Science of the Total Environment 651 (2019) 32–41

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Nitrogen deposition and decreased precipitation does not change total nitrogen uptake in a temperate forest

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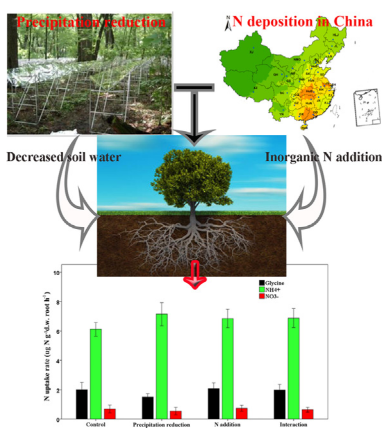
HIGHLIGHTS

- Trees showed a strong preference for NH_4^+ uptake over glycine and NO_3^- uptake.
- Plasticity in root traits use allowed trees to acclimation to environmental change.
- The change of root physiology may be the key to the increase of NH_4^+ uptake.
- The total amount of plant N uptake did not change after long-time treatments.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 8 July 2018
Received in revised form 11 September 2018
Accepted 12 September 2018
Available online 13 September 2018

Editor: Elena PAOLETTI

Keywords:
Nitrogen uptake
Decreased precipitation
Nitrogen addition
Root plasticity
Temperate forest

ABSTRACT

Decreased precipitation and increased anthropogenical by derived nitrogen (N) are important climate change factors that alter the availability of soil water and N which are crucial to root function and morphological traits. However, these factors are seldom explored in forests. To clarify how altered precipitation and N addition affect the uptake of organic and inorganic N by fine roots, a field hydroponic experiment using brief ^{15}N exposures was conducted in a temperate forest in northern China. The root traits related to nutrient foraging (root morphology and mycorrhizal colonization) were measured simultaneously. Our results showed that all three tree species preferred ammonium (NH_4^+) over glycine and nitrate (NO_3^-), and NH_4^+ contributed 73% to the total N uptake from the soil. Uptake of glycine was higher than that of NO_3^-. Decreased precipitation, N addition, and their interaction increased NH_4^+ uptake rate compared with the control. Decreased precipitation decreased the glycine and NO_3^- uptake rate. Moreover, N addition, decreased precipitation and their interaction changed root morphological traits and significantly decreased mycorrhizal colonization. Although our treatments resulted in changes to the root traits and the forms of N uptake by plants, the total amount of N uptake did not change among all treatments.

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https://doi.org/10.1016/j.scitotenv.2018.09.166

We conclude that although fine root traits of dominant tree species in temperate forests have high plasticity in response to climate change, nutrient balance in plants causes the total amount of N uptake to remain unchanged.

1. Introduction

Nitrogen (N) is a fundamental element regulating plant growth and development in terrestrial ecosystems, specifically in temperate and boreal forests, where N is generally considered as a major limiting factor for plant growth and development (Elser et al., 2007; LeBauer and Treseder, 2008). There are various N forms present in the soil, e.g., NH_4^+ and NO_3^- and organic N forms such as various amino acids (Nordin et al., 2001; Persson and Näsholm, 2001; Liu et al., 2017). Therefore, plants uptake a wide array of N forms, which is regarded as an acclimation to reduce limitations (Näsholm et al., 2009). More recently, the importance of plant strategies that use different forms of N has been increasingly acknowledged. Previous studies suggested that plant species may display various mechanisms to optimize the acquisition of N forms due to the complexity of plant N strategies (Näsholm et al., 2009). As a result, uptake patterns of inorganic and organic N may differ in various plant species and ecosystems (Inselsbacher and Näsholm, 2012; Liu et al., 2017). For example, plant species in the same ecosystem can avoid inter-species competition (competition theory) through the use of different N forms (McKane et al., 2002; Miller et al., 2007). Moreover, organic N in temperate forests is high due to low mineralization rates of soil organic matter, and but the contribution of organic N to plant N demands is inconsistent in different studies (Leduc and Rothstein, 2010; Liu et al., 2017). Therefore, a comprehensive understanding of various N forms contribution to plant N demands in various tree species of temperate forest remains incomplete.

In addition to ecosystem types and plant species, soil resource conditions also play an important role in regulating N uptake by plants (Xu et al., 2011). In recent decades, anthropogenically derived N and changes in precipitation regimes have been altered the availability of soil N and water resources that are crucial to plant performance and N uptake strategies (Larsen et al., 2011). Anthropogenic N deposition has led to an increase in soil N availability (Liu et al., 2013), which can alter uptake of various N forms and specific root traits to achieve effective N uptake (Lilleskov et al., 2002; Li et al., 2015). For example, N addition decreased the length, biomass and mycorrhizal colonization rates of the fine roots to regulate nutrient uptake (Li et al., 2015; Wang et al., 2017). Moreover, the quantity and forms of soil available N are very sensitive to reduced soil water availability (Gholamhoseini et al., 2013). Decreased water availability reduces soil N mineralization and N availability (Emmett et al., 2004; Sanaullah et al., 2012). Additionally, acquisition of N by living roots or mycorrhizal fungi is a complex process involving transport in soil via flow and diffusion. Decreased water availability can reduce/change the delivery of various N forms to the root surface through water flow due to the difference in the mobility of different N forms, which may effects on the uptake of various N forms (Buljovcic and Engels, 2001). For example, under drought conditions, plants become more reliant on inorganic N due to greater mobility (e.g., NO_3^- and NH_4^+) as an N source because it is more mobile than organic N (e.g., amino acids) (Tobar et al., 1994; Hawkins et al., 2000). The availability of water also affects root morphology, affecting uptake of N by roots (Kadam et al., 2017). However, this process is seldom explored in forests.

Atmosphere N deposition and decreased precipitation are altering the environment. Plant species can adjust to environmental changes through plasticity of root physiological and morphological traits. Under N additions and precipitation decreases, plasticity in N uptake might therefore be an adaptive strategy giving plants a competitive advantage associated with root tissue construction and maintenance, because they can meet their N demands with any N forms occurring in their root surface (Gutschick, 1981; Grime, 2006). Similarly, since future climate change and regional anthropogenic activity will involve changes in N deposition and precipitation patterns, to understand the possible interactions between different climate and anthropogenic drivers on soil N availability and plant N limitations becomes extra important. However, currently, few previous studies have examined the effects of N additions, precipitation decrease and their interactions on the quantity and forms of plant N absorption and the root traits related to N uptake simultaneously.

To clarify how the plasticity of the uptake of N forms in response to N deposition, decreased precipitation and their interaction in a temperate forest, we conducted an experiment with an N addition, a 30% of decreased precipitation and their interaction to quantify their effects on the uptake strategies for different N forms using field hydroponic experiments and root traits measurement in an old broad-leaved Korean pine (*Pinus koraiensis*) mixed forest in northern China. N addition increased soil inorganic N availability (Liu et al., 2013), we expected that inorganic N more likely to reach the root surface. Therefore, we hypothesize that N addition, will increase inorganic N (NH_4^+ and NO_3^-) uptake. Moreover, decreased precipitation decreased mass flow or diffusivity of organic and inorganic N (Hawkins et al., 2000), we hypothesize that decreased precipitation will decrease inorganic N uptake. Plants developed a suite of effective strategies for root acquiring nutrients and water from the soil by depending on specific root traits (Ostonen et al., 2017). Thus we also hypothesize that N addition, decreased precipitation and their interaction will increase the length of absorption root to increase the rate of root N uptake. Generally, our results provide an important opportunity to understand how the changes in precipitation patterns and anthropogenic alterations of N cycles affect root N uptake strategies.

2. Materials and methods

2.1. Site description and experimental treatments

The experimental sites are located in the Changbai Mountains Natural Reserve in Jilin Province, northeastern China (42°24′N, 128°06′E, and 738 m a.s.l.). This region belongs to a typical temperate-continental climate zone. The long-term (1982–2003) mean annual air temperature is 3.6 °C, with a mean growing season (from May to October) temperature of 15 °C, a mean winter season temperature of −0.6 °C, the highest monthly mean temperature of 21.5 °C occurring in August and the lowest monthly mean temperature of −17.3 °C occurring in January (Forest Ecosystem Research Station of Changbai Mountains, Chinese Academy of Science). Mean annual precipitation is approximately 790 mm, of which 630 mm occurs between May and August. The soil in the study sites was developed from volcanic ash and is classified as an Eutric Cambisol (FAO classification); the bulk density was 0.35 g cm^{-3} in the surface soil (0–10 cm) and 0.68 g cm^{-3} in the deep soil layer (10–20 cm); the contents of total carbon (C), N, phosphorus (P) and organic matter in the 0–20 cm soil layer were 156.6 g C kg^{-1}, 7.17 g N kg^{-1}, 12.20 g P kg^{-1}, 270.00 g kg^{-1}, respectively (Wang et al., 2012). The vegetation type is an old broad-leaved Korean pine mixed forest that is over 300 years old. The dominant tree species are *Pinus koraiensis* (PKS), *Tilia amurensis* (TAR), *Fraxinus mandshurica* (FMR) and *Quercus mongolica*. The mean canopy height and diameter at 1.3 m breast height for these three species were 26 m and 34.2 cm, respectively (Zheng et al., 2017). The tree density on the site was 432 trees hm^{-2}. The main shrub species include *Philadelphus schrenkii*, *Euonymus alatus*, *Lonicera japonica*, *Corylus mandshurica*, and *Deutzia scabra*, and the main herbaceous species include *Anemone raddeana*, *A. cathayensis*, *Cyperus microiria*, *Funaria officinalis*, *Adonis vernalis*, *Brachybotrys paridiformis*, and *Filipendula palmata*. The aboveground tree litterfall is 4.23 Mg hm^{-2}, and aboveground productivity is 9.46 Mg hm^{-2}.