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The presence of amino acids affects inorganic N uptake in non-mycorrhizal seedlings of European beech (*Fagus sylvatica*)

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Summary To investigate the impact of organic N compounds for inorganic nitrogen uptake in the rhizosphere, we fed ammonium nitrate with or without amino acids (i.e., glutamine or arginine) to the roots of non-mycorrhizal beech (*Fagus sylvatica* L.) seedlings under controlled conditions at different levels of N availability. Uptake of individual N sources was determined from ^{15}N (inorganic N) and $^{15}N^{13}C$ (organic N) accumulation in the roots. In addition, gene fragments encoding proteins involved in N uptake and metabolism were cloned from beech for gene expression analyses by quantitative real-time PCR in the roots. Generally, ammonium was preferred over nitrate as N source. Organic N sources were taken up by beech roots as intact molecules. Uptake of organic N was significantly higher than inorganic N uptake, thus contributing significantly to N nutrition of beech. Depending on the level of N availability, inorganic N uptake was negatively affected by the presence of organic N sources. This result indicates an overestimation of the contribution of inorganic N uptake to N nutrition of beech in previous studies. Apparently, association with mycorrhizal fungi is not essential for organic N uptake by beech roots. Gene expression analyses showed that transcriptional regulation of the amino acid transporters *FsCAT3*, *FsCAT5*, *FsAAT* and *FsAAP* and the ammonium transporter *FsAMT1.2* in the roots is involved in N nutrition of beech.

Keywords: ammonium, enzymes of N metabolism, N availability, N transporters, nitrate, organic N uptake.

Introduction

Tree growth and development are limited by the availability of N in many temperate forest ecosystems not exposed to anthropogenic N deposition (Rennenberg et al. 1998, 2009, Lovett et al. 2004, Chapman et al. 2006). Plants use a wide range of N forms to optimize N acquisition (Näsholm et al. 2009). Numerous studies under laboratory as well as field conditions have shown that plants acquire N not only as inorganic but also as organic N species (reviews by Näsholm et al. 2009, Rennenberg et al. 2009 and references therein). However, only little is known about how different N forms interact, how this interaction may change with N availability and how N uptake is regulated at the molecular level (Gessler et al. 2004, Rennenberg et al. 2009), in particular for temperate forest tree species.

In Central Europe, European beech (*Fagus sylvatica* L.) is the dominant tree species of the potential natural vegetation in moist to moderately dry areas of the sub-mountainous altitude range (Ellenberg 1996). Nowadays, beech is favoured by forest practitioners and governments (e.g., Fotelli et al. 2001, Gessler et al. 2007) since forest management practices in Central Europe have changed from supporting conifer monocultures to supporting mixed species stands thereby promoting the natural regeneration of deciduous tree species (e.g., Tarp et al. 2000, Fotelli et al. 2001). Inorganic N uptake has been investigated in beech under different environmental conditions, for example: drought (Fotelli et al. 2002), varying soil temperature (Gessler et al. 1998*a*), different rhizospheric NO concentrations (Simon et al. 2009*a*), different soil substrates (Gessler et al. 1998*a*, Dannenmann et al. 2009), differences in climate (Gessler et al. 2005), diurnal patterns (Gessler et al. 2002), forest management (Gessler et al. 2005) and in competition with soil microorganisms (Dannenmann et al. 2009) or other plant species (Fotelli et al. 2002, Simon et al. 2009*b*). In general, it has been found that ammonium is the main N form taken up by beech on soil substrates with high N availability (Gessler et al. 1998*a*), whereas nitrate is favoured on substrates with limited N supply, in particular when ammonium availability is low (Dannenmann et al. 2009, Simon et al. 2009*b*). Only recently, organic N uptake by beech has also been studied (Dannenmann et al. 2009, Simon et al. 2009*a*, 2009*b*), but studies considering the interaction between inorganic and organic N sources for N uptake by beech roots and the regulatory processes involved have not been reported.

Nitrate uptake is regulated by several feedback inhibitors such as nitrate itself (Siddiqi et al. 1989, King et al. 1993)