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ORIGINAL PAPER

Nitrate reductase activity and nitrogen compounds in xylem exudate of *Juglans nigra* seedlings: relation to nitrogen source and supply

Michael A. Nicodemus · K. Francis Salifu · Douglass F. Jacobs

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Abstract Nitrogen (N) limits plant productivity and its uptake and assimilation may be regulated by N source, N availability, and nitrate reductase activity (NRA). Knowledge of how these factors interact to affect N uptake and assimilation processes in woody angiosperms is limited. We fertilized 1-year-old, half-sib black walnut (*Juglans nigra* L.) seedlings with ammonium (NH_4^+) [as $(NH_4)_2SO_4$], nitrate (NO_3^-) (as $NaNO_3$), or a mixed N source (NH_4NO_3) at 0, 800, or 1,600 mg N plant^{-1} season^{-1}. Two months following final fertilization, growth, in vivo NRA, plant N status, and xylem exudate N composition were assessed. Specific leaf NRA was higher in NO_3^--fed and NH_4NO_3-fed plants compared to observed responses in NH_4^+-fed seedlings. Regardless of N source, N addition increased the proportion of amino acids (AA) in xylem exudate, inferring greater NRA in roots, which suggests higher energy cost to plants. Root total NRA was 37% higher in NO_3^--fed than in NH_4^+-fed plants. Exogenous NO_3^- was assimilated in roots or stored, so no difference was observed in NO_3^- levels transported in xylem. Black walnut seedling growth and physiology were generally favored by the mixed N source over NO_3^- or NH_4^+ alone, suggesting NH_4NO_3 is required to maximize productivity in black walnut. Our findings indicate that black walnut seedling responses to N source and level contrast markedly with results noted for woody gymnosperms or herbaceous angiosperms.

Keywords Black walnut · Nitrate · Nitrate reductase · Ammonium · Xylem exudate

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M. A. Nicodemus · K. F. Salifu · D. F. Jacobs (✉)
Department of Forestry and Natural Resources,
Hardwood Tree Improvement and Regeneration Center,
Purdue University, West Lafayette, IN 47907, USA
e-mail: djacobs@purdue.edu

Introduction

Black walnut (*Juglans nigra* L.) is one of the most valuable species of the Central Hardwood Forest Region of the United States. The species is used for high quality lumber and veneer, has value for nut production and serves as a food source for wildlife (Williams 1990). Considering the value and increasing significance of black walnut (Jacobs et al. 2004), optimizing growth and physiology of juvenile seedlings is important to enhance plantation productivity. Nitrogen (N) supply is a key factor limiting plant growth and appropriate N fertilization provides an opportunity to promote productivity of tree crops (Allen 1987), especially for young plantations.

Plants may assimilate organic N (Näsholm et al. 1998; Raab et al. 1999; Persson et al. 2006). However, the major source of N for plant uptake and assimilation is inorganic N as nitrate (NO_3^-) or ammonium (NH_4^+) (Hageman 1980; Walecka-Hutchison and Walworth 2007). Absorbed NH_4^+ is quickly assimilated into amino acids (AA) and proteins for storage in roots because low levels can cause NH_4^+ toxicity, such as ammonium-induced element deficiency associated with impaired uptake of other cations and rhizosphere acidification (Haynes 1986). By contrast, absorbed NO_3^- may be stored or assimilated into organic forms for storage in roots or transported in xylem exudate along with AA into leaves where it is reduced. These processes may be regulated by nitrate reductase activity (NRA), N source supplied to plants, and N application levels.

Studies have shown that preferred N source is largely species-specific. For example, woody gymnosperms