On Inorganic N Uptake by Vascular Plants: Can ^{15}N Tracer Techniques Resolve the NH_4^+ vs. NO_3^- 'Preference' Conundrum?

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Abstract

The relative uptake by plants of the two ionic N forms, NH_4^+ and NO_3^- , has been the subject of much interest during the past 50 years, resulting in a considerable scientific literature. The general idea is that plants have choice, resulting in *preference* for either one mineral N form or the other. Unfortunately, there is no specific definition of *preference* or agreement on how it should be measured. In this review, we critically examine the alternative techniques that have been used to measure the relative uptake of NH_4^+ and NO_3^- by plants, including those based on unlabelled sources, ^{15}N -enriched mineral N forms and variations in the ^{15}N natural abundance of mineral N sources. The main difficulty with using unlabelled N is the antecedent N in plant tissue prior to the imposition of treatments. While ^{15}N -enrichment overcomes this obstacle, it is nevertheless difficult to separate uptake as $^{15}\text{NH}_4^+$, uptake as $^{15}\text{NO}_3^-$, and uptake as $^{15}\text{NO}_3^-$ derived from the nitrification of $^{15}\text{NH}_4^+$. With ^{15}N natural abundance, isotopic fractionation during plant uptake complicates the interpretation of data. There is increasing evidence that plants exhibit *flexibility* or *plasticity* with respect to the use of mineral N forms rather than *preference*.

Highlights

- The concept of plant preference for ammonium or nitrate forms of mineral N is examined
- Experiments using ^{15}N enrichment and ^{15}N natural abundance are reviewed
- The direct uptake of $^{15}\text{NO}_3^-$ is confounded with the uptake of $^{15}\text{NO}_3^-$ derived from nitrified $^{15}\text{NH}_4^+$
- Plants exhibit plasticity rather than preference in the acquisition of ammonium and nitrate

RUNNING TITLE Ammonium or nitrate preference

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/ejss.13069](https://doi.org/10.1111/ejss.13069)

KEYWORDS Ammonium, Apportionment, Nitrate, ^{15}N , $\delta^{15}\text{N}$, Preference

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1 INTRODUCTION

The idea that vascular plants have *preference* with respect to the uptake of the two sources of available mineral N in the soil, NH_4^+ and NO_3^- , has been expressed in the titles and contents of many scientific papers published since the 1960s (e.g. Blair et al., 1970; Boudsocq et al., 2012; Cox & Reisenauer, 1973; Falkengren-Grerup, 1995; Kirkby, 1967; Olsson & Falkengren-Grerup, 2000; Wang & Macko, 2011). *Preference* implies that plants can actively discriminate between these two inorganic N sources, with benefit accrued from the uptake of either one or the other of the ionic N forms. The concept of *preference* seems to have gained general acceptance in the literature, without the benefit of a clear definition of its meaning or a review of the methodologies on which *preference* has been evaluated.

An equally valid concept is that the two mineral N sources are complementary rather than in competition. For example, Ali et al. (2001) found that a mixture of NH_4^+ and NO_3^- was necessary to obtain maximum N uptake of barley in solution culture compared with either N source alone. Others have proposed that *preference* is not a fixed attribute of plants, but they can exhibit *plasticity* in N resource use (Andersen & Turner 2013; Andersen et al., 2017; Ashton et al., 2010; Song et al., 2015). Yet others have proposed an inhibitory mechanism whereby the presence of NH_4^+ inhibits the uptake of NO_3^- (Kronzucker et al., 1999; Lee & Drew, 1989). Despite extensive research conducted over past decades, the concept of *preference* remains an enigma, a terminology in common usage, yet without definition or

clarity. Nevertheless, interest persists as evidenced by recent literature (e.g. Boschiero et al., 2018; Cui et al., 2017; Iqbal et al., 2020; Liu et al., 2019; Zhang et al., 2019).

At first glance, the solution to this question may appear to be straightforward. For example, plants can be grown in solution culture where either NH_4^+ or NO_3^- is individually supplied, or supplied together in various molar ratios, and some measure of relative plant performance is obtained (e.g. de Graaf et al., 1998; Griffith & Streeter, 1994). This type of experiment suffers from several limitations, including the artificial nature of hydroponics, and that in biologically-active soil in which plants normally grow, NH_4^+ is often rapidly converted to NO_3^- by soil nitrifying bacteria, archaea and fungi, the nitrification rate depending on environmental and edaphic factors. The concentrations of soil NO_3^- and NH_4^+ are therefore in temporal flux, while demand for N similarly varies with plant ontogeny. Given the biological coupling between NH_4^+ and NO_3^- , and the dynamic nature of the supply and demand of plant-available N, the quantitative apportionment of the sources of plant-derived soil inorganic-N becomes a complex issue, which cannot be easily resolved. It is nevertheless a relevant issue, given that in some countries nitrification inhibitors are combined with N fertilizers in an attempt to increase fertilizer use efficiency in agriculture by reducing soil concentrations of NO_3^- in favour of NH_4^+ (Qiao et al., 2015).

Of the many papers written on the subject of *preference*, some have employed unlabelled substrates while others have utilized ^{15}N tracer in an attempt to differentiate N sources. Two approaches have been pursued, the use of ^{15}N -enriched fertilizers in agroecosystems, and the use of natural variations in the relative ^{15}N abundance ($\delta^{15}\text{N}$) of mineral N in natural ecosystems. The objectives of this review are three-fold: (i) to critically examine the concept of *preference*; (ii) to outline the various experimental approaches, including both unlabelled and ^{15}N -labelled studies; and (iii) to highlight the efficacy or deficiencies of approaches taken to quantify the abstract idea of intrinsic plant *preference*.

The physiology of NH_4^+ and NO_3^- uptake by plants is briefly addressed, but the biochemistry N assimilation is beyond the scope of the present review. We briefly consider the uptake of organic N by plants, but only in relation to the measurement of inorganic N uptake.

2 PHYSIOLOGY OF AMMONIUM AND NITRATE UPTAKE BY PLANT ROOTS

As NH_4^+ and NO_3^- comprise about 80% of the total cations and anions taken up by plants, the form of mineral N supply has a strong impact on the uptake of other ionic species and on cellular and rhizosphere pH regulation (Marschner, 1995). Several authors have reviewed the extensive literature on the effects of mineral N source on plant physiology (Forde & Clarkson, 1999; Haynes & Goh, 1978; Li et al., 2013; Marschner, 1995). Marschner (1995) pointed out that many studies in solution culture have shown that plants grow better with a mixture of NH_4^+ and NO_3^- than with either form alone, but warned that results of single ion studies should be treated with caution, since the N concentrations used were sometimes far in excess of what would normally be found in the soil solution.

The physiological effects generally relate to competitive uptake between NH_4^+ and other essential plant cations (Ca^{2+} , Mg^{2+} , K^+) or between NO_3^- and other essential plant anions (H_2PO_4^- , HPO_4^{2-} , SO_4^{2-}), or to a change in rhizosphere pH due to efflux of protons (H^+) from roots when NH_4^+ is taken up or efflux of hydroxyl (OH^-) when NO_3^- is absorbed by roots. The energy costs associated with plant uptake of NH_4^+ vs. NO_3^- are different, and were reviewed by Raven (1985) and Andrews et al. (2013).

The pH effect can be important with respect to the ionic form of P or Al in the soil solution. Many authors have found that mineral N nutrition was of critical importance with respect to the tolerance of crop cultivars to Al toxicity in solution culture. For example, Taylor and Foy (1985) demonstrated a significant correlation between Al tolerance of 21 wheat cultivars and plant-induced pH of the nutrient solution, with the solubility of Al increasing with a pH change from 5.0 to 4.0. However, Klotz & Horst (1988) found that NH_4^+ supply increased the tolerance of sorghum to Al compared to NO_3^- supply when grown at constant solution pH. Similarly, Zhao et al. (2009) found that NH_4^+ alleviated Al toxicity in two rice cultivars. An increased NH_4^+ uptake would be expected to decrease solution pH and increase crop susceptibility to Al toxicity. Therefore, more than one mechanism of Al tolerance is indicated. Ma (2000) suggested that organic acids play a role in Al detoxification in both external and internal plant environments. A biotic-abiotic interaction with respect to Al tolerance has been proposed between the occurrence of mycorrhizae, the source of mineral N and P availability (Cumming & Weinstein, 1990). An in-depth review of plant-soil-microbe interactions as they affect N cycling in the plant rhizosphere was recently provided by Moreau et al. (2019).

3 HYDROPONIC STUDIES

The investigation of plant nutrition using hydroponics is a useful experimental technique, provided recognition is given to the limitations of such a system, compared with those existing in arable cropping. It is often difficult to translate results to the conditions pertaining in soil-cultured plants in pots or the field. Nevertheless, it is a logical starting point in the evaluation of *preference*.

3.1 Uptake of Unlabelled NH_4^+ or NO_3^-

The yields and N uptakes of a representative selection of cereals, trees, grasses and shrubs grown in hydroponic systems involving static / flowing solution or sand / solution culture when supplied with either NH_4^+ or NO_3^- mineral N forms are shown in Table 1. Static or flowing solution hydroponics present some difficulties as plants must be raised externally in a solid medium before transplanting to the hydroponic system, thus possessing an antecedent dry matter (DM) yield and N uptake, which could potentially mask the unlabelled NH_4^+ or NO_3^- treatment response. Perennials generally have a longer pre-treatment development period compared to annuals. Sand / solution culture is superior in this respect as plants can be raised from seed, thus avoiding transplanting and enabling treatments to be imposed at an earlier plant age.

Dry matter is a poor response parameter as it integrates many environmental and edaphic factors in addition to the treatments employed. While N uptake is potentially a better response parameter than DM it still has an antecedent N uptake background. In an attempt to overcome this impediment, several authors have estimated N uptake indirectly by measuring N depletion in the nutrient solution (e.g. Frith & Nichols, 1975; Malagoli et al., 2000; Marschner et al., 1991; Schortemeyer et al., 1993), which is based on the assumption that plant uptake is the only process that removes N from solution. In addition, N concentration in solution is notoriously difficult to maintain at a constant level due to plant uptake and evaporation (e.g. Schjørring, 1986). Care must also be exercised that concentrations of N are equal in NH_4^+ or NO_3^- solutions when mono-ionic and di-ionic N compounds are employed (e.g. KNO_3 and $(\text{NH}_4)_2\text{SO}_4$), as equal mM concentrations of these salts are unequal with respect to N concentration (e.g. Griffith & Streeter,

1994; Ta & Ohira, 1982). Generally, equal or nearly equal concentrations of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ have been used (Table 1).

Plant yields of perennials within the same study were species-dependent, showing either no difference or higher yields with NH_4^+ compared with NO_3^- (Kalcsits et al., 2015; Norisada & Kojima, 2005), or were inconsistent being either equal or higher for either NH_4^+ or NO_3^- for different tree species (Adams & Attiwill, 1982). Annual cereals and grasses were similarly inconsistent with respect to differences in DM between NH_4^+ and NO_3^- treatments (Table 1).

Therefore, variable results were obtained from a comparison of the NH_4^+ and NO_3^- nutrition of a range of species taken from representative examples of the published literature. Certainly, an equivocal conclusion could not be drawn from these studies regarding the so-called plant ‘preference’ for NH_4^+ or NO_3^- , because of the possibility that added NH_4^+ was nitrified and taken up as NO_3^- . In an attempt to retard nitrification, Townsend (1967) added an inhibitor (nitrapyrin) to the nutrient solution. In a meta-analysis of the impacts of external NH_4^+ vs. NO_3^- addition on plant growth in terrestrial ecosystems, Yan et al. (2019) found that the mineral N form had a differential effect on above- and below-ground biomass, with NH_4^+ being superior with respect to total plant DM.

3.2 Uptake of $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$

N uptake response to treatment can be determined independently of antecedent unlabelled N uptake by adding $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$. Plant yields and ^{15}N uptake can also be determined for treatments involving addition of ^{15}N -enriched NH_4^+ or NO_3^- together with the counterpart unlabelled form (i.e. of $^{15}\text{NH}_4^+ + ^{14}\text{NO}_3^-$ and $^{14}\text{NH}_4^+ + ^{15}\text{NO}_3^-$ (Arkoun et al., 2012; Morita et al., 1998). The yields and ^{15}N uptakes of cereals, grasses, oilseeds, vegetables and shrubs grown in hydroponic systems involving static solution or sand / solution culture when supplied with either $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ mineral N forms are shown in Table 2.

Short exposure periods (8 to 48 h) to labelled mineral N were used in several studies (Table 2), presumably to limit the period during which nitrification might occur, while in others the exposure ranged from 9 to 15 d. Stock & Lewis (1984) checked the leachate of the sand culture for $^{15}\text{NO}_3^-$ in the $^{15}\text{NH}_4^+$ treatment which would indicate nitrification. There was no consistency in the uptake of ^{15}N between $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ treatments, with barley, blueberry, tea and

seedlings of lowland rice showing significantly greater uptake of $^{15}\text{NH}_4^+$, while for the grass *Calamagrostis*, tomato, canola and lowland rice at tillering, the uptake of ^{15}N was greater for NO_3^- cf. NH_4^+ . Unlike results obtained for lowland rice (Lin et al., 2005), the relative uptake of the two mineral forms of N did not change during the growth of tomato, irrespective of whether the isotope was applied at the seedling, flowering, early fruiting or pre-harvest stages (Tan et al., 2000). Koppisch et al. (1993) commented that their results did not support the initial hypothesis that grasses may 'prefer' NO_3^- cf. NH_4^+ . Indeed, none of the results support the idea of plant 'preference' for NO_3^- vs. NH_4^+ . They merely illustrate divergent relative uptake of NO_3^- and NH_4^+ under the given experimental conditions. Labelling of the mineral N substrates with ^{15}N , while overcoming the problem of antecedent plant N, did not obviate the possibility that $^{15}\text{NH}_4^+$ was nitrified in non-sterile sand or static solution culture and then taken up as $^{15}\text{NO}_3^-$.

4 SOIL-CULTURED PLANTS

4.1 Uptake of $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$

Many short-term (2.5 to 48 h) comparisons of $^{15}\text{NH}_4^+$ vs $^{15}\text{NO}_3^-$ uptake have been conducted in natural ecosystems to compare the uptake of mineral N vs. organic N in the form of doubly labelled ($^{15}\text{N}^{13}\text{C}$) glycine or L-alanine (Table 3). Occasionally, longer exposure times were used (Wittich et al., 2015). These experiments involved low addition rates to plants of highly-enriched (> 98 atom %) labelled substrates and short exposure times, in order to permit estimation of the direct plant uptake of the doubly-labelled amino acid, because of its rapid biological transformation in soil.

Low addition rates and short exposure times led to insignificant uptake of isotope, which masked differences in % recovery between $^{15}\text{NH}_4^+$, $^{15}\text{NO}_3^-$ or ^{15}N -glycine treatments within species (Andersen et al., 2017, Table 3). The % recoveries of these three N sources within each of six species were not significantly different (Wittich et al., 2015). Recovery of $^{15}\text{NO}_3^-$ by barley was consistently greater than recovery of $^{15}\text{NH}_4^+$, irrespective of growth stage, and more $^{15}\text{NO}_3^-$ was recovered by oats at tillering compared with $^{15}\text{NH}_4^+$, but differences in recovery by oats between the two N forms were not significant at heading or milk stages (Cui et al., 2017).

N uptake or rates of N uptake were measured in some studies (Table 3). N uptake (mg g^{-1}) of $^{15}\text{NH}_4^+$, $^{15}\text{NO}_3^-$ or ^{15}N -glycine of two pasture species were inconsistent between shoots and roots (Näsholm et al., 2000). The rates of N uptake ($\mu\text{g g}^{-1} \text{h}^{-1}$) of $^{15}\text{NO}_3^-$ were greater than $^{15}\text{NH}_4^+$ or glycine, while the rate of uptake of $^{15}\text{NH}_4^+$ was either equal to or less than that of glycine within four species (Ashton et al., 2010). Among six species studied, the rate of N uptake of $^{15}\text{NH}_4^+$ was either less than, equal to or greater than uptake of $^{15}\text{NO}_3^-$ or glycine (Miller & Bowman, 2002). Thus, the relative uptake of $^{15}\text{NH}_4^+$, $^{15}\text{NO}_3^-$ or ^{15}N -labelled amino acid, whether expressed as an amount, rate or quantitative recovery, depended on several factors, including plant species, plant organ and growth stage.

As noted in the previous Section, plant uptake of $^{15}\text{NH}_4^+$ from hydroponic culture does not indicate whether it was taken up directly as $^{15}\text{NH}_4^+$ or indirectly as $^{15}\text{NO}_3^-$ derived from the nitrification of $^{15}\text{NH}_4^+$. The same principle applies to soil-cultured plants, with nitrification rates and microbial immobilization being potentially greater compared to plants grown in hydroponics. However, the short isotopic exposure times should constrain nitrification, and may give a better estimate of direct uptake. Nevertheless, there is no guarantee that uptake of labelled N sources in either hydroponic- or soil-cultured plants would provide an unequivocal estimate of direct and indirect uptake of mineral N forms. Therefore, a new conceptual framework is required to enable pathways to be quantified, if the ‘preference’ conundrum is to be resolved. Such an innovative approach was proposed by Barraclough and co-workers, as outlined in the following Section.

4.2 Uptake of (^{15}N -labelled + Unlabelled) NH_4^+ and NO_3^-

This approach differs from earlier studies on the plant uptake of $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ in that it estimates uptake from both ^{15}N -labelled + unlabelled NH_4^+ and NO_3^- pools (e.g. fertilizer + soil), not just the labelled fertilizer pools. It takes into account the nitrification rate (n) which affects the N concentration and isotopic composition of the NO_3^- pool, and the mineralization rate (m) which affects the N concentration and isotopic composition of the NH_4^+ pool, and it therefore represents a conceptual advance over previous techniques. The theory was developed and tested over several years by Barraclough and co-workers (Barraclough, 1988, 1991, 1995; Barraclough et al., 1985; Barraclough & Smith, 1987; Geens et al., 1991).

Estimation of the uptake of ^{15}N -labelled + unlabelled NH_4^+ or NO_3^- by plants is based on the exponential decline in the ^{15}N enrichment of the mineral N pool as shown for nitrate in well-aerated soil (Chalk et al., 1996) or ammonium in flooded soil (Pareek et al., 1990) according to Eq. 1.

$$E_t = E_0 e^{-kt} \quad (1)$$

where E_t and E_0 are the ^{15}N enrichments (atom % excess) of the $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ pools at times t and zero, respectively, k is the decline or first-order rate constant (d^{-1}) and t is time (d).

A plant growing in soil labelled with $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ would assimilate available N over the time interval t_0 to t_1 with an ^{15}N enrichment of E^* equivalent to the integral of E_t (Eqs. 2 and 3).

$$E^* = \int_{t_0}^{t_1} \frac{E_t dt}{t_1 - t_0} \quad (2)$$

$$= \frac{E_{t_0} (e^{-kt_0} - e^{-kt_1})}{k (t_1 - t_0)} \quad (3)$$

An alternative expression for the solution of E^* is given by Eq. 4 (Pareek et al., 1990).

$$E^* = \frac{E_{t_1} - E_{t_0}}{\ln \left(\frac{E_{t_1}}{E_{t_0}} \right)} \quad (4)$$

The technique is based on recognition of three pools of mineral N (Figure 1); direct uptake of $^{15}\text{NH}_4^+$ (U_1), direct uptake of $^{15}\text{NO}_3^-$ (U_3), and uptake of $^{15}\text{NO}_3^-*$ derived from the nitrification of $^{15}\text{NH}_4^+$ (U_2). It involves paired plots, one labelled with $^{15}\text{NH}_4\text{NO}_3$ and the other with $\text{NH}_4^{15}\text{NO}_3$. The procedure incorporates the estimation of gross rates of mineralization (m) and gross rates of nitrification (n) using a zero-order model first developed by Kirkham and Bartholomew (1955), and the so-called concept of “mean pool abundance” or E^* . Since E^* is based on ^{15}N -enrichment (atom % excess) rather than ^{15}N -abundance (atom %) it would be more accurately described as “integrated ^{15}N -enrichment” of the soil $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ pools over a time interval Δt .

N uptake by the plant and its ^{15}N enrichment are measured at times t_0 and t_1 . The size and ^{15}N enrichments of the soil NH_4^+ and NO_3^- pools are also measured at times t_0 and t_1 . Two calculation procedures are described by Barraclough (1991). Procedure A involves the $\text{NH}_4^{15}\text{NO}_3$ treatment, and an estimate of $U_2 + U_3$ (Figure 1) is obtained, while Procedure B

involves the $^{15}\text{NH}_4\text{NO}_3$ treatment, and an estimate of U_1 (Figure 1) is obtained. The equations (S1 to S11) used to arrive at these estimates are given in Supporting Information S1.

Several assumptions are used in the calculation of the relative uptakes of NH_4^+ and NO_3^- . (i) complete mixing of the added label and the equivalent unlabelled mineral N pool. i.e. uniform labelling. Barraclough (1991) predicted that this would not be a problem in shallow-rooted grasslands, but it could be under arable cropping where mineral N is exploited to a greater soil depth not equilibrated with the isotope (ii) loss of $^{15}\text{NO}_3^-$ by a process other than plant uptake (e.g. denitrification), thus interfering with the estimation of n . The same potential error applies to the loss of $^{15}\text{NH}_4^+$ via volatilization or loss of NO_x during the estimation of m . (iii) the models used for the estimation of m and n conform to zero-order kinetics. i.e. there is no remineralization of biologically immobilized ^{15}N . In order to avoid this error, short sampling intervals (e.g. several days up to 1 week) following addition of isotope are recommended. Barraclough (1991) found that estimates of U_n using procedures A and B were inconsistent, due to unequal values of U in each treatment, thus revealing a weakness of the paired plot approach.

Few studies have been conducted using the techniques described by Barraclough and co-authors, perhaps because of doubts about the validity of the assumptions underpinning the methodology. Barraclough (1988) reported the results of a grassland experiment conducted in 1986 involving addition of 90 kg N ha^{-1} as NH_4NO_3 to paired plots. Over a period of 20 d it was estimated that 61% of plant N was taken up as NH_4^+ . Crawford and Chalk (1993) found that the uptake of NH_4^+ by wheat (U_1) during 0 to 20 d in a clay soil with high biological activity was less, both in absolute amounts and relative proportions, than the uptake of NO_3^- ($U_2 + U_3$) in paired pots, but when the nitrification inhibitor nitrapyrin was added with the fertilizer, uptake of NH_4^+ increased and NO_3^- decreased, so that the relative proportions taken up by wheat were approximately equal. On the other hand, application of nitrapyrin to a pasture soil had little effect on the proportional uptake of NH_4^+ and NO_3^- by perennial ryegrass, because the soil had a low nitrification capacity (Geens et al., 1991). However, the proportional uptake as NH_4^+ increased in a linear fashion when the ratio of NH_4^+ to NO_3^- increased in the 90 kg N ha^{-1} N fertilizer treatment (Barraclough, 1995; Geens et al., 1991).

While the concepts described by Barraclough and co-workers represented an advance over previous studies involving uptake of $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$ (Sections 3.2 and 4.1) in that the uptake of both labelled and unlabelled mineral N forms were accounted for, compared with only labelled N, the separation of the two components of NO_3^- uptake (U_2 and U_3), as depicted in Figure 1, was generally not achieved. However, Barraclough and Smith (1987) claimed to have separated U_2 and U_3 by a combination of mathematical analysis and computer simulation.

It is also possible to estimate U_2 from the data of Crawford and Chalk (1993) by using the difference in the uptake of N in $\pm$ inhibitor treatments. For example, $U_2 = U_{n(-\text{inhibitor})} - U_{n(+\text{inhibitor})} = 50 - 31 = 19 \text{ mg N kg}^{-1} \text{ soil}$. The average N uptake of $\pm$ inhibitor treatments was $61 + 68 / 2 = 64.9$. Therefore, U_2 expressed as a percentage of average N uptake $= (19 / 64.9) \times 100 = 29\%$, represented a significant proportion of the total N uptake by wheat. In contrast, Barraclough and Smith (1987) estimated that U_2 was an insignificant component of N uptake over 39 days by ryegrass fertilized with 250 kg N ha^{-1} (0.7 to 2.0 kg N ha^{-1}) compared with NH_4^+ ($U_1 = 56$ to 67 kg N ha^{-1}) and NO_3^- ($U_3 = 25 \text{ kg N ha}^{-1}$) because of the low nitrification rate under pasture.

5 ^{15}N NATURAL ABUNDANCE TECHNIQUES

Strong isotopic fractionation occurs during the biological oxidation of NH_4^+ to NO_3^- in soil (Högberg, 1997; Robinson, 2001), resulting in the natural ^{15}N enrichment of the substrate relative to the product during nitrification. Thus, in the absence of other significant fractionation processes (e.g. denitrification) it is tempting to assume that the $\delta^{15}\text{N}$ value of plant foliage may reflect the uptake of either NH_4^+ or NO_3^- from the soil. However, many additional factors affect the $\delta^{15}\text{N}$ signature of the foliage of non-leguminous plants, including depth of acquisition within the soil profile, mycorrhizal dependence, absorption of depositional N by foliage (Vallano and Sparks, 2013), in addition to isotopic fractionation during the assimilation of acquired N. Within an ecosystem, all of the above factors can operate to determine the integrated value of $\delta^{15}\text{N}_{\text{foliage}}$ (Craine et al., 2015). Among ecosystems, variation in plant $\delta^{15}\text{N}$ can be affected by the same factors, but the form of mineral N is unlikely to drive variation in stand-level signatures when the majority of available N is acquired by plants (Craine et al., 2015).

5.1 Relationships among measurements of plant $\delta^{15}\text{N}_{\text{foliar}}$, enrichment factors, plant N concentration and soil N parameters

A variety of studies has been conducted within and between ecosystems globally to investigate the strength of relationships among plant and soil indices of potential N availability (Table 4). Significant positive linear correlations were found between $\delta^{15}\text{N}_{\text{foliage}}$ and enrichment factors, net mineralization rate, net N nitrification rate and $\delta^{15}\text{N}_{\text{soil}}$, which were themselves significantly correlated (Table 4), illustrating the strong influence that soil-derived N variables have on the relative ^{15}N abundance of foliar N. However, although the significant correlations involving net nitrification rate reinforce the role that mineral N form has on $\delta^{15}\text{N}_{\text{foliage}}$ signatures, they do not by themselves provide evidence that enables identification of the form of mineral N uptake, but can assist the interpretation when other evidence exists (e.g. Tateno et al., 2005).

On the basis that foliar $\delta^{15}\text{N}$ values were closer to soil NH_4^+ than soil NO_3^- values, Brearley (2013) suggested that trees in Jamaican forests may have a preference for NH_4^+ . Similarly, Schimann et al. (2008) surmised that *Dicorynia guianensis* preferentially used NH_4^+ on the basis of similar soil $\delta^{15}\text{NH}_4^+$ and leaf $\delta^{15}\text{N}$ ($\sim 3.5\text{‰}$) values, whereas similarity between leaf $\delta^{15}\text{N}$ of *Eperua falcata* and root $\delta^{15}\text{NO}_3^-$ (0.2 and -2.0‰ , respectively) suggested preferential use of NO_3^- in these tree species in a tropical rainforest in French Guiana. Given the many factors affecting $\delta^{15}\text{N}$ signatures of plant foliage, it is doubtful if simple comparisons such as those conducted by Brearley (2013) and Schimann et al. (2008) will provide reliable indicators of mineral N source. Perhaps the most important factors that need to be considered are pool size and the flux of N through each mineral N pool.

5.2 Estimating apportionment of plant N sources using end-member mixing models

Two-end-member mixing models are used to estimate proportions of plant N derived from mineral N forms, NH_4^+ and NO_3^- . Three-end-member mixing models are used to estimate the proportions of plant N derived from mineral N forms and dissolved organic N (DON). These models are based on Eqs. 5 and 6, respectively.

$$\delta^{15}\text{N}_{\text{foliage}} = \delta^{15}\text{NH}_4^+ \times f_{\text{NH}_4^+} + \delta^{15}\text{NO}_3^- \times f_{\text{NO}_3^-} \quad (5)$$

$$\delta^{15}\text{N}_{\text{foliage}} = \delta^{15}\text{NH}_4^+ \times f_{\text{NH}_4^+} + \delta^{15}\text{NO}_3^- \times f_{\text{NO}_3^-} + \delta^{15}\text{N}_{\text{DON}} \times f_{\text{DON}} \quad (6)$$

where $\sum f = 1$.

Several models have been used to estimate the proportional contribution of N sources to plant nutrition, including two-end- (IsoError) and three-end- (IsoSource and SIAR) members (Table 5). The IsoSource model version 1.3 is a Microsoft Visual Basic™ software package based on the original papers of Phillips & Gregg (2003) and Phillips et al. (2005). The model is used when the number of sources is too large to permit a unique solution ($> \text{number of isotope systems} + 1$). Several authors (Table 5) have used this model to apportion three N sources (Eq. 2). The apportionment of three N sources was also estimated by Zhu et al. (2019) using a Bayesian-isotope mixing model in R (SIAR) as described by Inger et al. in a Guide for Ecologists: https://maths.ucd.ie/~parnell_a/media/SIAR_For_Ecologists.pdf The IsoError model version 1.04, based on the original paper of Phillips & Gregg (2001), is a Microsoft Excel 2000™ spreadsheet that calculates estimates and confidence intervals of the proportional contributions of two mineral N sources to a mixture (Eq. 1). It ignores the potential contribution of DON to the N nutrition of the plant.

The proportional contribution of N source to plant nutrition is usually estimated on the plant leaves, which are the only plant parts that are easily harvested in trees. Errors will occur because atmospheric deposition also contributes to leaf $\delta^{15}\text{N}$ values, and isotopic fractionation during N assimilation from root uptake will also affect the leaf $\delta^{15}\text{N}$ signature. Attempts have been made to correct for isotopic fractionation depending on whether the plant is mycorrhizal or non-mycorrhizal as well as the type of mycorrhizae (Zhang et al., 2018; Zhu et al., 2019; Table 5). Takebayashi et al. (2010) and Yang et al. (2018) did not attempt to correct for fractionation. Zhang et al. (2018) found that the calculations of the proportional dependence of plants on N source were relatively insensitive to the uncertainty in the variation of the isotope fractionation effect.

Takebayashi et al (2010) and Zhang et al. (2018) used both two- and three-end-member models to estimate proportionality in N uptake form (Table 5). Although the absolute proportional values will necessarily differ between the two models unless αDON is zero, Zhang et al. (2018) found that the ratio of the proportions of $\text{NH}_4^+ : \text{NO}_3^-$ was similar in each treatment (variation from 0.5 to 1.3). Although the agreement found by Takebayashi was less precise, the

same general trend in the ratios was observed between treatments. Plant species had a marked effect on the proportions of NH_4^+ and NO_3^- estimated by the IsoError (Mayor et al., 2014) and SIAR (Zhu et al., 2019) models. In three of four species NO_3^- contributed the major proportion to foliar N (Zhu et al., 2019), while NH_4^+ or NO_3^- were the major contributors in two of four species (Mayor et al., 2014). Houlton et al. (2007) found that DON contributed only a small proportion ($\leq 5\%$) to the mean values of four plant species across a range of mean annual precipitation from 2200 to 5050 mm (Table 5). The tropical species with diverse growth strategies (trees and ferns) relied on a common pool of inorganic N, rather than specializing on different N pools. The species changed their dominant N source abruptly and in unison from NO_3^- to NH_4^+ in response to increasing precipitation (Houlton et al., 2007; Table 5). This threshold response indicates a coherent strategy among species to exploit the most available forms of N in soil.

Uncertainty associated with mixing models is often substantial (Moore & Semmens, 2008). Although these authors introduced a modification to explicitly account for uncertainty associated with multiple sources, fractionation and isotope signatures, it was criticised by Jackson et al. (2009). In response to this criticism, Semmens et al. (2009) fine-tuned their original modification. High standard errors of mean values have been observed in mixing model estimates of the proportional contributions of N sources to foliar $\delta^{15}\text{N}$ signatures, while individual proportions can sometimes exceed 100% (Zhang et al., 2018). Therefore, although mixing models provide estimates of the proportional contributions of soil N sources to plant nutrition, they are subject to the accuracy of the input data and have so far not accounted for foliar absorption of atmospheric N moieties.

6 CONCLUSIONS

Microorganisms compete with plants for mineral N. The ^{15}N -enrichment model of Barraclough and co-authors has shown that the soil nitrification rate affects ammonium vs. nitrate uptake by plants. In situations where nitrification is extremely low or absent, plants have little or no choice with respect to the uptake of the available inorganic forms of soil N. For example, in the flooded rice paddy, the plant uses NH_4^+ almost exclusively, because apart for a thin aerobic surface layer, the bulk soil is anaerobic and there is little or no autotrophic nitrification.

Certain plants have been identified as preferring NH_4^+ or NO_3^- . The current promotion of nitrification inhibitors to increase N fertilizer use efficiency implies that those plants that ostensibly ‘prefer’ NO_3^- , would be disadvantaged compared with those plants that ‘prefer’ NH_4^+ . Instead of causing negative effects, however, there is evidence across a range of crops and edaphic conditions that nitrification inhibitors can improve yield or N uptake by reducing the potential for N losses via NO_3^- leaching or denitrification. Thus, factors other than *preference* are presumably more important in the acquisition of mineral N by plants.

Evidence continues to accumulate that plants show *flexibility* or *plasticity* rather than *preference* in mineral N uptake. Plants can also acquire N through alternative sources. In harsh environments, plants roots can absorb low molecular weight organic N compounds, and in polluted environments plants can absorb atmospheric N through the foliage. Based on the evidence that the nitrification rate is the dominant factor affecting the form of mineral N taken up by soil-cultured plants, we suggest that the concept of *preference* is an anachronism, and we therefore discourage the use of the terminology.

CONFLICT OF INTEREST The authors declare no conflict of interest.

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FIGURE 1 Schematic of the uptake of N by plants as NH₄⁺ (U₁), as NO₃^{-*} derived from the nitrification of NH₄⁺ (U₂) and as NO₃⁻ (U₃)

TABLE 1 Dry matter (DM) yield and N uptake of non-leguminous plants in hydroponic systems supplied with either unlabelled NH_4^+ or NO_3^-

Reference (chronological)	Culture ^a	Species ^b	N source	N concentration (mg l ⁻¹) ^c		Plant age (d) ^d	DM yield (g) ^e	N uptake (mg) ^e
				NH_4^+	NO_3^-			
Kirkby (1967)	SS	<i>C. album</i>	NH_4^+	70	0	6 leaf - +28	9.9	415
			NO_3^-	0	70		29.6	639
Townsend (1967)	Sand / solution	Highbush blueberry	NH_4^+	(21)	0	300-379	43a	
			NO_3^-	0	(21)		25b	
Blair et al. (1970)	FS	Maize	NH_4^+	56	0	7-14	2.84a	3a
			NO_3^-	0	56		3.09a	17b
Cox & Reisenauer (1973)	FS	Wheat	NH_4^+	1.4	0	6-19	0.22a	12a
			NO_3^-	0	1.4		0.32b	11a
Adams & Attiwill (1982)	Sand / solution	<i>Eucalyptus regnans</i>	NH_4^+	(42)	0	28-98	6.4a	
			NO_3^-	0	(42)		8.1a	
		<i>Eucalyptus obliqua</i>	NH_4^+	(42)	0		20.9a	
			NO_3^-	0	(42)		15.7b	
		<i>Pinus radiata</i>	NH_4^+	(42)	0		19.4a	
			NO_3^-	0	(42)		26.4b	
Griffith & Streeter (1994)	Sand / solution	Italian ryegrass	NH_4^+	280	0	5-54	6.9a	
			NO_3^-	0	140		5.2b	
Norisada & Kojima (2005)	Sand / solution	<i>Anisoptera costata</i>	NH_4^+	56	0	400-472	10.4a	
			NO_3^-	0	51		10.0a	
		<i>Hopea odorata</i>	NH_4^+	56	0		3.1a	
			NO_3^-	0	51		2.2b	
		<i>Shorea roxburghii</i>	NH_4^+	56	0		3.0a	
			NO_3^-	0	51		1.9b	
		<i>Dipterocarpus obtusifolius</i>	NH_4^+	56	0		5.9a	
			NO_3^-	0	51		4.0b	
		<i>Shorea faguetiana</i>	NH_4^+	56	0		5.3a	
			NO_3^-	0	51		3.7a	
Kalcsits et al. (2015)	Sand / solution	<i>Populus tremuloides</i>	NH_4^+	2.8	0	Seed - 90	0.42a	
			NO_3^-	0	2.8		0.58b	
		<i>Pinus contorta</i>	NH_4^+	2.8	0		0.20a	
			NO_3^-	0	2.8		0.22a	
		<i>Picea glauca</i>	NH_4^+	2.8	0		0.06a	
			NO_3^-	0	2.8		0.08a	

^a SS, Static solution; FS, flowing solution

^b *C*, *Chenopodium*; Highbush blueberry, *Vaccinium corymbosum*; Maize, *Zea mays*; Wheat, *Triticum aestivum*; Italian ryegrass, *Lolium multiflorum*

^c Data in parentheses () are ppm

^d Age interval between start of NH_4^+ and NO_3^- treatments and harvest

^e Data within a column and species followed by different lower-case letters are significantly different ($P \leq 0.05$)

TABLE 2 Dry matter (DM) yield, ^{15}N uptake of non-leguminous plants in hydroponic systems supplied with either $^{15}\text{NH}_4^+$ or $^{15}\text{NO}_3^-$

Reference (chronological)	Culture ^a	Species ^b	^{15}N source	N concentration (mg l ⁻¹) ^c		Plant age (d) ^d	DM yield (g) ^{e,f}	^{15}N uptake (mg) ^{e,g}
				NH_4^+	NO_3^-			
Ta & Ohira (1982)	SS	Rice (Indica)	NH_4^+	56	0	28 + 1	(11.4)	
			NO_3^-	0	28		(17.2)	
		Rice (Japonica)	NH_4^+	56	0		(9.2)	
			NO_3^-	0	28		(7.4)	
Lewis & Chadwick (1983)	SS	Barley	NH_4^+	28	0	20 d + 8 h		0.20a
			NO_3^-	0	28			0.05b
Stock & Lewis (1984)	Sand / solution	<i>Protea repens</i>	NH_4^+	28	0	118 + 9	(3.9)	0.023
			NO_3^-	0	28		(3.6)	0.017
Deignan & Lewis (1988)	SS	Wheat	NH_4^+	28	0	34 d + 8 h		(0.35)
			NO_3^-	0	28			(0.25)
Koppisch et al. (1993)	Sand / solution	<i>Calamagrostis villosa</i>	NH_4^+	28	0	63 + 2	2.0a	21.2a
			NO_3^-	0	28		6.0b	66.5b
Merhaut & Darnell (1995)	Sand / solution	Blueberry	NH_4^+	(105)	0	2.5 y + 2 d		79a
			NO_3^-	0	(105)			40b
Morita et al. (1998)	SS	Tea	NH_4^+	50	0	520 d + 24 h		1.17a
			NO_3^-	0	50			0.52b
Tan et al. (2000)	SS	Tomato	NH_4^+	200	0	6-leaf + 24 h		1.79a
			NO_3^-	0	200			3.32b
Lin et al. (2005)	SS	Rice (lowland)	NH_4^+	0.06	0	Seedling + 4d		0.429a
			NO_3^-	0	0.06			0.225b
			NH_4^+	0.06	0	Tillering + 2d		0.348a
			NO_3^-	0	0.06			0.606a
Arkoun et al. (2012)	SS	Canola	NH_4^+	28	0	7-22	0.6a	35a
			NO_3^-	0	28		1.4b	50b
Zhang et al. (2019)	SS	Maize	NH_4^+	28	0	3-30	3.5a	
			NO_3^-	0	28		2.0b	

^a SS, Static solution^b Rice, *Oryza sativa*; Barley, *Hordeum vulgare*; Wheat, *Triticum aestivum*; Blueberry, *Vaccinium corymbosum*; Tea, *Camellia sinensis*; Tomato, *Lycopersicon esculentum*; Canola, *Brassica napus*; Maize, *Zea mays*^c Data in parentheses () are mg N^d Age interval between start of $^{15}\text{NH}_4^+$ and $^{15}\text{NO}_3^-$ treatments and harvest^e Data within a column and species followed by different lower-case letters are significantly different ($P \leq 0.05$)^f Data in parentheses () are fresh weight^g Data in parenthesis () are mg ^{15}N g⁻¹ fresh weight

TABLE 3 Short-term plant recovery, rate and amount of uptake of $^{15}\text{NH}_4^+$, $^{15}\text{NO}_3^-$ and $^{15}\text{N}/^{13}\text{C}$ -labelled amino acids by non-leguminous plants in soil-based natural- and agro-ecosystems

Reference	Ecosystem ^a	Sites	Species	¹⁵ N Source ^b	N added	Time ^c (h)	Treatment ^d	NH ₄ ⁺	NO ₃ ⁻	AA
								Plant recovery (%) ^e		
Wilkinson et al. (2015)	Grasslands UK	Field (2)	2 site 1 5 site 2	One of A+N+Al	1.4 mg	2.5	HP site 1	9.0	3.1	6.1
							LP site 2	3.1	1.6	2.0
Wittich et al. (2015)	Tropical montane forest trees EC	Pots (3)	6	Either A, N, Gl	300 mg	120	<i>P. torta</i>	<0.5a	<0.5a	<0.5a
							<i>H. sprucei</i>	3.0a	1.3a	3.2a
							<i>Myrica</i> sp.	<0.5a	<0.5a	<0.5a
							<i>H. transluc.</i>	4.4a	2.1a	6.0a
							<i>G. harlingii</i>	1.0a	0.8a	1.3a
							<i>H. purpur.</i>	1.0a	1.0a	1.3a
Andersen et al. (2017)	Pre-montane tropical forest PA	Field (1)	11	One of A+N+Gl	2 μg cm ⁻³ soil	48	<i>S. panam.</i>	<0.01	<0.01	0
							<i>V. guatam.</i>	0	0.015	0
							<i>C. macrad.</i>	<0.01	0.012	0
							<i>R. montana</i>	0.015	0.01	0
Cui et al. (2017)	Agro-Lhasa Experiment Station Tibet CN	Field (1)	2 at 3 growth stages	Either A, N	23.2 kg ha ⁻¹	24	Barley T	5a	16b	-
							Barley H	13a	29b	-
							Barley M	15a	29b	-
							Oat T	5a	17b	-
							Oat H	15a	16a	-
							Oat M	15a	17a	-
								¹⁵ N uptake rate ^{e,f}		
Miller & Bowman (2002) ^g	Dry meadow alpine tundra CO	Pots (2)	7	Either A, N, Gl	2.8 mg	6-14	<i>Aco. rossii</i>	1.7a	0.5b	<0.5b
							<i>Art. scopul.</i>	4.2a	6.2b	4.4a
							<i>F. brachy.</i>	4.0a	3.9a	8.2b
							<i>C. rupestris</i>	5.9a	4.5a	3.0b
							<i>K. myosur.</i>	6.4a	6.4a	3.6b
							<i>Luz. spicata</i>	14.0a	8.0b	8.5b
Ashton et al. (2010)	Dry meadow alpine tundra CO	Field (1)	4 (no neighbour)	One of A+N+Gl	2.4 mg kg ⁻¹ soil	6	<i>K. myosur.</i>	93a	223b	85a
							<i>Geum rossii</i>	45a	290b	134c
							<i>C. rupestris</i>	27a	259b	89c
							<i>M. lanceol.</i>	144a	268b	112a
								N uptake (mg g ⁻¹) ^e		
Näsholm et al. (2000)	Grassland SE	Pots in field (1)	2	Either A, N, Gl	1.4 mg	21	Timothy S	0.5a	1.4b	0.4a
							Timothy R	0.6a	1.4b	0.4a
							Buttercup S	1.3a	1.2a	0.6b
							Buttercup R	1.2a	1.4a	0.6b

^a UK, United Kingdom; EC, Ecuador; PA, Panama; CN, China; Co, Colorado USA; SE, Sweden

^b A, ammonium, N, nitrate, Al, alanine; Gl, glycine;

^c Time elapsed between ^{15}N addition and plant harvest

^d HP, high productivity pasture; LP, low productivity pasture; *H. Hedyosmum*, *H. translucidum*, *H. purpurascens*; *Sebastiania panamensis*, *Vochysia guatamalensis*, *Citharexylum macradenium*, *Roupala montana*; Barley, *Hordeum vulgare*; Oat, *Avena sativa*; T, tillering; H, heading; M, milk; *Aco.*, *Acomastylus*; *Art. scopul.*, *Artemisia scopulorum*; *F. brachy.*, *Festuca brachyphylla*; *C.*, *Carex*; *K. myosur.*, *Kobresia myosuroides*, *Luz.*, *Luzula*; *M. lanceol.*, *Mertensia lanceolata*; Timothy, *Phleum pratense*; Buttercup, *Ranunculus acris*; S, shoots; R, roots

^e Data with a row followed by different lower-case letters are significantly different ($P \leq 0.05$)

^f Units are $\mu\text{g g}^{-1} \text{h}^{-1}$

^g Used a mixture of sand: topsoil: vermiculite of 5:2:1

TABLE 4 Correlations among $\delta^{15}\text{N}_{\text{foliage}}$, enrichment factors, plant N concentration and soil N parameters in natural ecosystems

Reference	Location ^a	Sites	Species ^b	Variables ^c		n	r ^d
Garten (1993)	Walker Branch Watershed TN	5	Mixed (13)	$\delta^{15}\text{N}_{\text{foliage summer}}$	$\delta^{15}\text{N}_{\text{foliage spring}}$	13	0.97
				$\delta^{15}\text{N}_{\text{foliage}}$	NN	7	0.97
				EF	NN	7	0.94
Garten & Van Miegroet (1994)	Great Smoky Mountains National Park TN	20	Mixed (20)	$\delta^{15}\text{N}_{\text{foliage evergreens}}$	NM _{evergreens}	8	0.96***
				EF _{evergreens}	NM _{evergreens}	8	0.89**
				$\delta^{15}\text{N}_{\text{foliage ferns}}$	NM _{ferns}	6	0.85*
				EF _{ferns}	NM _{ferns}	6	0.94**
Roggy et al. (1999)	Rain forest St. Elie FG	1	<i>L. procera</i>	$\delta^{15}\text{N}_{\text{leaf}}$	[N] _{leaf}	7	0.84*
			Pioneers (4)			4-9	NS
Falkengren-Grerup et al. (2004)	Deciduous oak woodland SE	12	<i>G. urbanum</i>	$\delta^{15}\text{N}_{\text{leaf}}$	[N] _{leaf}	30-35	-0.70***
			<i>M. effusum</i>				-65***
			<i>D. flexuosa</i>				0.59***
			<i>G. urbanum</i>	[N] _{leaf}	NM	0.75***	
			<i>A. podagraria</i>			0.49**	
			<i>M. effusum</i>			0.79***	
			<i>C. majalis</i>			0.71***	
			<i>D. flexuosa</i>			0.41*	
			<i>P. nemoralis</i>			0.36*	
			<i>G. urbanum</i>	[N] _{leaf}	NN	0.76***	
			<i>A. podagraria</i>			0.51**	
			<i>M. effusum</i>			0.66***	
			<i>C. majalis</i>			0.65***	
			<i>P. nemoralis</i>			0.43**	
Kahmen et al. (2008)	Temperate montane grassland DE	18	Forbs	$\delta^{15}\text{N}_{\text{foliage}}$	$\delta^{15}\text{N}_{\text{soil}}$	>50	0.78***
			Grasses				0.79***
			Forbs	EF	NM		0.51***
			Grasses				0.49***
				$\delta^{15}\text{N}_{\text{soil}}$	NM	18	0.59**
	NN	0.57*					
Brearley (2013)	Montane Forest JM	2	Mor (8)	$\delta^{15}\text{N}_{\text{leaf}}$	[N] _{leaf}	8	0.56***
			Mull (8)				0.34*
Fang et al. (2013)	Forests east Asia, MY, CN, JP, KR	32	Tropical (2) Subtropical (16) Temperate (14)	$\delta^{15}\text{N}_{\text{leaf}}$	[N] _{leaf}	50	0.28*
					$\delta^{15}\text{N}_{\text{soil Oi layer}}$	45	0.66***
					$\delta^{15}\text{N}_{\text{soil 0-10 cm}}$	65	0.51***

^a TN, Tennessee, USA; FG, French Guiana; SE, Sweden; DE, Germany; JM, Jamaica; MY, Malaysia, CN, China, JP, Japan, KR, Korea

^b Mixed (13), Americam beech, black gum, blackjack oak, boxelder, dogwood, hickory, red bud, red maple, sweet gum, sugar maple, sycamore, white oak, yellow poplar; Mixed (20), Conifers and non-deciduous woody shrubs, Fraser fir, red spruce, eastern hemlock, mountain laurel, rhododendron; Deciduous trees and shrubs, mountain maple, striped maple, red maple, sugar maple, yellow birch, American beech, blueberry, red oak, white oak, chestnut oak, black gum, yellow buckeye, mountain ash; Ferns, Christmas fern, woodfern; *G. Geum*; *A. Aegopodium*; *M. Miliun*; *C. Convallaria*; *D. Deschampsia*; *P. Poa*; Mor (8), *Alchornea latifolia*, *Clethra occidentalis*, *Clusia thevetioides*, *Cyrilla racemiflora*, *Lyonia octandra*, *Pittosporum undulatum*, *Podocarpus urbanii*, *Schefflera sciadophyllum*; Mull (8), as for Mor (8) + *Hedyosmum arborescens*, minus *C. thevetioides*

^c NN, net nitrification rate; EF, enrichment factor ($\delta^{15}\text{N}_{\text{leaf}} - \delta^{15}\text{N}_{\text{soil}}$); NM, net N mineralization rate; [N], N concentration

^d ***, P<0.001, **, P<0.01, *, P<0.05, NS, not significant

TABLE 5 Estimates of the proportional contribution of N sources to foliar $\delta^{15}\text{N}$ signatures in natural ecosystems

Reference	Model	Ecosystem ^a	Species ^b	* $\delta^{15}\text{N}_{\text{leaf}}^c$	Treatment ^d	Proportion (%) ^f		
						NH ₄ ⁺	NO ₃ ⁻	DON
Houlton et al. (2007)	IsoSource	Tropical forest HI	<i>M. polymorpha</i> <i>Ch. trigynum</i> <i>Ci. glaucum</i> <i>M. clusiifolia</i>	+2‰	2200 mm	15	80	5
					2450mm	17	78	5
					2750 mm	15	80	5
					3350 mm	5	93	2
					4050 mm	93	5	2
					5050 mm	93	5	2
Takebayashi et al. (2010)	IsoError	Forest JP	<i>C. obtusa</i>	+0‰	NK-(0.1)	94	6	
	Isosource				OT-(0.7)	47	53	
					HO-(1.7)	0	100	
					NK-(0.1)	47	28	25
					OT-(0.7)	24	61	15
					HO-(1.7)	3	95	2
Mayor et al. (2014)	IsoError	Lowland tropical rainforest PA	<i>A. blackiana</i>	−0.9‰		56	44	
			<i>H. concinna</i>			43	57	
			<i>T. panamensis</i>			70	30	
			<i>O. mapora</i>			30	70	
Yang et al. (2018)	Isoerror	Plant succession CN	Grasses (4) Shrubs (8) Trees (18)	+0‰		Mean <50 ^e	mean >50 ^e	
Zhang et al. (2018)	IsoError	Plantations age 20-70 y CN	<i>Picea asperata</i> (spruce)	+6‰ ECM species	20 y	27a	73b	
					30 y	42a	58b	
					50 y	93a	7b	
	IsoSource				20 y	19b	38a	43a
					30 y	31b	46a	23b
					40 y	34a	30a	36a
					50 y	33a	33a	34a
					70 y	43a	18b	39a
Zhu et al. (2019)	SIAR	Glasshouse study CN	<i>P. koraiensis</i>	+3.2‰		33	24	43
			<i>L. keampferi</i>	ECM		6	74	20
			<i>Q. mongolica</i>	species		1	88	11
			<i>J. mandshurica</i>	+2‰ AM		11	68	21

^a HI, Hawaii; JP, Japan; PA, Panama; CN, China^b *M*, *Metrosideros*; *Ch*, *Cheirodendron*; *Ci*, *Cibotium*; *M*, *Melicope*; *C*, *Chamaecyparis* (Hinoki cypress); *A*, *Alseis*; *H*, *Heisteria*; *T*, *Tetragastis*; *O*, *Oenocarpus*; *P*, *Pinus*; *L*, *Larix*; *Q*, *Quercus*; *J*, *Juglans*^c Correction for isotopic fractionation; ECM, ectomycorrhizal; AM, arbuscular mycorrhizal^d mm, mean annual precipitation; Data in parentheses are NO_3^- concentration (mg N L^{-1}) in stream water; NK, Norikura; OT, Okutama; HO, Hachioji^e Equal proportions for shrub *Boehmeria dolichostachya*, and grasses *Monochoria vaginalis*, *Miscanthus floridulus*^f Different lower-case letters within a row denote significant difference ($P \leq 0.05$)

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Title:

On inorganic N uptake by vascular plants: Can N-15 tracer techniques resolve the NH₄⁺ versus NO₃⁻ "preference" conundrum?

Date:

2020-11-26

Citation:

Chalk, P. & Smith, C. (2020). On inorganic N uptake by vascular plants: Can N-15 tracer techniques resolve the NH₄⁺ versus NO₃⁻ "preference" conundrum?. EUROPEAN JOURNAL OF SOIL SCIENCE, 72 (4), pp.1762-1779. <https://doi.org/10.1111/ejss.13069>.

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