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Long-term N and P additions alter the scaling of plant nitrogen to phosphorus in a Tibetan alpine meadow

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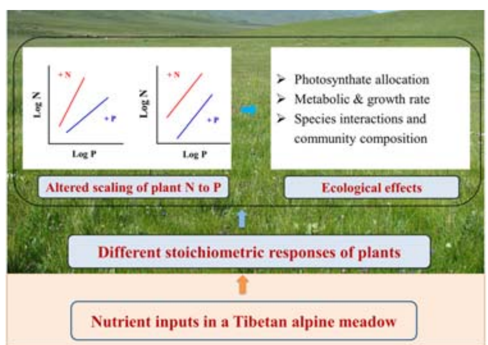
HIGHLIGHTS

- N&P inputs can significantly affect the plant N and P concentrations, N:P ratios and the scaling of plant N to P.
- The scaling of N to P under N additions was similar to the pattern previously reported with a uniform 2/3 slope.
- The scaling of N to P under P additions was significantly different with a smaller slope.
- Our findings suggest that soil N and P enrichment may differentially affect the stoichiometry of plants.

GRAPHICAL ABSTRACT



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ABSTRACT

Nitrogen and phosphorus are two important nutrient elements for plants. The current paradigm suggests that the scaling of plant tissue N to P is conserved across environments and plant taxa because these two elements are coupled and coordinately change with each other following a constant allometric trajectory. However, this assumption has not been vigorously examined, particularly in changing N and P environments. We propose that changes in relative availability of N and P in soil alter the N to P relationship in plants. Taking advantage of a 4-yr N and P addition experiment in a Tibetan alpine meadow, we examined changes in plant N and P concentrations of 14 common species. Our results showed that while the scaling of N to P under N additions was similar to the previously reported pattern with a uniform 2/3 slope of the regression between log N and log P, it was significantly different under P additions with a smaller slope. Also, graminoids had different responses from forbs. These results indicate that the relative availability of soil N and P is an important determinant regulating the N and P concentrations in plants. These findings suggest that alterations in the N to P relationships may not only alter plant photosynthate allocation to vegetative or reproductive organs, but also regulate the metabolic and growth rate of plant and promote shifts in plant community composition in a changing nutrient loading environment.

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1. Introduction

Terrestrial ecosystems are undergoing unprecedented increases in nutrient element inputs, such as nitrogen (N) and phosphorus (P) inputs through atmospheric deposition and fertilization (Fujimaki et al., 2009; Tipping et al., 2014; Vitousek et al., 1997; Peñuelas et al., 2012). Unbalanced inputs of nutrient elements can critically affect ecological stoichiometry - the elemental ratios of organisms, and further modify ecosystem functioning (Sardans et al., 2012; Finzi et al., 2011; Peñuelas et al., 2013). For example, N enrichment alters plant nutrient stoichiometry (Peñuelas et al., 2012; Wang et al., 2010) and accelerates P cycling (Marklein and Houlton, 2012). These effects may cascade to impact plant interactions (Brooker, 2006; Clark and Tilman, 2008) and plant productivity (Zaehle et al., 2010), and modify organic matter decomposition (Hobbie and Vitousek, 2000; Wild et al., 2014) and the terrestrial C and N cycling (Lu et al., 2011).

In terrestrial ecosystems, N and P are two major elements that often limit plant metabolic reactions and growth (Marschner, 2011). The plant N:P stoichiometry reflects biochemical constraints on relative investments in proteins (particular N rich) and the ribosomal RNA (sink for P) (Matzek and Vitousek, 2009). Tissue or organ N levels provide a reasonable indicator of the protein that must be synthesized to maintain balanced growth, whereas P levels offer a natural gauge of "machinery" driving growth (Niklas and Cobb, 2005). Plants with high growth rates will require an increased allocation of P-rich rRNA to support the energy demands of macromolecular (protein, rRNA) synthesis (Niklas et al., 2005; Elser et al., 2000; Elser et al., 2003). Moreover, the relative concentration of plant N to P (N:P ratio) is often used as an indicator for the changes of nutrient availabilities and the adaptation of plant to habitats (Wright and Westoby, 2003; Imran and Gurmani, 2011). For example, it is generally believed that a N:P ratio lower than 14 (on a mass basis) indicates that plant growth is limited by available N, while a ratio >16 indicates that plant growth is limited by available P (Güsewell, 2004; Koerselman and Meuleman, 1996; Cernusak et al., 2010; Aerts and Chapin, 1999).

How N and P were coupled and change with each other are particularly important in regulating nutrient limitation and the strategies of plant nutrient acquisition in changing environments (Niklas and Cobb, 2005; Sterner and Elser, 2002; Elser et al., 2007; Kerkhoff et al., 2005). Because P-rich RNA is preferentially required to support the elevated protein synthesis for rapid metabolism and growth, plants with greater metabolic and growth rates are disproportionately more P-rich than N-rich. Thus, an allometric scaling of N to P is expected according to Growth rate hypothesis (GRH) (Elser et al., 2000). Therefore, scaling relationships are widely used to explain the observed patterns of various plant traits, including metabolic and physical traits (Brown et al., 2004; Price et al., 2012; Wright et al., 2004; Xiang et al., 2013; Yang et al., 2013; Reich et al., 2006).

The scaling of N to P was reported to be conserved following a constant allometric trajectory across environments and plant taxa. Typically, plant N concentration scales as the3/4 or 2/3 power of plant P concentration within and across species (Wright et al., 2004; Ågren, 2008; Elser et al., 2010; Reich et al., 2010). The exponent value less than one in the power function indicates that plant N and plant N:P will decline relative to P when P concentration increases, because P increases faster than linearly with N, which is potentially important for understanding the effect of plant N:P on plant growth rate.

While stoichiometric relationships between N and P have been broadly reported by previous studies, the strategic differences of the scaling in plants in response to nutrient inputs from deposition and fertilization remain unclear. The overarching goal of this project is to evaluate the effects of altered nutrient inputs on the scaling of plant N to P. We hypothesize that altered N and P inputs may result in a change in the scaling of plant N to P between species. Specifically, P limitation would exacerbate with increasing N availability and result in an accelerated increase of N concentration, while N limitation would intensify with increasing P availability and result in a diminished increase of P concentration (Fig. 1a). Alternatively, the change rate of plant N and P with increasing N supply or inputs may remain constant if concentrations of N and P in plant tissues are linked each other, resulting in a greater coefficient of the scaling relationship (expressed as a power function) between N and P (Fig. 1b).

We conducted a long-term N and P addition experiment in an alpine meadow on the eastern Tibetan Plateau. The Tibetan Plateau is the region bordering China, with average altitude over 4000 m above sea level (Qiu, 2008; Li and Zhou, 1998; Zhang et al., 2002). The growth of alpine plants and community productivity are severely limited by available nutrients due to low microbial activity, litter decomposition and N mineralization at low temperature (Hobbie et al., 2000; Körner, 2003). Ecosystem functioning have been dramatically affected by nutrient inputs resulting from grazing and altered pasture management (Liu et al., 2013). However, the stoichiometric responses of alpine plants to the increased availability of N and P remain unclear. Our approach was to examine 14 common plant species in alpine meadow grassland in the eastern Tibetan Plateau, we attempt to address the following questions:

1) How do the plant N and P concentration and N:P ratios respond to N and P addition?

2) How does N or P addition affect the relationship between tissue N and P concentrations?

3) How does this scaling relationship vary among plant functional groups?

2. Materials and methods

2.1. Study site

The field experiment was conducted in 2014 at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University, located in an alpine meadow on the eastern Tibetan Plateau in Maqu (35°580′N, 101°530′E, altitude 3500 m a.s.l), China. The mean temperature ranges from ca. −10 °C in January to 11.7 °C in July, with ~620 mm of precipitation, mainly distributed during the short, cool summer. The vegetation of the meadow is mainly dominated by *Kobresia graminifolia* Clarke. (Cyperaceae), and *Elymus nutans* Griseb (Poaceae)and *Anemone rivularis Buch.-Ham* (Ranunculaceae). There are on average 20–35 vascular plant species per 0.25 m^2. The soil type in the study area is Mattic Cryic Cambisols (Gong et al., 2007).

2.2. Experimental design

The experimental study area for the experiment was fenced in 2011 to prevent grazing by large animals such as yak and sheep. The field experiment was a complete randomized block design with 2 blocks (each for N or P treatment). Twelve (12) plots (20 m × 10 m each) were arranged in a regular three by four matrix in each block. We added 0, 0.3571 and 1.0714 mol N m^{-2} yr^{-1} (NH_4NO_3) referring to Control, N5, N15 treatments, and 0.0645, 0.2580 mol P m^{-2} yr^{-1} (KH_2PO_4) referring to P2 and P8 treatments, respectively. Each treatment has four replicates. Fertilizers in solid were applied to the plot surfaces when raining in May once each year since 2011.

2.3. Plant and soil sampling and analyses

In early September 2014 when community biomass had reached its peak level, all aboveground parts of plants in 0.5 × 0.5 m^2 quadrats were clipped (Luo et al., 2006). Fourteen (14) species that appeared in all plots were selected for measuring above-ground plant nutrients. Here, we analyzed data in three different ecological scales including species, functional group and community levels. We did analyses at species level because species is the principal natural taxonomic unit and people are usually more interested in how specific species or taxon responds to