

VIEWPOINT

Ecological significance and complexity of N-source preference in plants

Dev T. Britto and Herbert J. Kronzucker*

Department of Biological Sciences, University of Toronto, 1265 Military Trail, Toronto, Ontario, Canada M1C 1A4

* For correspondence. E-mail: herbertk@utsc.utoronto.ca

Received: 29 April 2013 Returned for revision: 20 May 2013 Accepted: 29 May 2013

- **Background** Plants can utilize two major forms of inorganic N: NO_3^- (nitrate) and NH_4^+ (ammonium). In some cases, the preference of one form over another (denoted as β) can appear to be quite pronounced for a plant species, and can be an important determinant and predictor of its distribution and interactions with other species. In many other cases, however, assignment of preference is not so straightforward and must take into account a wide array of complex physiological and environmental features, which interact in ways that are still not well understood.
- **Scope** This Viewpoint presents a discussion of the key, and often co-occurring, factors that join to produce the complex phenotypic composite referred to by the deceptively simple term 'N-source preference'.
- **Conclusions** N-source preference is much more complex a biological phenomenon than is often assumed, and general models predicting how it will influence ecological processes will need to be much more sophisticated than those that have been so far developed.

Key words: Ammonium, nitrate, N-source preference, succession, competition, soils, amino acids, complexity.

INTRODUCTION

Terrestrial plants take up inorganic nitrogen from the soil mainly in the forms of ammonium, NH_4^+ and nitrate, NO_3^- , two ions that, when acquired, have highly distinct genetic and metabolic consequences in the plant (Haynes and Goh, 1978; Britto and Kronzucker, 2002, 2005a; Stitt *et al.*, 2002). Some plant species have been shown to produce more biomass, or accumulate greater quantities of nitrogen, when growing on one N source compared with another, i.e. they appear to display a preference. Despite the importance of N as a frequently growth-limiting nutrient in both agricultural and wild ecosystems (Tilman, 1985; Vitousek and Howarth, 1991), however, no precise definition of N-source preference (denoted here as β , after Boudsocq *et al.*, 2012) has emerged in the literature, nor has a robust, broad classification of plant species adapted to NO_3^- or NH_4^+ (although a few preliminary attempts have been made, e.g. Krajina *et al.*, 1973; Falkengren-Grerup, 1995; Britto and Kronzucker, 2002). This is in part because the interactions between plant acquisition of NO_3^- or NH_4^+ and multiple environmental variables, such as temperature, soil pH and nutrient supply, produce a complex of effects that can greatly influence and shift plant growth responses to variable N sources. In an ecological setting, this physiological complexity is compounded by the variability inherent in many ecosystems, where large changes in soil characteristics frequently occur over short distances and short spans of time (Hodge, 2004). In this paper we shall discuss the complexities involved in accurately modelling β within ecological contexts, and the significance of such preferences for ecological processes such as succession.

PHYSIOLOGICAL UNDERPINNINGS OF N-SOURCE DIFFERENCES

The reasons underlying apparent N-source preferences are poorly understood, but include ammonium toxicity in nitrate

specialists (Gerendás *et al.*, 1997; Britto and Kronzucker, 2002) and atrophied nitrate uptake systems in the roots of ammonium specialists (Kronzucker *et al.*, 1997). Fundamental questions remain unanswered in this branch of physiology, such as that of why many plants, especially agricultural crop species and early-successional pioneer species, appear to prefer NO_3^- to NH_4^+ , despite the fact that NO_3^- must be taken up against a steep electrochemical gradient, then reduced to NH_4^+ before entering the organic N pool. Both processes require a considerable additional expenditure of fixed carbon compared with NH_4^+ acquisition (Bloom *et al.*, 1992; Kurimoto *et al.*, 2004; Britto and Kronzucker, 2005a). One answer to this appears to lie in the rapid entry of NH_4^+ into roots, which occurs even in NO_3^- specialists, and can result in pronounced accumulation of NH_4^+ (Givan, 1979; Gerendás *et al.*, 1997; Britto *et al.*, 2001). Ammonium build-up can consequently have toxic effects, including the suppressed uptake of important cationic nutrients, such as K^+ , Ca^{2+} and Mg^{2+} (Kirkby, 1968; Salsac *et al.*, 1987; van Beusichem *et al.*, 1988; Lewis, 1992; Britto and Kronzucker, 2002). By contrast, NO_3^- toxicity is fairly uncommon and typically occurs at very much higher soil concentrations (Britto and Kronzucker, 2005b, and references therein). Among the strategies used by plants to decrease the amount of free NH_4^+ in tissues is increased NH_4^+ assimilation (Givan, 1979; Magalhaes *et al.*, 1995; Gerendás *et al.*, 1997; Schortemeyer *et al.*, 1997). However, this requires an elevated supply of carbohydrate to the roots, because only a small amount of NH_4^+ is translocated to shoots (Wang *et al.*, 1993; Kronzucker *et al.*, 1998; Finnemann and Schjoerring, 1999), leaving less reduced carbon available for growth and maintenance (Lewis, 1992). Another strategy is to increase the efflux of NH_4^+ to the external medium, which can, however, result in an energetically costly futile cycle (Britto *et al.*, 2001; Li *et al.*, 2012). Energy lost in this cycle, in addition to the frequently suggested uncoupling of energy gradients in cellular organelles by NH_4^+ (Krogmann *et al.*, 1959; Crofts, 1967; this possibility is disputed, however – see Gerendás *et al.*, 1997;

Britto and Kronzucker, 2002), may eliminate any energetic advantages conferred by the uptake of reduced N. Although elevated respiration under high- NH_4^+ conditions has been attributed to futile NH_4^+ cycling in roots (Britto *et al.*, 2001), the link between carbohydrate limitation and preference against NH_4^+ is not straightforward, since increased light intensity may aggravate rather than alleviate NH_4^+ toxicity (Gerendás *et al.*, 1997; Zhu *et al.*, 2000).

Deficiency, sufficiency and toxicity occur for both inorganic N forms, with very different set points, and growth optima are expected and commonly observed (Fig. 1; Gray, 1983; Eck, 1984; Westfall *et al.*, 1990; Miller and Timmer, 1994; Padgett and Allen, 1999; Cabrera, 2000; Gan *et al.*, 2012; Hall, 2002). Such optimum curves, and how they differ with N source for a given plant species, should inform any fundamental appraisal of the N-source preference(s) of that species, since they are directly linked with plant productivity. Root transport systems specific for NO_3^- and NH_4^+ acquisition fundamentally influence the shapes of growth–response curves, since their activities not only determine the amount of excessive, detrimental transport that may occur at high substrate concentrations (Britto *et al.*, 2001) but also govern the lowest soil N concentration from which a species can abstract the limiting resource and at which it can survive. This concentration minimum is frequently referred to as the C_{\min} , and may be as low as ~ 0.001 mM for both NO_3^- and NH_4^+ (Deane-Drummond and Chaffey, 1985; Marschner *et al.*, 1991). The C_{\min} concept is important in modelling processes such as competition and succession, and is similar to important ecological principles such as Justus von Liebig's 'law of the minimum', and Tilman's R^* rule, which predicts the outcome of competitive interactions between species based on their ability to survive on the lowest amount of a limiting resource (Tilman, 1982; McGill 2005; Wilson *et al.*, 2007). However, it should be emphasized here that C_{\min} (like β , as will be discussed) is not constant for a plant species, but varies with root activity, which in turn strongly depends on factors such as temperature and plant nutrient status (Drew *et al.*, 1984; Marschner *et al.*, 1991).

Because the regulation of inorganic N transport largely determines the uptake of nutrients at both limiting and toxic concentrations, it is crucial to examine it in the present context. Particularly important is the physiological principle that the transport systems moving inorganic N across root plasma membranes, as well as the metabolic systems assimilating N within the cell, are typically downregulated by increasing soil nutrient content, especially

that of N itself (Glass *et al.*, 2002; Tang *et al.*, 2012). The curves in Fig. 2 exemplify this pattern of regulatory feedback by long-term N supply and plant N status on the kinetics of N uptake (Wang *et al.*, 1993; Rawat *et al.*, 1999; Kronzucker *et al.*, 2000). Similar patterns are seen for both NO_3^- and NH_4^+ , but with unique kinetic parameters for each. It is important to note that these curves are typically hyperbolic in shape, as in Monod or Michaelis–Menten equations, under most ecologically relevant supply conditions; in other words, they saturate, as does the growth response to increasing soil N. Under toxicity or 'luxury consumption' conditions, however, linearly rising patterns of unidirectional influx are sometimes observed, but elevated influx is largely compensated for by elevated efflux under these conditions (Britto and Kronzucker, 2006) and does not translate into increased growth (Gezelius and Näsholm, 1993; de Mazancourt *et al.*, 2012). An added layer of regulatory complexity can be seen in the case of the nitrate acquisition apparatus, which is greatly downregulated in the absence of NO_3^- (Kronzucker *et al.*, 1999a; Glass *et al.*, 2001). The induction of this apparatus by the appearance of nitrate can be quite rapid in some species, taking only a few hours (Siddiqi *et al.*, 1989; Kronzucker *et al.*, 2000), while in others, such as white spruce, it can take several days (Kronzucker *et al.*, 1995; Min *et al.*, 1998). Once stimulated, NO_3^- transport is usually downregulated by further NO_3^- acquisition, but this is not well understood; there appear to be species-specific differences in the metabolites responsible for this effect (Glass *et al.*, 2002; Tang *et al.*, 2012). Regardless of the mechanism, it is well known that changes in soil N pools can exert powerful influences on N-acquisition characteristics, and bring changes in apparent N-source preferences, even at sub-toxic concentrations (Tylova-Munzarova *et al.*, 2005; Munzarova *et al.*, 2006; Houlton *et al.*, 2007).

Many other environmental factors influence the uptake of N, with divergent effects found for NO_3^- and NH_4^+ . One of the most important is soil temperature (Haynes and Goh, 1978; Sasakawa and Yamamoto, 1978; Clarkson and Warner, 1979; Kafkafi, 1990; Macduff and Jackson, 1991; Gessler *et al.*, 1998; Vaast *et al.*, 1998; Kumar *et al.*, 2008), which can fluctuate greatly on time scales of months, days or hours. In general, NO_3^- uptake appears to be more inhibited by low temperature than does NH_4^+ uptake (Frota and Tucker, 1972; Clarkson *et al.*, 1994), which can be explained by its higher energy requirement for

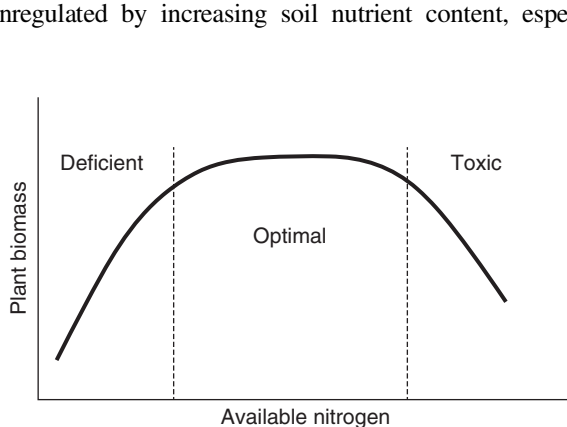


FIG. 1. Optimal curve relating plant biomass gain to N supply. Generalized from published data (see citations in text).

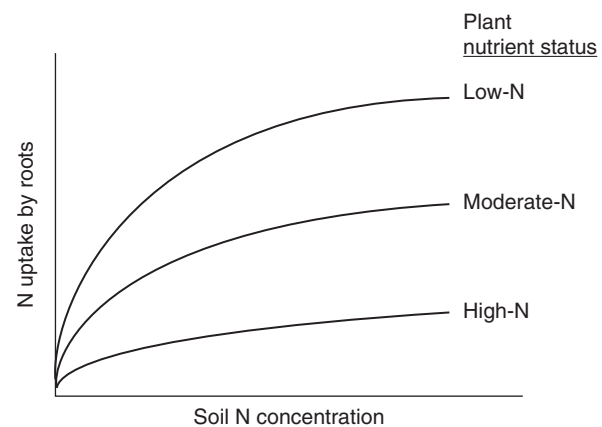


FIG. 2. Influence of plant N status on concentration-dependent N-uptake kinetics by plant roots. Generalized from published data (see citations in text).

acquisition and reduction (see above). Soil pH also shows high variability (Farley and Fitter, 1999) and affects NO_3^- and NH_4^+ transport differentially, with optima tending to be more alkaline for NO_3^- uptake than for NH_4^+ uptake (Haynes and Goh, 1978; von Wirén *et al.*, 1997; Hawkins and Robbins, 2010). This is somewhat surprising given that there is a higher proton requirement for NO_3^- uptake than for NH_4^+ , since it is driven by a proton-symport mechanism (McClure *et al.*, 1990; Britto and Kronzucker, 2006; Miller *et al.*, 2007), while NH_4^+ uptake probably occurs in a uniport manner, in exchange for protons (though not directly coupled to H^+ transport), under most conditions [Ludewig *et al.*, 2002; Mayer *et al.*, 2006; at very low concentrations, NH_4^+ uptake involves a symport mechanism with protons (Ortiz-Ramirez *et al.*, 2011), while at high concentrations NH_3 permeation may be possible through aquaporins (Jahn *et al.*, 2004)]. The mechanisms of transport for the two ions themselves have distinct consequences for soil pH: alkalization by NO_3^- nutrition and acidification by NH_4^+ nutrition (Raven and Smith, 1976; Runge, 1983; van Beusichem *et al.*, 1988; Marschner *et al.*, 1991; Falkengren-Grerup, 1995; Britto and Kronzucker, 2002). These processes can result in unpredictable feedback cycles that can be intensified by other factors, such as (1) inhibition of nitrification rates by soil bacteria as the rhizosphere acidifies (Haynes and Goh, 1978; Falkengren-Grerup, 1995) and (2) changes in the availability of nutrients, such as P, or toxicants, such as Al, as soil pH changes differentially depending on which N source dominates in plant acquisition patterns (Riley and Barber, 1971; Ruan *et al.*, 2000).

Other major components of plant nutrition interact profoundly with plant roots to produce divergent effects when grown on NO_3^- or NH_4^+ . One of the most notable examples of this is the alleviation of NH_4^+ toxicity by K^+ supply (Mengel *et al.*, 1976; Santa-Maria *et al.*, 2000; Roosta and Schjoerring, 2008; Balkos *et al.*, 2010; ten Hoopen *et al.*, 2010; Li *et al.*, 2012). Another lies in the interactions between NH_4^+ and NO_3^- themselves, such as the significant, and variable, inhibition of NO_3^- uptake by NH_4^+ (Minotti *et al.*, 1969; Lee and Drew, 1986; Marschner *et al.*, 1991; Kreuzwieser *et al.*, 1997; Kronzucker *et al.*, 1999a) and the synergistic effect on N uptake and growth often seen when the two N sources are combined (Cox and Reisenauer, 1973; Kronzucker *et al.*, 1999a, b). A third important example is seen in the strong interactions between carbohydrate supply and growth on different N sources (Haynes and Goh, 1978; Aslam *et al.*, 1979; Givan, 1979; Kafkafi, 1990), while a fourth is that between inorganic and organic N. Regarding this last example, inorganic vs. organic, the soil N content in some ecosystems, such as boreal forests, can be predominantly in the form of amino acids, which can be taken up by roots in substantial quantities (Näsholm *et al.*, 1998; Lipson and Näsholm, 2001). This has significance in terms of providing an alternative source of N when this resource is limiting, thus reducing plant demand for NO_3^- and NH_4^+ . Moreover, the downregulatory effect of amino acids on the uptake of NO_3^- and NH_4^+ is well known (Imsande and Touraine, 1994; Padgett and Leonard, 1996; Rawat *et al.*, 1999; Gessler *et al.*, 2004).

Further complex nutritional interactions of broad significance should be mentioned here, and can be considered in three groups. The first group consists of interactions among N source, soil moisture and water use. For instance, increased drought adaptation has been observed with NH_4^+ nutrition in some cereals

(Mihailović *et al.*, 1992; Yin and Raven, 1998; Guo *et al.*, 2008), while other studies, mainly in dicotyledons, have shown decreased water-use efficiency under NH_4^+ (Raven *et al.*, 1992; Høgh-Jensen and Schjoerring, 1997; Claussen, 2002; Lu *et al.*, 2005). Moreover, in a striking study of N-source preference among a functionally diverse group of tropical forest species, Houlton *et al.* (2007) showed abrupt community-wide changes in β resulting from changes in precipitation. These authors found that NO_3^- was the preferred source for all species under dry conditions, while in the wettest soils NH_4^+ was almost exclusively used.

The second group of interactions are those between N source and light intensity. Light plays a key role in regulating key components of the NO_3^- -acquisition pathway (Stitt *et al.*, 2002), while NH_4^+ -grown plants tend to be more sensitive to light stress than NO_3^- -grown plants (Magalhaes and Wilcox, 1983; Zornoza *et al.*, 1987; Zhu *et al.*, 2000).

The third group of interactions are those between N source and changes in atmospheric CO_2 : this topic, of considerable recent interest, has yielded mixed results, but elevated CO_2 can produce considerable differential effects on the acquisition of NO_3^- and NH_4^+ , at times causing switches in plant preference (Bassirirad *et al.*, 1996, 1997; Zerihun and Bassirirad, 2001).

The plasticity of plant responses to environmental variability reflects the complexity inherent in all ecosystems. This is particularly true in the case of the multifarious environmental factors influencing β , which must be included when comprehensively modelling the ecological consequences of such preferences. For example, even a seemingly simple agricultural system such as a rice paddy can be dauntingly complex in terms of modelling nitrification and nitrate use (Kirk and Kronzucker, 2005), since these activities, and the resulting magnitudes of N pools, can vary substantially over temporal and spatial scales. Indeed, the modelling of nitrification alone can require the consideration of as many as nine independent processes (Vitousek and Melillo, 1979). Moreover, the horizontal and vertical patchiness of soils with respect to water and nutrients is well known (Hodge, 2004); the variability of resources can be as great over the rooting zone of a plant as it is over a 120-m² plot (Jackson and Caldwell, 1993). Such patchiness extends to substantial, and unpredictable, temporal variations in nutrient availability, including that of NH_4^+ and NO_3^- (Drew and Saker, 1975; Farley and Fitter, 1999). An additional layer of complexity arises from the ability of vegetation to strongly influence the nutrient composition of soils; in one study, 10-fold variation in net mineralization was observed within 3 years in initially identical soils, as a result of the presence of different plant species (Wedin and Tilman, 1990). In all these considerations, it is important to understand that nutrient pool sizes do not necessarily reflect the importance of a pool in an ecosystem. While some pools may be small, this may simply be due to the very rapid turnover caused by intensive utilization and replenishment of the pool (Robertson and Vitousek, 1981; Schulze *et al.*, 1994; Eviner and Chapin, 1997; Hart and Stark, 1997; Kirk and Kronzucker, 2005).

Taken together, the above considerations strongly indicate that the concept of N-source preference cannot be easily defined, but depends on a wide and dynamic range of environmental and physiological factors that overlap simultaneously. Strictly speaking, any assignment of a rigid preference index is valid only for the composite of conditions under which it was experimentally

determined. Moreover, it may be valid only for a given plant variety or subspecies (e.g. Zornoza *et al.*, 1996) or developmental stage (Haynes and Goh, 1978; Jing *et al.*, 2012).

MODELLING THE INFLUENCE OF N-SOURCE PREFERENCE ON ECOLOGICAL PROCESSES

Despite the complex physiological nature of β values, plants have certainly evolved nutritional adaptations to NO_3^- or NH_4^+ , and thus can often be found on soils enriched in the particular N source to which they are most adapted for a given condition. Indeed, some plants appear to be so well adapted to a specific N source that they appear to prefer it under a wide range of conditions. For example, in one study seedlings of *Picea glauca* and *Pinus radiata* showed greater growth and N uptake with NH_4^+ than with NO_3^- , regardless of pH, temperature or type of growth medium (McFee and Stone, 1968). The slow growth of these late-successional conifers on NO_3^- may be particularly limited due to highly atrophied transport systems for the ion, as has been demonstrated in *P. glauca* (Kronzucker *et al.*, 1997), while their superior growth on NH_4^+ reflects the high NH_4^+ content and low nitrification potential of boreal forest soils and other climax systems (Rice and Panchoy, 1972; Haynes and Goh, 1978). Other studies have indicated at times extraordinary plant preferences for one inorganic N source over another, at various developmental stages and under differing nutritional conditions (Rygiewicz and Bledsoe, 1986; Knoepp *et al.*, 1993; van den Driessche and Ponsford, 1995; Gessler *et al.*, 1998).

In such species and under such conditions, where N-source preferences appear to be pronounced, soil nitrogen speciation (and changes in it) has been shown to be a significant determinant of plant productivity, competition, coexistence and ecological succession (McFee and Stone, 1968; Rice and Panchoy, 1972; Haynes and Goh, 1978; Lodhi, 1979; Lodhi and Killingbeck, 1980; Robertson and Vitousek, 1981; Kronzucker *et al.*, 1997, 2003; Kirk and Kronzucker, 2005; Kahmen *et al.*, 2008). Such work extends to interactions among plant species and soil

microorganisms in terms of their competition, cooperation and N-source preferences, which can change depending on the presence or absence of mycorrhizal associations (Plassard *et al.*, 1991; Stewart *et al.*, 1993; Clemmensen *et al.*, 2008; Warren, 2009; Paulding *et al.*, 2010; Piao *et al.*, 2012; Wu *et al.*, 2013).

Nevertheless, many other plants have eluded simple classification as preferring NO_3^- or NH_4^+ . For example, some apparent NO_3^- specialists can thrive on NH_4^+ when K^+ provision is sufficiently high (Britto and Kronzucker, 2002). Most strikingly in this regard, a quintessentially ‘ NH_4^+ -preferring’ plant such as rice (*Oryza sativa*) can show significant variations in its apparent β , depending on factors such as soil depth and nutritional composition, and can be very effective in NO_3^- utilization (Kronzucker *et al.*, 2000; Kirk and Kronzucker, 2005; Balkos *et al.*, 2010). Another such example is that of *Vaccinium* species, which are often considered to be NH_4^+ specialists (Claussen and Lenz, 1999; Britto and Kronzucker, 2002), but in some studies the co-presence of NO_3^- and NH_4^+ appears to be preferable (Ingestad, 1973). Thus, the development of a general model to predict the effect of β on ecological outcomes (e.g. of competition) should assume the multifactorial nature of N-source preference or, more precisely, a set of preferences rather than a fixed singularity.

The sheer complexity of possible plant responses to inorganic N source is a major reason why no comprehensive models yet exist to map and predict the effects of β on ecological processes. Recently, an attempt was made to model species replacement dynamics and ecosystem-level plant productivity, using a measure of N-source preference (Boudsocq *et al.*, 2012). Unfortunately, a very simple designation of β was used in the process; it was defined as a linear coefficient for NH_4^+ uptake, ranging from 0 to 1, while $(1 - \beta)$ was assigned to be the corresponding coefficient for NO_3^- uptake. A fixed N-source preference was thereby assumed for a given plant species, as was a linear proportionality between uptake and substrate concentrations. As discussed here, however, a fixed β value does not take into account the genetic and physiological plasticities of plant responses to NO_3^- or NH_4^+ within the matrix of changing environmental conditions

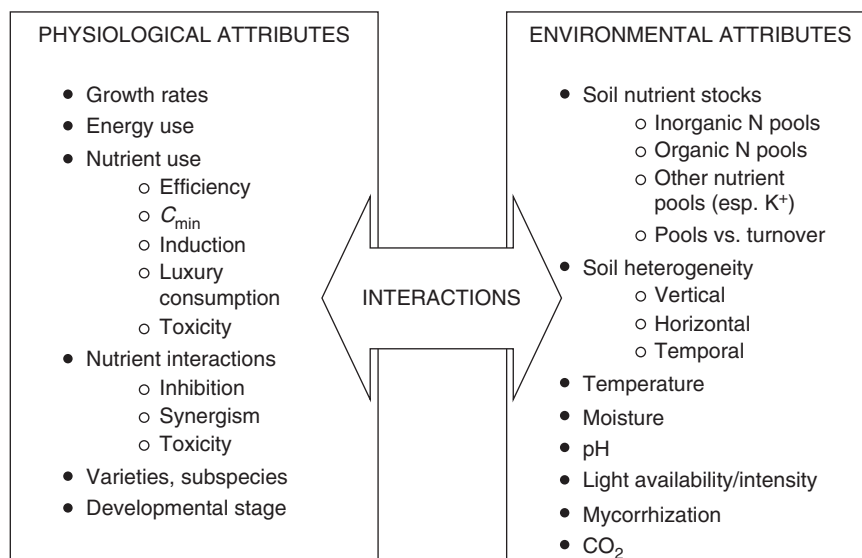


FIG. 3. Physiological and environmental factors influencing N-source preferences (β values) in plants.

(e.g. Fig. 2). In addition, this definition neither considers Monod-like (or Michaelis–Menten-like) growth and uptake patterns nor allows for luxury or toxic consumption (Fig. 1).

For purposes of ecosystem management and study, it is worthwhile to develop general models that describe and predict effects of N source on plant populations and their competitive interactions. What must be kept in mind is that pronounced differences exist in plant responses to NO_3^- or NH_4^+ , but how these translate into ‘preferences’ depends on many complex, and interacting, factors. Indeed, a simple assessment of β is not generally feasible or applicable to realistic models, despite recent effort to do so (Boudsocq *et al.*, 2012). The numerous factors, physiological and environmental, that coalesce to influence N-source preference are outlined in Fig. 3; each has its own set of complexities and interactions with other factors. In some cases, such as that of many boreal conifers, a strong specialization emerges despite myriad complexities (but cf. Heiskanen, 2005), while in cases like tropical lowland rice apparent preferences are not so clear-cut. To conclude, a quotation from D. Tilman (1985) is instructive: ‘Clearly, the uniqueness of the species involved in successions in different areas, the uniqueness of each particular habitat, and various historical factors all limit the potential predictive ability of any model of vegetation dynamics and structure’.

ACKNOWLEDGEMENTS

We thank the Natural Sciences and Engineering Council of Canada (NSERC; grant #217277-2009) and the Canada Research Chairs programme (CRC) for supporting this work.

LITERATURE CITED

- Aslam M, Huffaker RC, Rains DW, Rao KP. 1979. Influence of light and ambient carbon dioxide concentration on nitrate assimilation by intact barley seedlings. *Plant Physiology* **63**: 1205–1209.
- Balkos KD, Britto DT, Kronzucker HJ. 2010. Optimization of ammonium acquisition and metabolism by potassium in rice (*Oryza sativa* L. cv. IR-72). *Plant, Cell & Environment* **33**: 23–34.
- Bassirirad H, Thomas RB, Reynolds JF, Strain BR. 1996. Differential responses of root uptake kinetics of NH_4^+ and NO_3^- to enriched atmospheric CO_2 concentration in field-grown loblolly pine. *Plant, Cell & Environment* **19**: 367–371.
- Bassirirad H, Griffin KL, Reynolds JF, Strain BR. 1997. Changes in root NH_4^+ and NO_3^- absorption rates of loblolly and ponderosa pine in response to CO_2 enrichment. *Plant and Soil* **190**: 1–9.
- Bloom AJ, Sukrapanna SS, Warner RL. 1992. Root respiration associated with ammonium and nitrate absorption and assimilation in barley. *Plant Physiology* **99**: 1294–1301.
- Boudsocq S, Niboyet A, Lata JC, *et al.* 2012. Plant preference for ammonium versus nitrate: a neglected determinant of ecosystem functioning? *American Naturalist* **180**: 60–69.
- Britto DT, Kronzucker HJ. 2002. NH_4^+ toxicity in higher plants: a critical review. *Journal of Plant Physiology* **159**: 567–584.
- Britto DT, Kronzucker HJ. 2005a. Nitrogen acquisition, PEP carboxylase, and cellular pH homeostasis: new views on old paradigms. *Plant, Cell & Environment* **28**: 1396–1409.
- Britto DT, Kronzucker HJ. 2005b. Plant nitrogen transport and its regulation in changing soil environments. *Journal of Crop Improvement* **15**: 1–23.
- Britto DT, Kronzucker HJ. 2006. Futile cycling at the plasma membrane: a hallmark of low-affinity nutrient transport. *Trends in Plant Science* **11**: 529–534.
- Britto DT, Siddiqi MY, Glass ADM, Kronzucker HJ. 2001. Futile transmembrane NH_4^+ cycling: a cellular hypothesis to explain ammonium toxicity in plants. *Proceedings of the National Academy of Sciences, USA* **98**: 4255–4258.
- Cabrera RI. 2000. Evaluating yield and quality of roses with respect to nitrogen fertilization and leaf tissue nitrogen status. *Acta Horticulturae* **511**: 133–141.
- Clarkson DT, Warner A. 1979. Relationship between root temperature and the transport of ammonium and nitrate ions by Italian and perennial ryegrass (*Lolium multiflorum* and *Lolium perenne*). *Plant Physiology* **64**: 557–561.
- Clarkson DT, Hopper MJ, Jones HP. 1994. The effect of root temperature on the uptake of nitrogen and the relative size of the root system in *Lolium perenne*. I. Solutions containing both NH_4^+ and NO_3^- . *Plant, Cell & Environment* **9**: 535–545.
- Claussen W. 2002. Growth, water use efficiency, and proline content of hydroponically grown tomato plants as affected by nitrogen source and nutrient concentration. *Plant & Soil* **247**: 199–209.
- Claussen W, Lenz F. 1999. Effect of ammonium or nitrate nutrition on net photosynthesis, growth, and activity of the enzymes nitrate reductase and glutamine synthetase in blueberry, raspberry and strawberry. *Plant & Soil* **208**: 95–102.
- Clemmensen KE, Sorensen PL, Michelsen A, Jonasson S, Strom L. 2008. Site-dependent N uptake from N-form mixtures by arctic plants, soil microbes and ectomycorrhizal fungi. *Oecologia* **155**: 771–783.
- Cox WJ, Reisenauer HM. 1973. Growth and ion uptake by wheat supplied nitrogen as nitrate, or ammonium, or both. *Plant & Soil* **38**: 363–380.
- Croft AR. 1967. Amine uncoupling of energy transfer in chloroplasts. *Journal of Biological Chemistry* **242**: 3352–3359.
- de Mazancourt C, Schwartz MW. 2012. Starve a competitor: evolution of luxury consumption as a competitive strategy. *Theoretical Ecology* **5**: 379–49.
- Deane-Drummond CE, Chaffey NJ. 1985. Characteristics of nitrate uptake into seedlings of pea (*Pisum sativum* L. cv. Feltham First). Changes in net NO_3^- uptake following inoculation with *Rhizobium* and growth in low nitrate concentrations. *Plant, Cell & Environment* **8**: 517–523.
- Drew MC, Saker LR. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. *Journal of Experimental Botany* **26**: 2679–2690.
- Drew MC, Saker LR, Barber SA, Jenkins W. 1984. Changes in the kinetics of phosphate and potassium absorption in nutrient-deficient barley roots measured by a solution depletion technique. *Planta* **160**: 490–499.
- Eck HV. 1984. Irrigated corn yield response to nitrogen and water. *Agronomy Journal* **76**: 421–428.
- Eviner VT, Chapin FS. 1997. Nitrogen cycle: plant-microbial interactions. *Nature* **385**: 26–27.
- Falkengren-Grerup E. 1995. Interspecies differences in the preference of ammonium and nitrate in vascular plants. *Oecologia* **102**: 305–311.
- Farley RA, Fitter AH. 1999. Temporal and spatial variation in soil resources in a deciduous woodland. *Journal of Ecology* **87**: 688–696.
- Finnemann J, Schjoerring JK. 1999. Translocation of NH_4^+ in oilseed rape plants in relation to glutamine synthetase isogene expression and activity. *Physiologia Plantarum* **105**: 469–477.
- Frota JNE, Tucker LC. 1972. Temperature influence on ammonium and nitrate absorption by lettuce. *Soil Science Society of America Proceedings* **36**: 97–100.
- Gan J, Smith CT, Langeveld JW. 2012. Effects of considering greenhouse gas consequences on fertilizer use in loblolly pine plantations. *Journal of Environmental Management* **113**: 383–389.
- Gerendás J, Zhu Z, Bendixen R, Ratcliffe RG, Sattelmacher B. 1997. Physiological and biochemical processes related to ammonium toxicity in higher plants. *Zeitschrift für Pflanzenernährung und Bodenkunde* **160**: 239–251.
- Gessler A, Schneider S, von Sengbusch D, *et al.* 1998. Field and laboratory experiments on net uptake of nitrate and ammonium by the roots of spruce (*Picea abies*) and beech (*Fagus sylvatica*) trees. *New Phytologist* **138**: 275–285.
- Gessler A, Kopriva S, Rennenberg H. 2004. Regulation of nitrate uptake at the whole-tree level: interaction between nitrogen compounds, cytokinins and carbon metabolism. *Tree Physiology* **24**: 1313–1321.
- Gezelius K, Näsholm T. 1993. Free amino acids and protein in Scots pine seedlings cultivated at different nutrient availabilities. *Tree Physiology* **13**: 71–86.
- Givan CV. 1979. Metabolic detoxification of ammonia in tissues of higher plants. *Phytochemistry* **18**: 375–382.
- Glass ADM, Britto DT, Kaiser BN, *et al.* 2001. Nitrogen transport in plants, with an emphasis on the regulation of fluxes to match plant demand. *Journal of Plant Nutrition and Soil Science* **164**: 199–207.

- Glass ADM, Britto DT, Kaiser BN, *et al.* 2002. The regulation of nitrate and ammonium transport systems in plants. *Journal of Experimental Botany* **53**: 855–864.
- Gray JT. 1983. Nutrient use by evergreen and deciduous shrubs in southern California: I. Community nutrient cycling and nutrient-use efficiency. *Journal of Ecology* **71**: 21–41.
- Guo S, Zhou Y, Li Y, Gao Y, Shen Q. 2008. Effects of different nitrogen forms and osmotic stress on water use efficiency of rice (*Oryza sativa*). *Annals of Applied Biology* **153**: 127–134.
- Hall JL. 2002. Cellular mechanisms for heavy metal detoxification and tolerance. *Journal of Experimental Botany* **53**: 1–11.
- Hart JM, Stark SC. 1997. High rates of nitrification and nitrate turnover in undisturbed coniferous forests. *Nature* **385**: 61–64.
- Hawkins BJ, Robbins S. 2010. pH affects ammonium, nitrate and proton fluxes in the apical region of conifer and soybean roots. *Physiologia Plantarum* **138**: 238–247.
- Haynes RJ, Goh KM. 1978. Ammonium and nitrate nutrition of plants. *Biological Reviews* **53**: 465–510.
- Heiskanen J. 2005. Effect of nitrate and ammonium on growth of transplanted Norway spruce seedlings: a greenhouse study. *Annales Botanici Fennici* **42**: 1–9.
- Hodge A. 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist* **162**: 9–24.
- Høgh-Jensen H, Schjoerring JK. 1997. Effects of drought and inorganic N form on nitrogen fixation and carbon isotope discrimination in *Trifolium repens*. *Plant Physiology and Biochemistry* **35**: 55–62.
- Houlton BZ, Sigman DM, Schuur EAG, Hedin LO. 2007. A climate-driven switch in plant nitrogen acquisition within tropical forest communities. *Proceedings of the National Academy of Sciences, USA* **104**: 8902–8906.
- Imsande J, Touraine B. 1994. N demand and the regulation of nitrate uptake. *Plant Physiology* **105**: 3–7.
- Ingestad T. 1973. Mineral nutrient requirements of *Vaccinium vitis idaea* and *V. myrtillus*. *Physiologia Plantarum* **29**: 239–246.
- Jackson RB, Caldwell MM. 1993. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* **74**: 612–614.
- Jahn TP, Møller ALB, Zeuthen T, *et al.* 2004. Aquaporin homologues in plants and mammals transport ammonia. *FEBS Letters* **574**: 31–36.
- Jing J, Zhang F, Rengel Z, Shen J. 2012. Localized fertilization with P plus N elicits an ammonium-dependent enhancement of maize root growth and nutrient uptake. *Field Crops Research* **133**: 176–185.
- Kafkafi U. 1990. root temperature, concentration and the ratio $\text{NO}_3^-/\text{NH}_4^+$ effect on plant development. *Journal of Plant Nutrition* **13**: 1291–1306.
- Kahmen A, Wanek W, Buchmann N. 2008. Foliar $\delta^{15}\text{N}$ values characterize soil N cycling and reflect nitrate or ammonium preference of plants along a temperate grassland gradient. *Oecologia* **156**: 861–870.
- Kirk GJD, Kronzucker HJ. 2005. The potential for nitrification and nitrate uptake in the rhizosphere of wetland plants: a modelling study. *Annals of Botany* **96**: 639–646.
- Kirkby EA. 1968. Influence of ammonium and nitrate nutrition on the cation-anion balance and nitrogen and carbohydrate metabolism of white mustard plants grown in dilute nutrient solutions. *Soil Science* **105**: 133–141.
- Knoepp JD, Turner DP, Tingey DT. 1993. Effects of ammonium and nitrate on nutrient uptake and activity of nitrogen assimilating enzymes in western hemlock. *Forest Ecology and Management* **59**: 179–191.
- Krajina VJ, Madoc-Jones S, Mellor G. 1973. Ammonium and nitrate in the nitrogen economy of some conifers growing in Douglas-fir communities of the Pacific North-West of America. *Soil Biology and Biochemistry* **5**: 143–147.
- Kreuzwieser J, Herschbach C, Stulen I, Wiersma P, Vaalburg W, Rennenberg H. 1997. Interactions of NH_4^+ and L-glutamate with NO_3^- transport processes of non-mycorrhizal *Fagus sylvatica* roots. *Journal of Experimental Botany* **48**: 1431–1438.
- Krogmann DW, Jagendorf AT, Avron M. 1959. Uncouplers of spinach chloroplast photosynthetic phosphorylation. *Plant Physiology* **34**: 272–277.
- Kronzucker HJ, Siddiqi MY, Glass ADM. 1995. Nitrate induction in spruce: an approach using compartmental analysis. *Planta* **196**: 683–690.
- Kronzucker HJ, Siddiqi MY, Glass ADM. 1997. Conifer root discrimination against soil nitrate and the ecology of forest succession. *Nature* **385**: 59–61.
- Kronzucker HJ, Schjoerring JK, Erner Y, Kirk GJD, Siddiqi MY, Glass ADM. 1998. Dynamic interactions between root NH_4^+ influx and long-distance N translocation in rice: insights into feedback processes. *Plant & Cell Physiology* **39**: 1287–1293.
- Kronzucker HJ, Glass ADM, Siddiqi MY. 1999a. Inhibition of nitrate uptake by ammonium in barley: analysis of component fluxes. *Plant Physiology* **120**: 283–292.
- Kronzucker HJ, Siddiqi MY, Glass ADM, Kirk GJD. 1999b. Nitrate-ammonium synergism in rice: a subcellular analysis. *Plant Physiology* **119**: 1041–1046.
- Kronzucker HJ, Siddiqi MY, Glass ADM, Kirk GJD. 2000. Comparative kinetic analysis of ammonium and nitrate acquisition by tropical lowland rice: implications for rice cultivation and yield potential. *New Phytologist* **145**: 471–476.
- Kronzucker HJ, Siddiqi MY, Glass ADM, Britto DT. 2003. Root ammonium transport efficiency as a determinant in forest colonization patterns: an hypothesis. *Physiologia Plantarum* **117**: 164–170.
- Kumar S, Sterner RW, Finlay JC. 2008. Nitrogen and carbon uptake dynamics in Lake Superior. *Journal of Geophysical Research* **113**: pG04003.
- Kurimoto K, Day DA, Lambers H, Noguchi K. 2004. Effect of respiratory homeostasis on plant growth in cultivars of wheat and rice. *Plant, Cell & Environment* **27**: 853–862.
- Lee RB, Drew MC. 1986. ^{15}N studies of nitrate fluxes in barley roots. 2. Effect of plant N status on the kinetic parameters of nitrate influx. *Journal of Experimental Botany* **37**: 1768–1779.
- Lewis OAM. 1992. *Plants and nitrogen*. Cambridge, UK: Cambridge University Press.
- Li GJ, Dong GQ, Li BH, Li Q, Kronzucker HJ, Shi WM. 2012. Isolation and characterization of a novel ammonium overly sensitive mutant, *amos2*, in *Arabidopsis thaliana*. *Planta* **235**: 239–252.
- Lipson D, Näsholm T. 2001. The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. *Oecologia* **128**: 305–316.
- Lodhi MAK. 1979. Inhibition of nitrifying bacteria, nitrification and mineralization in spoil soils as related to their successional stages. *Bulletin of the Torrey Botanical Club* **106**: 284–289.
- Lodhi MAK, Killingbeck KT. 1980. Allelopathic inhibition of nitrification and nitrifying bacteria in a ponderosa pine (*Pinus ponderosa* Dougl.) community. *American Journal of Botany* **67**: 1423–1429.
- Lu YX, Li CJ, Zhang FS. 2005. Transpiration, potassium uptake and flow in tobacco as affected by nitrogen forms and nutrient levels. *Annals of Botany* **95**: 991–998.
- Ludewig U, von Wirén N, Frommer WB. 2002. Uniport of NH_4^+ by the root hair plasma membrane ammonium transporter LeAMT1;1. *Journal of Biological Chemistry* **277**: 13548–13555.
- Macduff JC, Jackson SB. 1991. Growth and preference for ammonium or nitrate uptake by barley in relation to root temperature. *Journal of Experimental Botany* **42**: 521–530.
- Magalhaes JS, Wilcox GE. 1983. Tomato growth and nutrient uptake patterns as influenced by nitrogen form and light intensity. *Journal of Plant Nutrition* **6**: 941–956.
- Magalhaes JR, Machado AT, Huber DM. 1995. Similarities in response of maize genotypes to water logging and ammonium toxicity. *Journal of Plant Nutrition* **18**: 2339–2346.
- Marschner H, Häussling M, George E. 1991. Ammonium and nitrate uptake rates and rhizosphere pH in non-mycorrhizal roots of Norway roots (*Picea abies* L. Karst.). *Trees* **5**: 14–21.
- Mayer M, Schaaf G, Mouro I, *et al.* 2006. Different transport mechanisms in plant and human AMT/Rh-type ammonium transporters. *Journal of General Physiology* **127**: 133–144.
- McClure PR, Kochian LV, Spanswick RM, Shaff JE. 1990. Evidence for cotransport of nitrate and protons in maize roots: I. Effects of nitrate on the membrane potential. *Plant Physiology* **93**: 281–289.
- McFee WW, Stone EL. 1968. Ammonium and nitrate as nitrogen sources for *Pinus radiata* and *Picea glauca*. *Soil Science Society of America Proceedings* **32**: 879–884.
- McGill B. 2005. A mechanistic model of a mutualism and its ecological and evolutionary dynamics. *Ecological Modelling* **187**: 413–425.
- Mengel K, Viro M, Hehl G. 1976. Effect of potassium on uptake and incorporation of ammonium-nitrogen of rice plants. *Plant & Soil* **44**: 547–558.
- Mihailović N, Jelić G, Filipović R, Djurdjević M, Dželetović Ž. 1992. Effect of nitrogen form on maize response to drought stress. *Plant & Soil* **144**: 191–197.
- Miller AJ, Fan X, Orsel M, Smith SJ, Wells DM. 2007. Nitrate transport and signalling. *Journal of Experimental Botany* **58**: 2297–2306.
- Miller BD, Timmer VR. 1994. Steady-state nutrition of *Pinus resinosa* seedlings: response to nutrient loading, irrigation and hardening regimes. *Tree Physiology* **14**: 1327–1338.

- Min XJ, Siddiqi MY, Guy RD, Glass ADM, Kronzucker HJ. 1998. Induction of nitrate uptake and nitrate reductase activity in trembling aspen and lodgepole pine. *Plant, Cell & Environment* **21**: 1039–1046.
- Minotti PL, Williams DC, Jackson WA. 1969. Nitrate uptake by wheat as influenced by ammonium and other cations. *Crop Science* **9**: 9–14.
- Munzarova E, Lorenzen B, Brix H, Vojtiskova L, Votrubova O. 2006. Effect of $\text{NH}_4^+/\text{NO}_3^-$ availability on nitrate reductase activity and nitrogen accumulation in wetland helophytes *Phragmites australis* and *Glyceria maxima*. *Environmental and Experimental Botany* **55**: 49–60.
- Näsholm T, Ekblad A, Nordin A, Giesler R, Högborg M, Högborg P. 1998. Boreal forest plants take up organic nitrogen. *Nature* **392**: 914–916.
- Ortiz-Ramirez C, Mora SI, Trejo J, Pantoja O. 2011. PvAMT1;1, a highly selective ammonium transporter that functions as H^+/NH_4^+ symporter. *Journal of Biological Chemistry* **286**: 31113–31122.
- Padgett PE, Allen EB. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology* **144**: 93–101.
- Padgett PE, Leonard RT. 1996. Free amino acid levels and the regulation of nitrate uptake in maize cell suspension cultures. *Journal of Experimental Botany* **47**: 871–883.
- Paulding EM, Baker AJM, Warren CR. 2010. Competition for nitrogen by three sympatric species of *Eucalyptus*. *Annals of Forest Science* **67**: 406.
- Piao HC, Liu CQ, Wang SJ. 2012. Isotopic evaluation of the role of arbuscular mycorrhizae in the nitrogen preference in Chinese fir seedlings. *Pedobiology* **55**: 167–174.
- Plassard C, Scherom P, Mousain D, Salsac L. 1991. Assimilation of mineral nitrogen and ion balance in the two partners of ectomycorrhizal symbiosis: data and hypothesis. *Experientia* **47**: 340–349.
- Raven JA, Smith FA. 1976. Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. *New Phytologist* **76**: 415–431.
- Raven JA, Wollenweber B, Handley L. 1992. A comparison of ammonium and nitrate as nitrogen sources for photolithotrophs. *New Phytologist* **121**: 19–32.
- Rawat SR, Silim SN, Kronzucker HJ, Siddiqi MY, Glass ADM. 1999. *AtAMT1* gene expression and NH_4^+ uptake in roots of *Arabidopsis thaliana*: evidence for regulation by root glutamine levels. *Plant Journal* **19**: 143–152.
- Rice EL, Pancholy SK. 1972. Inhibition of nitrification by climax ecosystems. *American Journal of Botany* **59**: 1033–1040.
- Riley D, Barber SA. 1971. Effect of ammonium fertilization on phosphorus uptake as related to root-induced pH changes at the root-soil interface. *Soil Science Society of America Proceedings* **35**: 301–306.
- Robertson GP, Vitousek PM. 1981. Nitrification potentials in primary and secondary succession. *Ecology* **62**: 376–386.
- Roosta HR, Schjoerring JK. 2008. Effects of nitrate and potassium on ammonium toxicity in cucumber plants. *Journal of Plant Nutrition* **31**: 1270–1283.
- Ruan JY, Zhang FS, Wong MH. 2000. Effect of nitrogen form and phosphorus source on the growth, nutrient uptake and rhizosphere soil property of *Camellia sinensis* L. *Plant & Soil* **223**: 63–71.
- Runge M. 1983. Physiology and ecology of nitrogen nutrition. In: Lange OL, Nobel PS, Osmond CB, Ziegler H. eds. *Physiological plant ecology*, III, Vol. 12C. New York: Springer, 163–200.
- Rygiewicz PT, Bledsoe CS. 1986. Effects of pretreatment conditions on ammonium and nitrate uptake by Douglas-fir seedlings. *Tree Physiology* **1**: 145–150.
- Salsac L, Chaillou S, Morot-Gaudry JF, Lesaint C, Jolivoe E. 1987. Nitrate and ammonium nutrition in plants. *Plant Physiology & Biochemistry* **25**: 805–812.
- Santa-Maria GE, Danna CH, Czibener C. 2000. High-affinity potassium transport in barley roots. Ammonium-sensitive and -insensitive pathways. *Plant Physiology* **123**: 297–306.
- Sasakawa H, Yamamoto Y. 1978. Comparison of uptake of nitrate and ammonium by rice seedlings: influences of light, temperature, oxygen concentration, exogenous sucrose, and metabolic inhibitors. *Plant Physiology* **62**: 665–669.
- Schortemeyer M, Stamp P, Feil B. 1997. Ammonium tolerance and carbohydrate status in maize cultivars. *Annals of Botany* **79**: 25–30.
- Schulze ED, Chapin FS, Gebauer G. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia* **100**: 406–412.
- Siddiqi MY, Glass ADM, Ruth TJ, Fernando M. 1989. Studies of the regulation of nitrate influx by barley seedlings using $^{13}\text{NO}_3^-$. *Plant Physiology* **90**: 806–813.
- Stewart GR, Pate JS, Unkovich M. 1993. Characteristics of inorganic nitrogen assimilation of plants in fire-prone Mediterranean-type vegetation. *Plant, Cell & Environment* **16**: 351–363.
- Stitt M, Müller C, Matt P, et al. 2002. Steps towards an integrated view of nitrogen metabolism. *Journal of Experimental Botany* **53**: 959–970.
- Tang Z, Fan X, Li Q, Feng H, Miller AJ, Shen Q, Xu G. 2012. Knockdown of a rice nitrate transporter alters long-distance translocation but not root influx. *Plant Physiology* **160**: 2052–2063.
- ten Hoopen F, Cuin TA, Pedas P, et al. 2010. Competition between uptake of ammonium and potassium in barley and *Arabidopsis* roots: molecular mechanisms and physiological consequences. *Journal of Experimental Botany* **61**: 2303–2315.
- Tilman D. 1982. *Resource competition and community structure*. Princeton, NJ: Princeton University Press.
- Tilman D. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* **125**: 827–852.
- Tylova-Munzarova E, Lorenzen B, Brix H, Votrubova O. 2005. The effects of NH_4^+ and NO_3^- on growth, resource allocation and nitrogen uptake kinetics of *Phragmites australis* and *Glyceria maxima*. *Aquatic Botany* **81**: 326–342.
- Vaast P, Zasoski RJ, Bledsoe CS. 1998. Effects of solution pH, temperature, nitrate/ammonium ratios, and inhibitors on ammonium and nitrate uptake by arabica coffee in short-term solution culture. *Journal of Plant Nutrition* **21**: 1551–1564.
- van Beusichem ML, Kirkby EA, Baas R. 1988. Influence of nitrate and ammonium nutrition on the uptake, assimilation, and distribution of nutrients in *Ricinus communis*. *Plant Physiology* **86**: 914–921.
- van den Driessche R, Ponsford D. 1995. Nitrogen induced potassium-deficiency in white spruce (*Picea glauca*) and Engelmann spruce (*Picea engelmannii*) seedlings. *Canadian Journal of Forest Research* **25**: 1445–1454.
- Vitousek PM, Howarth RW. 1991. Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry* **13**: 87–115.
- Vitousek PM, Melillo JM. 1979. Nitrate losses from disturbed forests: patterns and mechanisms. *Forest Science* **25**: 605–619.
- von Wirén N, Gazzarrini S, Frommer WB. 1997. Regulation of mineral nitrogen uptake in plants. *Plant & Soil* **196**: 191–199.
- Wang MY, Siddiqi MY, Ruth TJ, Glass ADM. 1993. Ammonium uptake by rice roots (1. Fluxes and subcellular distribution of $^{13}\text{NH}_4^+$). *Plant Physiology* **103**: 1249–1258.
- Warren CR. 2009. Uptake of inorganic and amino acid nitrogen from soil by *Eucalyptus regnans* and *Eucalyptus pauciflora* seedlings. *Tree Physiology* **29**: 401–409.
- Wedin DA, Tilman D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* **84**: 433–441.
- Westfall DG, Whitney DA, Brandon DM. 1990. Plant analysis as an aid in fertilizing small grains. In: Westerman RL. ed. *Soil Testing and Plant Analysis*, 3rd edn. SSSA Book Series, No. 3. Madison, WI: Soil Science Society of America, 495–519.
- Wilson JB, Spijkerman E, Huisman J. 2007. Is there really insufficient support for Tilman's R* concept? A comment on Miller et al. *American Naturalist* **169**: 700–706.
- Wu J, Ma H, Xu X, et al. 2013. Mycorrhizas alter nitrogen acquisition by the terrestrial orchid *Cymbidium goeringii*. *Annals of Botany* **111**: 1181–1187.
- Yin ZH, Raven JA. 1998. Influences of different nitrogen sources on nitrogen- and water-use efficiency, and carbon isotope discrimination in C_3 *Triticum aestivum* L. and C_4 *Zea mays* L. plants. *Planta* **205**: 574–580.
- Zerihun A, Bassirirad H. 2001. Interspecies variation in nitrogen uptake kinetic responses of temperate forest species to elevated CO_2 : potential causes and consequences. *Global Change Biology* **7**: 211–222.
- Zhu Z, Gerendás J, Bendixen R, et al. 2000. Different tolerance to light stress in NO_3^- and NH_4^+ -grown *Phaseolus vulgaris* L. *Plant Biology* **2**: 558–570.
- Zornoza P, Cusellas J, Carpena O. 1987. Response of pepper plants to $\text{NO}_3^-:\text{NH}_4^+$ ratio and light intensity. *Journal of Plant Nutrition* **10**: 773–783.
- Zornoza P, Gonzalez M, Serrano S, Carpena O. 1996. Inter-varietal differences in xylem exudate composition and growth under contrasting forms of N supply in cucumber. *Plant & Soil* **178**: 311–317.