



Vegetation affects pool size and composition of amino acids in Tibetan alpine meadow soils



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ARTICLE INFO

Handling Editor: Jan Willem Van Groenigen

Keywords:

Amino acid
Temporal variation
Vegetation
Plant-soil feedback
Mycorrhiza
Alpine meadow

ABSTRACT

Soil amino acids are of great importance for nitrogen cycling and plant nutrition, especially in the nitrogen-limited ecosystems. However, the factors that influence amino acid pools in alpine meadow soils remain unclear. The aims of this study were to answer the following questions: (1) Do soil amino acid pools under different vegetation cover show appreciable differences in their concentration and composition during the growing season? (2) Is the pool size of soil amino acids in the alpine meadow smaller or larger than those in other ecosystems? Soils were sampled from three sites dominated by three typical types of plants (*Kobresia graminifolia*, *Polygonum viviparum* and *Elymus nutans*) in a Tibetan alpine meadow, respectively, during the growing season. Soils were extracted with water and 2 M KCl solution, respectively, and amino acids were quantitatively determined by high performance liquid chromatography. The results show that the pool size of soil exchangeable amino acids extracted by 2 M KCl in this alpine meadow is comparable to those in other N-limited ecosystems. The pool size of soil amino acids across the three sites displayed temporal dynamics during the growing season, with the pool size increased from May to July and decreased in August. The *P. viviparum* soil had the largest amino acid pool among the three sites in May, whereas the largest pool in July and August was found in the *K. graminifolia* soil. The composition of the soil amino acid pools across the sites changed over the season, with acidic amino acids being abundant (63.6–84.3%) in spring, and neutral amino acids dominating (53.7–66.0%) in summer. The three sites shared five dominant amino acids (lysine, glutamic acid, leucine, alanine, and serine) through June to August; however, the other dominant amino acids (glycine, valine and threonine) varied among the sites and the months. These results suggest that the concentration and composition of amino acid pools in the Tibetan alpine meadow soils could be significantly influenced by the vegetation cover. Additionally, soil sampling time and extraction methods could also exert pronounced effect on the results. The information obtained in this study may help in understanding the influence of plant-soil feedback on soil amino acid pools, and the mechanisms of organic nitrogen uptake by alpine plants.

1. Introduction

Soluble nitrogen (N) is of great importance for N fluxes and plant nutrition in ecosystem (Huang and Schoenau, 1998). In the view of the traditional N cycling, mineral N is the primary form of N absorbed by plants (Schimel and Bennett, 2004). However, recent studies have demonstrated that many plant species in several ecosystems, in spite of their mycorrhizal types, can directly take up soluble organic N, especially amino acids from soil (Jones et al., 2005; Näsholm et al., 2009). These ecosystems include arctic tundra (Chapin et al., 1993; Schimel

and Chapin, 1996), boreal forest (Kielland et al., 2006; Näsholm et al., 1998; Nordin et al., 2001; Persson et al., 2003), alpine meadow (Lipson et al., 1999a; Raab et al., 1999), temperate grassland (Harrison et al., 2007; Streeter et al., 2000; Weigelt et al., 2005). In most of these regions, the decomposition of soil organic matter and N mineralization are slow due to high altitude/latitude and low temperature. Plant growth is heavily restricted and the total N demand of plants cannot be met through assimilating inorganic ions alone (Raab et al., 1999). At the same time, many plants are capable of directly absorbing amino acids from soil through an active proton symport mechanism (Reinhold

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Table 1
Concentrations ($\mu\text{g N g}^{-1}$ dry soil) of amino acid-N pools in different soil horizons and ecosystems.

Ecosystem	Vegetation	Horizon (soil depth)	Amino acid-N	Soil extractant	Reference
Alpine	Graminoid	MS (0–10 cm)	0.5–2.0 ^a	Water	Lipson et al. (1999b)
Arctic	Lichen, shrub, graminoid	O (0–10 cm)	1.57–8.29	Water	Kielland (1995)
Arctic	Graminoid, shrub	O (0–15 cm)	3–28	Water	Weintraub and Schimel (2005)
Boreal	Dwarf shrub-herb forest	O	1–6 ^a	Water	Nordin et al. (2001)
Boreal	Hardwood-conifer forest	O (0–20 cm)	0.44–4.87	Water	Werdin-Pfisterer et al. (2009)
Temperate	Grassland	MS (0–10 cm)	8.33–11.41	Water	Bardgett et al. (2003)
Boreal	Conifer forest	MS (0–10 cm)	0.17	Water	Inselsbacher et al. (2011)
			3.47	1 M KCl	
Temperate	Hardwood forest	MS (0–10 cm)	0.7–1.1	Water	Warren and Adams (2007)
			3.8–6.2	2 M KCl	
Subalpine	Conifer forest	O	3.75–11.88	2 M KCl	Zhang et al. (2017)
		MS (0–15 cm)	1.2–7.5 ^a		
Temperate	Conifer forest	O	14.93	2 M KCl	Finzi and Schlesinger (2003)
		MS (0–15 cm)	4.04		
		MS (15–30 cm)	1.17		
Temperate	Conifer-hardwood forest	O	45.6–51.2	2 M KCl	Berthrong and Finzi (2006)
		MS (0–15 cm)	1.97–3.67		
Temperate	Grassland	MS (0–15 cm)	0.84–6.3	1 M KCl	Warren and Taranto (2010)
Temperate	Hardwood-conifer forest	O	19.54–26.07	2 M KCl	Brzostek and Finzi (2011)
		MS (0–15 cm)	1.49–2.26		

For soil horizons: MS, mineral soil; O, organic horizon.

^a Data are estimated from the figure plots in the references.

and Kaplan, 1984). Some plants such as *Eriophorum vaginatum* in the Arctic tundra even preferred amino acids to inorganic N as their N source (Chapin et al., 1993). In these ecosystems, the direct uptake of amino acids by plants may contribute significantly to a plant's N budget (Chapin et al., 1993; Christou et al., 2006; Kielland, 1994; Lipson et al., 2001).

Amino acids in soil come from many sources, which mainly include the hydrolysis of soil protein and peptides by extracellular enzymes, exudation and leakage from plant root, leaching and decomposition of litter, and microbial excretion and turnover (Kielland, 1995; Lipson and Näsholm, 2001; Näsholm and Persson, 2001). The fate of these amino acids within the soil system usually involves uptake by soil microbes and plant roots (Bardgett et al., 2003; Harrison et al., 2007; Lipson et al., 1999a), and adsorption on the soil colloid surface (Jones and Hodge, 1999). The concentrations of soil amino acids in different ecosystems have been investigated by several studies (Table 1). Most of the studies were focused on the seasonal pattern of the pool size of soil amino acids, while very limited information is available on the effect of vegetation type on the concentration and composition of soil amino acids.

The availability of N determines species composition as well as production (McKane et al., 2002; Ohlson et al., 1995). In plant-soil feedback, vegetation may influence soil available N, especially amino acids through the following pathways: (1) Change of plant cover may lead to considerable shifts in soil chemistry by altering soil temperature and water relations (Roberts et al., 2009), and therefore, may influence soil enzyme activities and the production rate of amino acids. (2) Different plant litter contain different amounts and types of amino acids (Nykqvist, 1963; Rajendran and Kathiresan, 2000), which leads to different ways of amino acid leaching (Hicks et al., 1991), and different mechanisms of amino acid production by organic matter decomposition. (3) Different plant species produce diverse amount and composition of root exudates that include a large proportion of amino acids (Hertenberger et al., 2002). The difference in root exudates also selects for distinct rhizosphere community structures (Marschner et al., 2004), exerting specific influence on amino acid production and consumption. (4) The amino acid transporters present in plant roots are substrate-specific (Fischer et al., 1998), which makes the preference of different plant species for certain types of amino acids as nutrient sources (Kielland, 1994; Weigelt et al., 2005). Overall, vegetation cover may influence the relative availability of different forms of amino acid in

soil, ultimately inducing shifts in competitive ability and changes in plant diversity (Roberts et al., 2009).

In this study, to probe the factors that influence the pool size and composition of soil amino acids in alpine meadows, for further understanding the mechanisms of organic N uptake by alpine plants, we examined the soil amino acids at three community sites dominated by three typical types of plants, respectively, in the Tibetan alpine meadow, to answer the following scientific questions: (1) Do the soil amino acid pools under different vegetation cover show appreciable differences in their concentration and composition during the growing season? (2) Is the pool size of soil amino acids in the alpine meadow smaller or larger than those in other ecosystems?

2. Materials and methods

2.1. Site description

The research was conducted at the Maqu Alpine Meadow System Station, which is located in the eastern Qinghai-Tibetan Plateau, China (33°40'N, 101°53'E, altitude 3585 m). The soil in this area is classified as alpine meadow soil. The mean annual temperature is 1.2 °C. The lowest mean temperature is –10 °C in January and the highest is 11.7 °C in July (Wu et al., 2010). The mean annual precipitation is 620 mm, mainly occurs during the short, cool summer, and the mean annual evaporation is 1000–1500 mm. This region has 2580 h of sunshine and over 270 d of frost in a year. The plant growing season is between May and September in each year.

The alpine meadow on the Tibetan Plateau is the highest and largest pasture in the world (Li et al., 2016). Three plants, *Kobresia graminifolia* C.B. Clarke, *Polygonum viviparum* L. and *Elymus nutans* Griseb., are typical dominant plants in the eastern Tibetan alpine meadow (Liu et al., 2016). The communities dominated by species in the genus *Kobresia* cover the largest area in this alpine meadow (Li et al., 2016; Miede et al., 2014), and *P. viviparum* is the dominant species in forb meadow. In contrast to the two indigenous species, *E. nutans* is the invaded dominant species in some degraded meadow, where the degradation was caused by human disturbance such as improper cultivation or overgrazing. In addition, the three plants are different in mycorrhizal association. Usually, *K. graminifolia* in the family *Cyperaceae* is non-mycorrhizal (Chapin et al., 1993; Raab et al., 1999, 1996), *P. viviparum* is ectomycorrhizal (Massicotte et al., 1998; Mühlmann et al., 2008) and

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