



Divergent responses of biological nitrogen fixation in soil, litter and moss to temperature and moisture in a karst forest, southwest China

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ABSTRACT

Free-living biological N₂ fixation (BNF) in soil, litter and moss is an important pathway for external nitrogen (N) inputs to unmanaged terrestrial ecosystems. However, how free-living BNF responses to temperature, moisture and their interaction have not been well understood, especially in the subtropical regions. Here we investigated the responses of BNF in soil, litter and moss to temperature (15, 25 and 35 °C) and moisture (low, intermediate and high levels) over a one-week period under laboratory conditions. The samples were collected in a subtropical karst forest, southwest China. We found that the responses of BNF in moss, litter and soil to temperature and moisture were divergent. Litter and soil BNF rates increased with temperature under the three moisture levels. However, moss BNF rates were decreased, not changed or increased by warming under low, intermediate and high moisture levels, respectively. At each temperature, the BNF rates increased with moisture for moss and litter. However, the patterns of moisture responses were different at the three temperatures for soil BNF, which was not changed and increased by moisture at 15 °C and 25 °C, respectively; and was greatest under intermediate moisture, but lowest under low moisture at 35 °C. The temperature sensitivity of BNF was generally highest for litter, intermediate for soil and lowest for moss. In contrast, the moisture sensitivity of BNF was generally highest for moss, intermediate for soil, and lowest for litter. Our findings suggest that different temperature or moisture sensitivities of BNF for the three substrates should be integrated into terrestrial ecosystem models in order to better predict N inputs via BNF under climate change.

1. Introduction

Nitrogen (N) is the major limiting element for net primary productivity (NPP) in terrestrial ecosystems (LeBauer and Treseder, 2008). The dynamics of N availability is usually expected to have substantial impacts on an ecosystem's structure, functions and processes (Xia and Wan, 2008; Liu and Greaver, 2009, 2010; Bobbink et al., 2010; Niu et al., 2016). In addition, N availability is crucial in determining long-term terrestrial carbon (C) sequestration under climate change (Hungate et al., 2003; Luo et al., 2004). Therefore, understanding the dynamics of ecosystem N inputs, which relate directly to N availability, is undoubtedly important for predicting climate change-C cycle feedbacks.

Biological N₂ fixation (BNF hereafter) is a major pathway of external N inputs to unmanaged terrestrial ecosystems (Fowler et al., 2013; Houlton and Morford, 2015). BNF may be performed by

symbiotic and free-living organisms (Reed et al., 2011). According to Reed et al. (2011), symbiotic BNF is defined as BNF occurring via relationships between plants and the N₂-fixing symbionts in plant root nodules either as *Rhizobia* or *Frankia*. Free-living BNF, includes BNF carried out by cyanobacteria in association with moss or by other free-living diazotrophs in soil and litter (Reed et al., 2011). The free-living BNF rates vary from 0.01 to 60 kg N ha⁻¹ yr⁻¹ depending on climate and ecosystem type, but are generally lower than symbiotic BNF rates (Cleveland et al., 1999; Reed et al., 2011). However, for those ecosystems lacking (or with a low abundance of) N₂-fixing plants, free-living BNF may be the dominant pathway of external N inputs.

Free-living BNF is affected by a few abiotic factors (Reed et al., 2011), including the climate related factors, e.g., temperature (Bjerke et al., 2003; Sorensen and Michelsen, 2011; Rousk et al., 2017), and precipitation (Gundale et al., 2012b; Whiteley and Gonzalez, 2016; Rousk et al., 2017). Global warming and subsequent changes in

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precipitation patterns have been well documented and will continue in the near future with some regions becoming wetter while others are predicted to become dryer (IPCC, 2014). How BNF responds to climate change could directly affect plant production and ecosystem C sequestration (Hungate et al., 2003; Smith et al., 2014). However, the current treatment of BNF in terrestrial models is entirely empirical, and mostly based on the empirical relationships between BNF rates and NPP, evapotranspiration (ET) or other variables (William et al., 2015). There is large uncertainty in terms of how BNF will respond to climate change, which unavoidably increases the uncertainty in predicting climate change-C cycle feedbacks (Hungate et al., 2003; Thornton et al., 2007).

So far, most of the studies investigating free-living BNF responses to temperature and/or moisture have focused on BNF of bryophyte-cyanobacteria associations, especially moss BNF (Bjerke et al., 2003; Gundale et al., 2012b; Lindo et al., 2013; Rousk et al., 2017). According to these studies, BNF of bryophyte-cyanobacteria associations may be enhanced (Gundale et al., 2012a; Lett and Michelsen, 2014; Rousk et al., 2017), remain unchanged (Bjerke et al., 2003; Deslippe et al., 2005; Sorensen and Michelsen, 2011; Whiteley and Gonzalez, 2016) or decreased (Sorensen et al., 2012) by warming. In contrast, moisture has often been found to have a strong impact on BNF with BNF rates increasing with moisture (Gundale et al., 2009; Whiteley and Gonzalez, 2016; Rousk et al., 2017). To our knowledge, only one study has investigated the response of soil BNF to warming under controlled conditions, and found that soil BNF increased exponentially with increasing temperature (Diáková et al., 2016). However, the available studies, which investigated the responses of free-living BNF to climate change, have generally been conducted in boreal or arctic regions. In these regions, the mean annual air temperature is much lower than 10 °C. However, some of the studies show that the optimum temperature for free-living BNF is between 20 °C and 30 °C (Gundale et al., 2012a; Rousk et al., 2017), but others have found that the optimum temperature differs according to cyanobacteria-moss associations. For example, Gentili et al. (2005) found that *Nostoc* sp. had a maximum BNF rate at 13 °C while *Calothrix* sp. had maximum at 30 °C. It remains unclear whether free-living BNF in tropical or subtropical regions responds to climatic changes in a similar manner. Furthermore, since no study has simultaneously explored the responses of BNF in soil, litter and moss to climate change, it remains unclear whether BNF in these ecosystem compartments respond similarly or not.

In order to address the above uncertainties, the responses of soil, litter and moss BNF to temperature and moisture were investigated under laboratory conditions. Samples were collected from a secondary forest with a very limited abundance of N₂-fixing plants in a subtropical karst region, southwest China. This region has experienced an increase in temperature over the past decades and is predicted to become warmer in the 21st century (IPCC, 2014). Data from 70 meteorological stations show that different areas have higher risk of extreme drought or wet events in the southwest China (Liu et al., 2014). Nevertheless, how climate change influences BNF has not been investigated in this region. Therefore, the main objectives of the present study were to address: (i) How does BNF in moss, litter and soil respond to variation in temperature and moisture? (ii) Are there interaction effects of temperature and moisture on BNF? (iii) Are there differences in the temperature sensitivity or moisture sensitivity of BNF?

2. Materials and methods

2.1. Sampling site

Samples were collected from a secondary forest at Mulun National Nature Reserve (107°53′–108°05′ E, 25°06′–25°12′ N) in Guangxi Zhuang Autonomous Region, southwest China. The region is located in the subtropical humid forest life zone and has a monsoon climate. Mean annual air temperature is 17.8–21.1 °C, with the lowest monthly mean in January (7.8–11.2 °C) and the highest in July (25.8–29.0 °C). Mean annual precipitation ranges from 1346 to 1498 mm with a distinct seasonal pattern. The period from April to August is the wet season (accounting for about 71% of the annual precipitation) while September to March is the dry season (accounting for about 29% of the annual precipitation). Total atmospheric N deposition is about 37 kg N ha⁻¹ yr⁻¹ (Zhu et al., 2015). The studied area is characterized by a typical karst landscape with gentle valleys flanked by steep hills. The bedrock is mostly limestone nested with dolomite. The soil is classified as a calcareous lithosol (limestone soil) according to the FAO/UNESCO classification system (Li et al., 2017). Soil depth varies from 0 to 80 cm in the valley and ranges from 0 to 30 cm on the slopes. The selected forest site was about 35 years old at an elevation of 420 m. The forest had naturally regenerated from an abandoned maize-soybean rotation field. The dominant tree species included *Cladrastis platycarpa* (Maxim.) Makino, *Liquidambar formosana* Hance, *Cryptocarya chinensis* (Hance) Hemsl., *Eurycorymbus cavaleriei* (Levl.) Rehd. et Hand. and *Itoa orientalis* Hemsl. Moss species occur on rocks, dead trunks, downed wood and the forest floor (Fig. S1). The soil texture was silt loam.

2.2. Sample collection and experimental design

Samples of soil, litter and moss (hereafter referred to as substrate) were collected from six randomly selected plots (20 m × 20 m each) within an area of 100 m × 100 m in July 2016. Ten locations of 50 cm × 50 cm were randomly selected in each plot. At each location, all the bulk leaf litter was collected. Soil samples from the surface 2 cm were collected with a soil corer (5 cm in diameter) upon removal of the litter layer. The green branches of the dominant moss (*Hypnum plumaeforme*) were collected from the rock surface with a knife. Upon transporting to the laboratory, the soil (or litter/moss) within a plot was mixed thoroughly to form a composite sample, and left in the laboratory for one or two days to lower the moisture to the low level of respective substrate (Table 1) if necessary. Some physicochemical properties of soil, leaf litter and moss are presented in Table 2.

The experiment employed a full factorial design, including three air temperature levels (15, 25 and 35 °C) and three levels of moisture for each category of substrates (Table 1). The three air temperature levels were within the range of air temperature reported in this region with mean minimum daily air temperature of 8 °C (January) – 25 °C (July) and mean maximum daily air temperature of 15 °C (January) – 33 °C (July) across the year. The low, mid and high levels of moisture for soil and litter were adjusted to be close to the lowest (28.4% for soil, and 36.4% for litter; moisture is based on dry weight basis hereafter), average (35.1% for soil, and 59.7% for litter) and maximum (44.2% for soil, and 80.2% for litter) gravimetric moisture values recorded in four field campaigns in January, April, July and October. For moss, the low

Table 1
Temperature (°C) and moisture (%) treatments applied to moss, litter and soil, respectively, in the incubation experiment.

	Moss		Litter		Soil	
	Temperature	Moisture	Temperature	Moisture	Temperature	Moisture
Low level	15	74.3	15	19.7	15	28.8
Mid-level	25	84.5	25	53.9	25	37.2
High level	35	93.6	35	73.6	35	42.8

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