



Research article

Nitrogen use strategies of seedlings from neotropical tree species of distinct successional groups



Halley Caixeta Oliveira ^{a,*}, Ligia Maria Inocência da Silva ^a, Letícia Dias de Freitas ^a, Tatiane Viegas Debiassi ^a, Nidia Mara Marchiori ^b, Marcos Pereira Marinho Aidar ^b, Edmilson Bianchini ^a, José Antonio Pimenta ^a, Renata Stolf-Moreira ^a

^a Department of Animal and Plant Biology, UEL – University of Londrina, Londrina, PR, Brazil

^b Plant Physiology and Biochemistry Section, Institute of Botany, São Paulo, SP, Brazil

ARTICLE INFO

Article history:

Received 17 January 2017

Received in revised form

2 March 2017

Accepted 3 March 2017

Available online 6 March 2017

Keywords:

Ammonium

Ammonium toxicity

Nitrate

Nitrate reductase

Nitrogen metabolism

Plant succession

ABSTRACT

Few studies have analyzed the strategies of neotropical tree seedlings for absorbing, translocating and assimilating the nitrogen. Here, we compared the nitrogen use strategies of seedlings from six tree species that are native to the Brazilian Atlantic Forest and that belong to different successional groups: *Trema micrantha*, *Heliocarpus popayanensis* and *Cecropia pachystachya* (pioneers), *Cariniana estrellensis*, *Eugenia brasiliensis* and *Guarea kunthiana* (non-pioneers). The effects of cultivating seedlings with nitrate or ammonium on the growth, physiology and nitrogen metabolism were analyzed. Nitrate-grown pioneer species had much higher leaf nitrate reductase activity than non-pioneer ones, but non-pioneer seedlings were also able to use nitrate as a nitrogen source. In addition to this remarkable difference between the groups in the capacity for leaf nitrate assimilation, substantial variations in the nitrogen use strategies were observed within the successional classes. Differently from the other non-pioneers, the canopy species *C. estrellensis* seemed to assimilate nitrate mainly in the leaves. Morpho-physiological analyses showed a gradient of ammonium toxicity response, with *E. brasiliensis* as the most tolerant species, and *T. micrantha* and *H. popayanensis* as the most sensitive ones. *Guarea kunthiana* showed a relatively low tolerance to ammonium and an unusual high translocation of this cation in the xylem sap. In contrast to the other pioneers, *C. pachystachya* had a high plasticity in the use of nitrogen sources. Overall, these results suggest that nitrogen use strategies of neotropical tree seedlings were not determined solely by their successional position.

© 2017 Elsevier Masson SAS. All rights reserved.

1. Introduction

Nitrogen (N) has been widely recognized as an important resource that determines the performance and distribution of plant species in natural ecosystems (Britto and Kronzucker, 2013; Dias et al., 2014). N is the root-absorbed nutrient that is required in the highest amounts in plant tissues, and it contributes to the composition of several biomolecules, such as proteins, chlorophylls

and nucleotides (Kraiser et al., 2011). Thus, plant N status has a great influence over a range of processes, such as carbon metabolism, leaf gas exchange, growth and development (Guo et al., 2007b; Kraiser et al., 2011).

Nitrate (NO_3^-) and ammonium (NH_4^+) are the primary inorganic N forms in the soil used by the plants (Miller and Cramer, 2004). The NO_3^- taken up by the roots is reduced to nitrite (NO_2^-) by the cytosolic nitrate reductase (NR) enzyme. NO_2^- is then reduced to NH_4^+ in the plastids by nitrite reductase enzyme. The NH_4^+ resulting from this reaction and the NH_4^+ absorbed from the soil by the roots is assimilated into amino acids through the sequential action of the enzymes glutamine synthetase and glutamine-2-oxoglutarate aminotransferase (Krapp, 2015). The N uptake and its assimilation involve a high energetic cost for plant cells, and this cost is higher when nitrate is used instead of the direct utilization of NH_4^+ (Guo et al., 2007a). However, the internal NH_4^+ accumulation in tissues

Abbreviations: DW, dry weight; FW, fresh weight; N, nitrogen; NH_4^+ , ammonium; NO_2^- , nitrite; NO_3^- , nitrate; NR, nitrate reductase; NRA, nitrate reductase activity.

* Corresponding author. Department of Animal and Plant Biology, Center of Biological Sciences, University of Londrina - UEL, Rodovia Celso Garcia Cid - PR445, km 380, Campus Universitário, Londrina, PR 86057-970, Brazil.

E-mail address: halley@uel.br (H.C. Oliveira).

<http://dx.doi.org/10.1016/j.plaphy.2017.03.003>

0981-9428/© 2017 Elsevier Masson SAS. All rights reserved.

can exert toxic effects on plants commonly associated with ionic, metabolic and hormonal imbalances (Britto and Kronzucker, 2002; Andrews et al., 2013). Thus, the cultivation of many plant species with NH_4^+ as the sole N source can be associated with toxicity symptoms, which may include leaf chlorosis and impaired growth (Britto and Kronzucker, 2002; Andrews et al., 2013). NH_4^+ accumulation is prevented by its rapid assimilation after uptake or formation (Oliveira et al., 2013; Sarasketa et al., 2016), whereas NO_3^- can be stored at high concentrations in cells (Dechorgnat et al., 2011). Moreover, NO_3^- can be translocated in large quantities by xylem sap, and it can be assimilated into amino acids in the roots or leaves depending on the species (Miller and Cramer, 2004). By contrast, the NH_4^+ absorbed from the soil is usually assimilated in the roots, and the resulting amino acids are translocated in the xylem (Oliveira et al., 2013).

Different plant species or functional groups may have specific patterns of N use strategies, which may represent an important adaptive response to the environment in which they live (Britto and Kronzucker, 2013). For example, Kronzucker et al. (2003) found that seedlings from early successional temperate trees were more sensitive to NH_4^+ toxicity than *Picea glauca*, a conifer found in NH_4^+ -rich soils of the late stages of succession. Moreover, many tree species from Australian ecosystems with NH_4^+ predominance in the soil (as in eucalypt woodlands) have been shown to have a preference for using this cation (Schmidt and Stewart, 1998). Conversely, *Ficus* spp. have a high capacity to use NO_3^- , which is associated with their distribution across soils with high nitrification rates (Schmidt et al., 1998).

In one of the few studies with neotropical tree species dedicated to this subject, Aidar et al. (2003) observed a continuum of N use strategies in a successional community in the Brazilian Atlantic Forest. These authors proposed that pioneer tree species have a high capacity for NO_3^- assimilation, as indicated by the high NRA in the leaves and the translocation of considerable amounts of NO_3^- in the xylem sap. On the other extreme of the continuum, the late secondary species had a reduced capacity for NO_3^- assimilation in the leaves, thereby incurring the use of other N sources (possibly NH_4^+) in the roots. The differences in N use strategies by these functional groups are in accordance with the normally observed reduction of the $\text{NO}_3^-/\text{NH}_4^+$ ratio in the soils over the course of forest succession (Kronzucker et al., 2003). However, tropical forests have a high complexity of microsites, with a significant horizontal and vertical heterogeneity in their soils (Davies et al., 1998). Thus, variations in N acquisition strategies among species from the same successional position might occur, allowing the occupation of specific niches. In accordance with this hypothesis, two late successional tree species of the Guianese tropical rainforest were shown to have different N use strategies, with *Eperua falcata* preferentially using litter-derived NO_3^- and *Dicorynia guianensis* using the NH_4^+ in the soil (Schimann et al., 2008).

The study by Aidar et al. (2003) was performed entirely in the field with adult individuals, and it is still necessary to evaluate the N use strategies of neotropical tree seedlings that are grown under controlled greenhouse conditions. In addition to allowing the analysis of root N metabolism and the NH_4^+ tolerance/sensitivity response, greenhouse studies would be able to verify whether the model proposed by Aidar et al. (2003) could be extrapolated for tree seedlings. The capacity of tree seedlings to acclimatize or not to different N sources may affect their ability to colonize new habitats, and may be of great interest in restoration programs. An important example of the necessity of knowing N relations of seedlings comes from Kronzucker et al. (1997), who showed that the low capacity for NO_3^- utilization by *Picea glauca* seedlings compromises their establishment in degraded areas with a predominance of NO_3^- in the soil.

Here, we aimed to analyze the N use strategies of seedlings from six neotropical tree species belonging to distinct successional groups (pioneer or shade-intolerant and non-pioneer or shade tolerant). For this purpose, we evaluated the effects of cultivation with NO_3^- or NH_4^+ on the growth, physiology and N metabolism of the seedlings. We hypothesized that variations in N use strategies would occur not only between but also within the successional groups.

2. Materials and methods

2.1. Plant material and growth conditions

Six tree species native to the Brazilian Atlantic Forest were chosen for this study. *Trema micrantha* (L.) Blume (Cannabaceae), *Heliocarpus popayanensis* Kunth (Malvaceae) and *Cecropia pachystachya* Trécul (Urticaceae) are pioneer or shade-intolerant species, whereas *Cariniana estrellensis* (Raddi) Kuntze (Lecythidaceae), *Eugenia brasiliensis* Lam. (Myrtaceae) and *Guarea kunthiana* A. Juss. (Meliaceae) are considered non-pioneer or shade-tolerant plants. These species make part of the floristic composition of fragments of seasonal semideciduous forest (Silva and Soares-Silva, 2000; Lopes et al., 2012). The three pioneer species are abundant in the border and are restricted to large gaps within the fragments. *C. pachystachya* stands out in floristic inventories of alluvial forests of South and Southeast Brazil (Silva et al., 2007). *C. estrellensis* is a canopy species, whereas *E. brasiliensis* and *G. kunthiana* are typical of understory. The six species are used together in the restoration of degraded areas (Cavalheiro et al., 2002).

The seeds were kindly provided by the Laboratory of Biodiversity and Ecosystem Restoration (LABRE) of the State University of Londrina. The seeds were germinated in water-irrigated sand, and seedlings with a pair of fully developed leaves were transferred to individual pots (10.5 cm high, 9.5 cm lower diameter, 14 cm upper diameter) filled with sterilized sand for the beginning of the treatments. The pots were irrigated twice a week with 90 mL of the nutritive solution, which was composed of 1 mM KH_2PO_4 , 2 mM K_2SO_4 , 2 mM MgSO_4 , 2 mM CaCl_2 , the micronutrients described by Hoagland and Arnon (1950) and KNO_3 or $(\text{NH}_4)_2\text{SO}_4$ as the N source (total [N] = 4 mM). The pH was adjusted to 5.5 using KOH. The solution was supplemented with 100 μM N-allylthiourea to prevent nitrification in the pots (Ginestet et al., 1998). Once per week, the pots were irrigated with distilled water to prevent desiccation and the accumulation of nutrients in the sand. The scheme of irrigation of the pots with nutritive solution and distilled water was also important to prevent the acidification of the substrate of NH_4^+ -grown seedlings. The plants were kept for two months at the greenhouse of the Department of Animal and Plant Biology of the University of Londrina, municipality of Londrina (23°19'29"S, 51°11'51"W). The experiments were performed from February to May 2014 and 2015 (summer-autumn). The average daily values and standard deviations of the temperature, relative humidity, and accumulated global solar radiation were 21.7 ± 2.9 °C, $83.2 \pm 10.5\%$, and 14.1 ± 4.9 MJ m⁻², respectively (data kindly provided by the Laboratory of Agrometeorology, Embrapa Soja, Londrina).

2.2. Leaf gas exchange measurements

Eight weeks after the beginning of the N treatments, the net photosynthesis and stomatal conductance of the seedlings were measured during the early mornings (8–10 a.m.) of sunny days using a Portable LI-6400XT Photosynthesis System (LI-COR Biosciences, Lincoln, NE, USA). The leaves were placed in a 6 cm² 6400-02B measuring chamber in which they were exposed to a saturating PAR (1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and a flow rate of 400 mL min⁻¹.

Download English Version:

<https://daneshyari.com/en/article/5515584>

Download Persian Version:

<https://daneshyari.com/article/5515584>

[Daneshyari.com](https://daneshyari.com)