densiflora* and subjected to air warming (ambient or +3 °C) in combination with precipitation treatments (reduced by 30%, ambient or elevated by 30%). Soil microbial biomass and four extracellular enzyme activities were measured. Additionally, the structure and composition of microbial communities were assessed. Warming increased microbial biomass concentration by 22.3% in precipitation control plots and by 17.9% in elevated precipitation plots. Warming lowered the extracellular enzyme activity in precipitation control plots, but increased their activity in elevated precipitation plots. Warming had a differential effect on the composition of bacterial and fungal communities under different precipitation treatments, with significant changes in the relative abundance of Proteobacteria and Acidobacteria. Meanwhile, the alpha diversity index of both bacterial and fungal communities were affected by warming, with variation among the precipitation treatments. Changes in enzyme activities and microbial communities were correlated with shifts in soil environmental conditions (e.g., moisture, temperature, and available nutrients). In conclusion, changes in soil environmental conditions may select for distinct soil microbial communities, further reshaping soil ecosystem processes and functions in a warmer world.

1. Introduction

Ongoing global climate change is predicted to alter the soil microbial communities through direct and indirect pathways (Brockett et al., 2012). Changes in soil microbial assemblages may alter terrestrial ecosystem processes, including the decomposition of soil organic matter (SOM), carbon (C) sequestration, and nutrient cycling (Allison and Treseder, 2008; Schindlbacher et al., 2011). Direct effects of climate change are the result of altered microbial metabolism and substrate availability (Classen et al., 2015), while indirect effects arise from soil microbial-plant interactions that reflect the change in growth, phenology, and species composition of plants due to climate change (Brockett et al., 2012; Classen et al., 2015).

Temperature and precipitation are the most important climate change drivers that alter the structure and composition of soil microbial communities in terrestrial ecosystems. Increases in temperature can enhance the activity, biomass, alpha diversity, and respiration of soil microbes by accelerating metabolic rates, thereby favoring microbial communities adapted to warmer environments (Zhang et al., 2005; Bell

et al., 2010; Chen et al., 2015). Meanwhile, previous studies suggested that drought may reduce the microbial activity and population size by reducing soil moisture (Schimel et al., 2007; Sheik et al., 2011; Manzoni et al., 2012), while elevated precipitation may enhance the microbial respiration by increasing soil available substrates (Xiang et al., 2008). Alteration of the precipitation pattern may also affect the soil microbial community by increasing the ratio of fungi to bacteria by as much as 50% due to the changes in C inputs to soil from plants, altering the microbial community composition (Castro et al., 2010; Zhao et al., 2016).

Extracellular enzymes are useful indicators of soil fertility as they are major drivers of the decomposition of soil organic matter: β -1,4-glucosidase (BG) is involved in C acquisition by catalyzing cellulose degradation; N-acetyl-glucosaminidase (NAG) and L-leucine aminopeptidase (LAP) are involved in the mineralization of nitrogen (N) from chitin and proteins, as well as the breakdown of fungal cell walls; acid phosphatase (AP) is involved in the mineralization of phosphorus (P; Zhou et al., 2013). Though both microbes and plant roots may secrete extracellular enzymes, the activity of extracellular enzymes is often

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representative of microbial functions (Puissant et al., 2015; Souza et al., 2017). Higher soil temperature could either increase or decrease the soil extracellular enzyme activities. It can not only stimulate enzyme production, resulting in greater potential for soil extracellular enzyme activity (Henry, 2013), but also reduce the rate of enzyme-substrate binding, decelerating enzyme-mediated reactions. These contradictory effects may occur because not all enzymes respond consistently to increases in temperature. Higher soil temperature can increase the activities of NAG and AP by enhancing the soil microbial activity (Brzostek and Finzi, 2011; Zhou et al., 2013), whereas it can decrease the activities of BG, NAG, and LAP by reducing soil moisture through elevated evapotranspiration (Allison and Treseder, 2008; Zhou et al., 2013; Machmuller et al., 2016). Similarly, soil extracellular enzyme activities do not respond consistently to altered precipitation. Sardans and Peñuelas (2005) showed that drought significantly decreased the activity of BG by 47%, but did not induce significant shifts in AP activity. Conversely, Kreyling et al. (2008) found that elevated precipitation significantly increased NAG activity, while neither elevated precipitation nor drought induced significant changes in BG and AP activities. Zhou et al. (2013) also reported that 30% elevated precipitation significantly decreased BG activity, but increased NAG, LAP, and AP activities.

In many parts of the world, concurrent changes in temperature and precipitation patterns are occurring due to climate change, leading to interactive effects of temperature and precipitation on soil properties, microbial communities, and extracellular enzyme activities (Zhang et al., 2016a). However, it is challenging to predict the outcome of emerging temperature and precipitation regimes. For instance, soil warming of 3.0 °C increased the soil temperature by as much as 2.3 °C and also stimulated evapotranspiration, which made the soil drier despite a concurrent 30% increase of precipitation (Li et al., 2017a). Meanwhile, higher precipitation (30% more than the ambient conditions) also had a cooling effect on soil temperature, reducing it by 0.7 °C compared to soils with warming alone (Li et al., 2017a). Lower precipitation (50% less than the ambient conditions) is expected to limit water availability and reduce the diffusion of substrates, thereby constraining microbial biomass and enzyme (BG, NAG, and LAP) activities, resulting in similar microbial and enzymatic responses in soil warmed by 4 °C compared to soils with no water limitation (Steinweg et al., 2013). Since soil biological responses are dependent upon the interaction between temperature and precipitation, it is essential to evaluate warming effects on soil microbes and extracellular enzymes while considering a precipitation gradient that includes drier and wetter regimes (Brockett et al., 2012; Henry, 2013; Zhang et al., 2016a).

To investigate how warmer air temperature and precipitation manipulation affect the soil microbial communities and extracellular enzyme activities, we set out to sample a constructed open-field experimental site planted with *Pinus densiflora* seedlings, which was established two years prior to this study. Previous results from this experimental site demonstrated that warming increased soil respiration, but the magnitude of warming-induced respiration varied among precipitation (Li et al., 2017b). The specific goals of the present study were (1) to quantify the main and interactive effects of warming and precipitation regimes on soil microbial biomass, composition, and structure, and (2) to evaluate the main and interactive effects of warming and precipitation regimes on four extracellular enzymes, namely the hydrolytic enzymes BG, NAG, LAP, and AP involved in organic C, N and P cycling. The study was predicated upon four hypotheses: (1) warming will increase soil microbial biomass and extracellular enzyme activity, (2) elevated precipitation will increase soil microbial biomass and extracellular enzyme activity, whereas lower precipitation will reduce soil microbial biomass and extracellular enzyme activity, (3) due to the interaction of warming and precipitation, the greatest soil microbial biomass and extracellular enzyme activity will occur in the warmest, wettest soil conditions, and the lowest soil microbial biomass and extracellular enzyme activity will occur in the

coolest, dry soil conditions, and (4) the diversity and structure of different soil microbial communities (i.e., bacterial and fungal communities) will respond differently to warming and precipitation manipulation.

2. Materials and methods

2.1. Experimental site description and design

The experiment was conducted at a nursery located at Korea University, Seoul, South Korea (37°35'36" N, 127°1'31" E). The nursery was used to study the effect of warming on the representative tree species in South Korea from 2010 to 2013. The interactive effects of warming and precipitation manipulation were evaluated in the nursery from 2013 to 2015. At this site, the long-term (1981–2010) annual air temperature was 12.5 °C and annual natural precipitation was 1450.5 mm, which is cooler and wetter than the mean air temperature of 13.6 °C and annual precipitation of 792.1 mm recorded in Seoul in 2015 (Tables S1 and S2; Korea Meteorological Administration, 2017). Before the site for this study was established in April 2013, the soil was plowed to a depth of 50 cm and all vegetation was removed. The experiment consisted of 18 plots (1.5 m × 1.5 m with a 50 cm buffer between the plots) that were planted with 45 seedlings (at a spacing of 15 cm between the seedlings) of 2-year-old *P. densiflora* with a similar size (i.e., 22.1–24.0 cm height and 5.3–5.8 mm root collar diameter) in April 2013. *P. densiflora* is a common coniferous tree in temperate regions and a dominant, economically important species in mixed and natural coniferous forests of South Korea, covering approximately 23.1% (1,477,000 ha) of the total forest area and 55% of the coniferous forest area in South Korea (Noh et al., 2016; Lee et al., 2017). The soil is a loamy sand (80% sand, 14% clay, and 6% silt) with slightly acidic pH (6.5 ± 0.0 ; mean \pm standard error), low cation exchange capacity (CEC; 6.1 ± 0.1 cmol_c kg⁻¹) and total C and N concentrations of 1.9 ± 0.0 g kg⁻¹ and 0.1 ± 0.0 g kg⁻¹ with C:N ratio of 16.0 ± 0.2 .

The field plots were monitored from April 2013 to December 2015. The experimental design was a complete factorial with six treatments and three replicates (18 plots in total), consisting of two levels of air warming (control (C) and +3 °C based on air temperature (W)) in combination with three levels of precipitation manipulation (–30% (P-), control (P0), and +30% (P+)). Factorial treatments with ambient air temperature are referred to as C*P-, C*P0 and C*P+, and those with air warming were designated as W*P-, W*P0 and W*P+, which reflects the combined effects of warming and precipitation regimes. Air warming and precipitation manipulation treatments were selected based on the climate change scenario RCP 8.5 for South Korea, which simulates climate change for the next 50 years (Kim et al., 2014). The air warming treatment was achieved with an infrared lamp heater consuming 1000 W of electric power (FTE-1000; Mor Electric Heating Instrument Inc., Grand Rapids City, Michigan, USA), which was set at a height of 60 cm above the *P. densiflora* seedling canopy to increase air temperature by 3 °C. A controller consisting of a data logger and a relay automatically turned on the heater if the difference in air temperature between the unwarmed and warmed plots was lower than 3 °C. Nonetheless, the actual difference in air temperature (2.8 ± 0.1 °C; verified with an infrared temperature sensor, see subsection 2.3) was slightly lower than 3 °C due to time lag between data logging and heating as well as seasonally intensive rainfall events that cause cooling at the site (Yun et al., 2014).

Precipitation was manipulated with polycarbonate panels, an automatic pump, and a drip-irrigation system. The transparent polycarbonate panels were installed above the reduced precipitation plots and covered 30% of the plot area to block precipitation, reducing annual precipitation to the reduced precipitation plots by 30%. The blocked precipitation was immediately diverted to the elevated precipitation plots by an automatic pump and a drip-irrigation system, which added 30% more precipitation to the elevated precipitation

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