



Seasonal variations in the soil amino acid pool and flux following the conversion of a natural forest to a pine plantation on the eastern Tibetan Plateau, China



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ABSTRACT

Although the importance of amino acids to plant nitrogen (N) nutrition in most terrestrial ecosystems is being increasingly recognized, the availability and seasonal variations of soil amino acids in subalpine coniferous forests are poorly understood. Few studies have investigated the differences in the soil amino acid pool and the cycling between forest types caused by land-use changes. In this study, we quantified the concentrations and fluxes of soil amino acids in a dragon spruce plantation and an adjacent natural forest (NF) on the eastern Tibetan Plateau, China. Soil samples from organic and mineral soil horizons were collected in May, July, September, and December of 2015 and March of 2016. The pools and fluxes of soil amino acids in the plantation converted from NF decreased significantly during the growing season and increased during the non-growing season. Meanwhile, greater pools and fluxes of soil amino acids were observed in the organic horizon than in the mineral soil horizon in both forest types. Our results indicate that distinct nutrient economies were likely formed in the plantation compared with the NF because the quality of the input litter decreased in the plantation. In addition, the importance of soil amino acids in the subalpine coniferous forest ecosystem was evaluated based on published literature. The ratios of amino acids to dissolved inorganic N (DIN) in the soils from the two studied forests were generally much lower than the range of ratios reported for other ecosystems. However, the relative high amino acid: DIN ratio in the plantations during the non-growing season suggests that the plants in the plantation may have the potential to modify their strategies for acquiring N due to the changed relative dominance between the DIN and amino acids in the soils.

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1. Introduction

Nitrogen (N) is an essential element for plant growth and has an important impact on net primary productivity in terrestrial ecosystems (Reich et al., 1997; Elser et al., 2007). Any change in the soil N availability can markedly influence plant productivity and consequently affect ecosystem functions (Esser et al., 2011), especially in N-limited regions. Studies of soil N pools and cycling have

largely focused on inorganic N forms (i.e., NH_4^+ and NO_3^-) (Burton et al., 2007a; Fagotti et al., 2012; Li et al., 2014), partly due to the belief that trees can only take up inorganic N. However, recent studies have indicated that some plant species (with or without associated mycorrhiza) that occur in a wide range of ecosystems have the physiological capacity to directly compete with soil microbes for organic N by assimilating amino acids (Nasholm et al., 2009; Warren, 2012; Hill et al., 2013). Previous studies have also shown that amino acids generally comprise approximately 20–60% of the total soil N pool, both as free and bound amino acids (Amelung et al., 2006; Bol et al., 2008), and represent an important potential N source and sink in terrestrial ecosystems. These observations have led to the hypothesis that amino acids and

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inorganic N may play equally critical roles in soil N cycling (Jones et al., 2004; Weigelt et al., 2005). The phenomenon that plants can acquire N from multiple sources has also caused the re-evaluation of the N cycling model of terrestrial ecosystems (Schimel and Bennett, 2004; Jones et al., 2005a).

Soil N pools and cycles are microbially and abiotically mediated, which means they are affected by various factors, including vegetation coverage, soil microbial community composition, the soil microclimate, and soil conditions (Templer et al., 2003; Cheng et al., 2011; Butterbach-Bahl et al., 2013; Li et al., 2014). The soil amino acid pool has been demonstrated to be significantly influenced by the temporal variations involved with root exudation and turnover, the activity of extracellular enzymes responsible for amino acid production, and litter inputs (Abuarghub and Read, 1988; Lipson and Nasholm, 2001; Schimel and Bennett, 2004; Jones et al., 2005b). Previous studies have also indicated that the amino acid pool and the functions of soil enzymes in amino acid production are closely related to soil temperature (Warren and Taranto, 2010; Brzostek et al., 2012). Thus, seasonal shifts accompanied by soil temperature changes may largely affect the size of the soil amino acid pool by influencing the microbial and enzymatic activities. However, most previous studies of soil amino acids that have been conducted are limited to the growing season, and few studies have attempted to resolve the seasonal dynamics of the soil amino acid pool, especially during the non-growing season (Burton et al., 2007a; Werdin-Pfisterer et al., 2009; Wang et al., 2013; Xue et al., 2013). This may cause partial quantification of the soil amino acid pools, because even in the same ecosystem completely different results could be observed regarding the relative pool sizes of the inorganic N and amino acids (Kielland, 1995; Nordin et al., 2004). Therefore, a thorough evaluation of the soil amino acid pool and its proportions relative to inorganic N during the growing season and non-growing season would help create a better understanding of the roles of amino acids in the soil N cycle and forest nutrient supply.

Subalpine coniferous forest ecosystems play a critical role in the terrestrial ecosystems in China (Zhang et al., 2011). Meanwhile, the subalpine zone of southwestern China is considered an important ecological zone of defence for the Upper Changjiang River Valley. During the last century, natural coniferous forests in southwestern China were deforested to meet the increasing demands of the timber market for fuel materials and other forest products. After deforestation, a monoculture of dragon spruce (*Picea asperata* Mast.) was immediately planted on the cut area. Currently, over one million hectares of dragon spruce plantation exists in Western Sichuan, accounting for approximately 50% of the forest area in this region (Xu et al., 2010, 2012b). The long-term sustainability and productivity of forest plantations depends on the soil nutrient (mainly N) supply (Burton et al., 2007b). N limitations were previously reported to occur in the plantations in this region because the pools and turnover rates of soil available inorganic N significantly decline following the conversion of natural forests (NFs) to plantations (Xu et al., 2010, 2014). However, little research has been conducted on the impacts of this type of land-use change on the cycling of N in another important N pool, soil amino acids. Therefore, as a special forest type on the eastern Tibetan Plateau, it is important to assess the pools and cycling of soil amino acids in plantations relative to their adjacent NFs to understand the nutrient acquisition strategies of the plantation plants when soil inorganic N is limiting.

In this study, we quantified the soil amino acid pools and fluxes along with their importance relative to the soil inorganic N pools in plantation forests and NFs during the growing and non-growing seasons. Our aim was to determine whether plantations derived from land-use change from NFs have the potential to modify their

strategies for acquiring N to compensate for severely limited N availability. In addition, to evaluate whether soil amino acids are a N source for plants in this study area, the pool of amino acid N and the ratio of the amino acid pool to the inorganic N pool were compared with those measured in other ecosystems. We hypothesized that (1) compared with NFs, the plantation forest would have a larger soil amino acid pools and a greater turnover rates in response to the lower inorganic N availability; (2) the amino acid N would dominate the soil N pools available for plants uptake during the non-growing season because N mineralization is constrained in cold climates; and (3) amino acid N could be an important potential N source in subalpine coniferous forest ecosystems.

2. Materials and methods

2.1. Study sites

This research was conducted on two sites that were within approximately 300 m distance of each other. Both experimental sites are located in the Miyaluo Experimental Forest in Lixian County on the eastern Tibetan Plateau in Sichuan, China (31° 35'N, 102° 35'E, and 3150 m a.s.l.). One site consists of a spruce-fir-dominated NF (c. 200 years old) and the other site is a dragon spruce plantation (c. 70 years old). The spruce plantation originated from NF that was clear-cut in the 1950s, and since then, there has not been any management practice, such as forest tending and thinning, performed in this region. The understory of the NF is dominated by *Acer mono*, *Lonicera* spp., and *Betula albo-sinensis*, occurrence of the herb *Anemone rivularis* and the sedge *Carex capilliformis*. In the plantation, less vegetation is present, with *Festuca ovina*, *Deyeuxia arundinacea*, and *Carex capilliformis* mainly growing under the plantation canopy. The two study sites provide a natural platform for assessing the differences of the soil N pool and N cycling between the forest types caused by land-use change. The climate at the study site is hilly monsoon, with a mean annual precipitation of 800 mm and a mean annual temperature of 6.8 °C (the mean temperatures in January and July are −8 °C and 12.6 °C, respectively). The growing season lasts approximately six months, extending from late-April to late-October. Snow cover is typical from late-November to mid-February. The soils at both sites are typical brown forest soils and are classified as a Cambic Umbrisols according to the IUSS Working Group (2007). The basic soil properties at both sites were determined in July 2015 and are shown in Table 1.

2.2. Sample collection

At each site, four 20 m × 20 m plots separated by more than 50 m were delineated. The plots were sampled during the growing season (i.e., 10 May, 19 July, and 18 September of 2015), and the non-growing season (25 December in 2015 and 1 March in 2016). On each sample date, five sampling points were randomly chosen in each plot. The sampling points were >5 m apart, and the organic horizon was sampled at each site by obtaining a 10 × 20 cm monolith. The mineral soil was sampled directly beneath the organic horizon to a depth of 15 cm by using a 5-cm diameter soil sampler. The samples from the five points chosen in each plot were mixed thoroughly, and then the mixed samples were immediately brought to the laboratory (with ice bags). Each composite sample was passed through a 2-mm sieve and then visible living plant materials and rocks were manually removed from the samples. Subsamples of each sieved soil sample were immediately frozen at −80 °C for later extracellular enzyme activity assays. All extractions (except net fluxes) were completed within 36 h of sample collection. Proteolytic rates were analysed within 48 h of sample

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