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Responses of understory plant physiological traits to a decade of nitrogen addition in a tropical reforested ecosystem

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ABSTRACT

Reforested ecosystems are becoming a dominant forest cover type in the tropics where anthropogenic nitrogen (N) deposition has been increasing greatly. Although understory plants play an important role in ecosystem structure and functioning, it remains unclear how long-term N deposition affects eco-physiological traits of understory species. To address this question, we expanded a ten-year simulated N deposition experiment in a tropical reforested ecosystem, with variable N addition levels as Control (no addition, N0), 50 kg N ha^{-1} yr^{-1} (N50), and 100 kg N ha^{-1} yr^{-1} (N100). Leaf physiological traits associated with photosynthetic capacity, foliar elements and N storage of seven dominant understory species were measured. Results showed that both medium-light species and shade-tolerant species had little physiological responses to N addition. However, one high-light species (*Alchornea trewioides*) responded significantly to N addition, showing decreases foliar N and Pmax. We further found that Pmax of *Alchornea trewioides* was negatively correlated with the canopy closure which increased under long-term N addition. Our findings suggest that understory plant growth may be more limited by light rather than N availability, particularly under chronic high N deposition; and N deposition can suppress understory high-light species through accelerating canopy closure in some tropical reforested ecosystems.

1. Introduction

Plant physiological features could reflect fundamental processes and ecological strategies in their niches. Foliar physiological traits, such as photosynthetic capacity and foliar nutrients, are commonly very sensitive to variation of environmental factors (Bazzaz, 1979; Reich et al., 1995; Bauer et al., 2004; Poorter and Bongers, 2006; Pérez-Harguindeguy et al., 2013). Therefore, measurements of physiological traits can be employed as a useful tool to explore ecological questions.

Nitrogen (N) is regarded as one of the most important nutrients to limit net primary production in terrestrial ecosystems (Elser et al., 2007). There generally exists a positive correlation between foliar N concentration and photosynthetic capacity, because photosynthetic enzymes account for a large proportion of the foliar N content (Chapin III et al., 2011). Therefore, increased N availability is suggested to increase foliar N and simulate photosynthetic capacity. With the globalization of elevated N deposition, terrestrial N availability has been increasing worldwide (Galloway et al., 2004). Elevated N deposition is expected to affect natural and semi-natural ecosystems at different scales ranging from individual physiology to community composition (Aber and Magill, 2004; Bobbink et al., 2010; Stevens et al., 2011; Liu et al., 2011). It has been addressed well that excess N deposition can lead to nutrient imbalance, decrease in plant growth and decline in biodiversity (Aber et al., 1989; Matson et al., 2002; Magill et al., 2004; Hogberg et al., 2006; Elvir et al., 2006; Bobbink et al., 2010). Noticeably, foliar physiological traits are very sensitive to high N inputs (Bauer et al., 2004; Elvir et al., 2006).

Several studies showed that N inputs below a critical threshold increased foliar N and photosynthetic capacity of tree species due to satisfying plant requirement for N (Bauer et al., 2004; Mo et al., 2008; Fleischer et al., 2013). However, increased foliar N is not always parallel to increased photosynthetic capacity, and species differ in their responses to N additions even growing in the same forests. At the Bear Brook Watershed, for example, Elvir et al. (2006) reported higher N concentrations in all three tested species (*Acer saccharum*, *Fagus grandifolia*, *Pinus resinosa*) after a decade of N inputs, but only *Acer saccharum* showed significantly higher photosynthetic rates. At Harvard Forest, Bauer et al. (2004) found that increased foliar N concentration in red pine (*Pinus resinosa*) under

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the high N treatment did not optimize its photosynthetic capacity. Instead, increased foliar N was mainly reserved as soluble protein, amino acids and chlorophyll. In four mature northern hardwood forests, Talhelm et al. (2011) concluded that chronic N additions (14 years) significantly increased foliar N of the dominant species (*Acer saccharum*), but did not stimulated their photosynthesis. Similarly, Mo et al. (2008) reported that net photosynthetic rate of two dominant tree seedlings (*Schima superba* and *Cryptocarya concinna*) to simulated N deposition varied depending on rate of N addition and species-N-requirement. Down regulation or non-response in net photosynthesis to N addition is attributed to decoupling in allocation of photosynthetically used, or decreased foliar calcium (Ca) and/or magnesium (Mg) causing by N-induced soil acidification processes (Bauer et al., 2004; Elvir et al., 2006).

Until now, however, most studies on responses of physiological traits to N addition were based on measurements in a few dominant tree species in temperate forests or in young seedlings grown in artificial environments, where light was relatively abundant. There is still a lack of information on how long-term N deposition affects understory species in tropical reforested ecosystems. Understory layer, which consists of a continuum in species of light requirements (Poorter and Bongers, 2006), contributes a large proportion of biodiversity in forest ecosystems (Gilliam, 2007). Meanwhile, understory species are considered to be sensitive to changes of environmental factors (Scheller and Mladenoff, 2002), and play important roles in succession of reforested ecosystems (Royo and Carson, 2006). Therefore, the potentially divergent responses of understory species to elevated N deposition would have profound implications for reforested ecosystems.

In the tropics, various stages of reforestation have become an important forest type due to anthropogenic land use (Brown and Lugo, 1990; Achard et al., 2002). For example, the total forest area is 9.06 million ha in Guangdong Province in southern China, while the area of planted forests is 5.58 million ha, accounting for 61.6% (Chinese Forestry Database; 2017/06/01, http://data.forestry.gov.cn/lysjk/indexJump.do?url=view/moudle/dataQuery/dataQuery). Masson pine (*Pinus massoniana*) plantations are widely distributed in this region, accounting for about 45% of total plantation area in Guangdong Province (Kuang et al., 2008). Reforested ecosystems play a critical role in restoration and buffering the anthropogenic direct disturbance to adjacent primary forests (Brown and Lugo, 1990). At the same time, anthropogenic atmospheric N deposition in tropical and subtropical regions will continue to increase in the following decades due to the increasing population, intensive agricultural and industrial activities (Galloway et al., 2004; Hietz et al., 2011). In Asia, from 1961 to 2000, the anthropogenic reactive N production increased from 14.4 Tg N y^{-1} to 67.7 Tg N y^{-1}, and was predicted to be 105.3 Tg by the year of 2030 (Zheng et al., 2002). In southern China, high N deposition in precipitation has been reported to range from 30 to 73 kg N ha^{-1} yr^{-1} (Lü and Tian, 2007; Xie et al., 2010; Lu et al., 2013; Zhao et al., 2017), which means large areas of tropical forests are projected to experience high rates of N deposition. Furthermore, many tropical ecosystems are rich in N but poor in other nutrients (e.g., P, Ca, Mg), and are suggested to be acid sensitive (Matson et al., 1999; Lu et al., 2015). Therefore, it is necessary to deepen understanding on how long-term N deposition affects plants in tropics.

This study is aimed to explore how long-term N deposition affects understory plant species in tropical reforested ecosystems. In 2002, we established a long-term N research site in a pine forest at Dinghushan reserve of southern China. Seven understory species with different light adaptive characteristics were selected (Table. 1). Specially, we measured leaf physiological traits including photosynthetic capacity, foliar elements and N storage. In a previous vegetation survey, decreasing abundance of *Alchornea trewioides* (heliophyte or high-light species) was detected in N-treatment plots (Lu et al., 2011; data unpublished). Here we experimentally test the following two hypotheses: (1) understory plant species are less limited by N availability, considering high ambient N deposition and relative shortage of other resources (such as light availability); (2) long-term N addition would negatively affect high-light species through increases in canopy closure.

2. Methods

2.1. Study site

This study was conducted in Dinghushan biosphere reserve (DHSBR), an UNESCO/MAB site located in center of the Guangdong Province in southern China (112°10′E, 23°10′N). Monsoon climate of this site averages 1927 mm precipitation per years with approximately 75% occurring between March and August, and 6% between December and February (Huang and Fan, 1983). Mean annual temperature is 21.0 °C, with an average coldest (January) and warmest (July) temperature of 12.6 °C and 28.0 °C, respectively. The soils are oxisol with variable depths which usually less than 40 cm (Mo et al., 2003). Monitoring records showed that the study areas of DHSBR experienced high N deposition since 1990s (Huang et al., 1994; Zhou and Yan, 2001). In 2009–2010, the reactive N compounds in the rainfall are 34.4 kg N ha^{-1} yr^{-1} with 18.2 kg ha^{-1} dissolved inorganic N (7.7 kg ha^{-1} NO_3^--N and 10.5 kg ha^{-1} NH_4^+-N, respectively) and 16.2 kg ha^{-1} dissolved organic N (Lu et al., 2013).

In the reserve, long-term N addition experiment site was established in 2002 in a reforested pine forest, which is a typical forest type in southern China. The pine forest located on a slope ranged from 10° to 20° at 100–150 m above sea level, occupies approximately 20% of the reserve (Mo et al., 2003). This forest was originated from clear cutting in 1930s and subsequent planting of pine trees (*Pinus massoniana*), so extensive erosion and degradation occurred since 1930s. This pine forest was continuously under disturbance by human activities such as harvesting of understory

Table 1
Ecological characteristic of all measured species in a reforested tropical ecosystem at Dinghushan natural reserve of southern China.

Species	High (m)	Growth form	Family	Light demand	Abundance	Code
Alchornea trewioides	~3	Dicotyledon shrub	Euphorbiaceae	***	2	*AT*
Rhodomyrtus tomentosa	~2.5	Dicotyledon shrub	Myrtaceae	***	5	*RT*
Dicranopteris dichotoma	~1	Fern forb	Gleicheniaceae	**	1	*DD*
Evodia lepta	~5	Dicotyledon shrub	Rutaceae	**	3	*EL*
Gahnia tristis	~1.5	Grass	Cyperaceae	**	4	*GT*
Lophatherum gracile	~0.5	Grass	Gramineae	**	6	*LG*
Schizoloma heteropyllum	~0.5	Fern forb	Lindsaeaceae	*	7	*SH*

*** High-light species (heliphytes), which are fast-growing in the open;
** Medium-light species;
* Shade-tolerant species (sciophytes), which are extremely shade tolerant. The classification of species in light demanding is based on studies from Zhang (1995), Deng et al. (2010), Yan et al. (2011), and also confirmed by substantial observation in study areas. Code for each species consists with the first letter of genus name and specific name.