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Calculating Nitrogen Uptake Rates in Forests: Which Components Can Be Omitted, Simplified, or Taken from Trait Databases and Which Must Be Measured In Situ?

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Abstract

Quantifying nitrogen uptake rates across different forest types is critical for a range of ecological questions, including the parameterization of global climate change models. However, few measurements of forest nitrogen uptake rates are available due to the intensive labor required to collect in situ data. Here, we seek to optimize data collection efforts by identifying measurements that must be made in situ and those that can be omitted or approximated from databases. We estimated nitrogen uptake rates in 18 mature monodominant forest stands comprising 13 species of diverse taxonomy at the Morton Arboretum in Lisle, IL, USA. We measured all nitrogen concentrations, foliage allocation, and fine root biomass in situ. We estimated wood biomass increments by in situ stem diameter and stem core measurements combined with allometric equations. We estimated fine root turnover rates from database values. We analyzed similar published data from monodominant forest FACE sites. At least in monodominant forests, accurate estimates of forest nitrogen uptake rates appear to require in situ measurements of fine root productivity and are appreciably better paired with in situ measurements of foliage productivity. Generally, wood productivity and tissue nitrogen concentrations may be taken from trait databases at higher taxonomic levels. Careful sorting of foliage or fine roots to species is time consuming but has

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little effect on estimates of nitrogen uptake rate. By directing research efforts to critical in situ measurements only, future studies can maximize research effort to identify the drivers of varied nitrogen uptake patterns across gradients.

Key words: fine root turnover; forest mensuration; forest productivity; nitrogen dynamics; nitrogen uptake rate; plant tissue nitrogen.

Highlights

- Insightful but labor-intensive nitrogen uptake rate measurements may be simplified.
- In situ measurements of fine root and foliage productivity appear necessary.
- Wood productivity and tissue N concentrations may be taken from trait databases.

Introduction

Nitrogen commonly limits primary production in forests (LeBauer and Treseder 2008), and nitrogen uptake into dominant canopy trees is thought to play an important role in carbon sequestration (Finzi and others 2007; Zaehle and others 2014; Walker and others 2021; Wang and Wang 2021). Many factors may affect plant nitrogen uptake, but their mechanisms and relative importance in different ecological contexts are poorly understood (Freschet and others 2021). Early research efforts focused on plant litter feedbacks as the dominant control of nitrogen availability and uptake (Pastor and others 1984; Hobbie 1992). However, a range of newly discovered mechanisms and possibilities have been identified in recent decades (Hobbie 2015), including plant–microbe competition (Schimel and Bennett 2004), organic nitrogen uptake (Schimel and Bennett 2004), priming effects (Phillips and others 2012; Cheng and others 2014; Meier and others 2017; Henneron and others 2020; Wen and others 2022), mycorrhizal uptake (Näsholm and others 2013), non-growing-season uptake (Ma and others 2021), water interactions (Joseph and others 2021), uptake at depth (Iversen 2010), game theoretic root overproliferation (Cabal 2022), and even significant foliage nitrogen uptake via direct absorption (Guerrieri and others 2021). Because of the myriad factors potentially impacting forest nitrogen dynamics, we need more stand-level measurements of nitrogen uptake rate to understand the relative contributions and context dependencies of these mechanisms.

Three common approaches for measuring or approximating nitrogen uptake rates all present critical challenges or shortcomings. First, under the classic leaf litter feedback paradigm, researchers sometimes equated plant uptake with availability by making the now-questionable assumptions that (1) net nitrogen mineralization in bulk soil was the only mode of nitrogen availability that mattered and (2) that all available nitrogen would be taken up. Nadelhoffer and others (1984), Nadelhoffer and others (1985), Pinay and others (1995), Ruess and others (1996), and Usman and others (1999) ostensibly concern plant nitrogen uptake, but their measures of uptake are actually measures of net nitrogen mineralization in bulk soil. Second, studies that focus on the relative partitioning of nitrogen among the many possible sinks involved in plant nitrogen uptake have made great use of ^{15}N tracers (for example, Näsholm and others 2013), whereby labeled nitrogen is injected into soils and its uptake and allocation to different plant tissues are subsequently analyzed. However, ^{15}N tracer studies use a short-term pulse of nitrogen that does not reflect integrated uptake across an entire growing season, and they do not account for retranslocation and the use of stored nitrogen within a plant. As such, and despite the tremendous strength of ^{15}N tracer studies to discriminate the relative partitioning of labeled nitrogen, these studies must be treated cautiously when interpreting absolute nitrogen uptake.

The third method, calculating absolute nitrogen uptake, sidesteps these shortcomings but requires measuring the growth increments of a stand's foliage, wood (including branch, bole, and coarse roots), fine roots, and reproductive structures, along with the nitrogen concentrations in those structures (Whittaker and others 1979). The calculation must also account for nitrogen redeployed from storage each year (for example, Dybzinski and others 2019). Stand heterogeneity invariably complicates the calculation, requiring study design decisions that hinge on statistical power that can seldom be known in a given stand a priori. For example, growth increments and nitrogen concentrations of various tissues will likely differ between individuals of different sizes and different species and may even differ within a single individual both in space (for example, a sunlit branch versus a shaded branch) and time (for example, at different times within a given growing season or across different growing seasons).

Because calculating absolute nitrogen uptake is so challenging and labor-intensive, insights into forest nitrogen uptake are only available from a handful of studies at a handful of sites (Whittaker and others 1979; Finzi and others 2007; Tateno and Takeda 2010). Finzi and others (2007) found that forest nitrogen uptake increased under elevated CO_2 in three of four Free-Air CO_2 Enrichment (FACE) sites and that the site that did not show an increase was not nitrogen limited. Tateno and Takeda (2010) found that nitrogen uptake into aboveground tissues increased with increasing nitrogen mineralization rate but that nitrogen uptake into belowground tissues decreased with increasing nitrogen mineralization rate, such that total nitrogen uptake did not change with increasing nitrogen mineralization rate.

Given the ecological importance of forest nitrogen uptake—especially in the context of global change factors—researchers would benefit from more measurements at more and varied sites. Indeed, a network of sites using commensurate protocols to measure forest nitrogen uptake would allow researchers to distinguish generalities from special cases (Borer and others 2014). However, the complications and labor involved in the standard method for calculating absolute forest nitrogen uptake rate stand in the way, and we are not aware of any networks that are yet undertaking nitrogen uptake measurements. Can the method be simplified by omitting certain components, by making simplifying assumptions, or by obtaining certain components not from in situ measurements, but rather from trait databases?

Here, we report on the nearly complete in situ measurements of absolute forest nitrogen uptake in 18 mature, monodominant stands at the Morton Arboretum (Lisle, Illinois, USA)and draw on published data on the nearly complete in situ measurements of absolute forest nitrogen uptake in four forest FACE sites (Finzi and others 2007). Our goal is to find ways to simplify the method without substantially changing either the total nitrogen uptake estimate or the ranking of sites by total nitrogen uptake, either of which would represent paths forward to greater researcher uptake (pun intended) of absolute forest nitrogen uptake calculations at more and varied sites. To find the most promising simplifications, we systematically omit components, simplify assumptions, and replace components with trait database values. Broadly, we ask the following questions, where ''need'' is defined as important for accurately calculating total nitrogen uptake and/or maintaining ranking of sites by total nitrogen uptake:

- Are foliage, fine root, and wood nitrogen uptake measurements all needed?
- Are in situ nitrogen concentrations needed or can trait database values be substituted? If trait database values are used, what is the best taxonomic level?
- Can allometric relationships or stand-level database values replace the need for in situ leaf litter, fine root, and/or wood production measurements?
- How much do assumptions about fine root turnover rates matter to the total nitrogen uptake estimate and/or the ranking of sites by total nitrogen uptake?
- Is careful sorting of fine roots and leaf litter needed, and is it necessary to include nitrogen uptake into reproductive structures?
- Are the results of any simplifications systematically different for major plant groups, including mycorrhizal associations or plant divisions?

We compare both the accuracy and correlation of the resulting simplified calculations of forest nitrogen uptake with those made using the nearly complete in situ measurements (''nearly complete'' because we used allometric equations to estimate wood increment and because we used database fine root turnover values). Accuracy measures the quantitative agreement between estimates with a given simplification and the nearly complete in situ measurements. Correlation measures the ability to correctly rank forest stands by their nitrogen uptake rates with a given simplification as compared with the nearly complete in situ measurements.

Materials and Methods

Overview

In what follows, we first explain the calculations that we use to estimate nitrogen uptake rate from empirical measurements. Second, we describe the Morton Arboretum study site in detail, as well as an overview of the four forest FACE sites from which we repurpose published data. Third, we describe the TRY and FluxNet databases used in some of the analysis scenarios. Finally, we describe the rationale and details of the analysis scenarios that test different possible simplifications of the most comprehensive approach to measuring nitrogen uptake rates. The supplemental online material contains additional details on in situ field measurements at the Morton Arboretum, error propagation in analyses, the rationale and details regarding our measures of accuracy and correlation for comparing different simplification scenarios, and details on a power analysis for measuring fine root biomass and nitrogen concentration.

General Framework for Measuring Absolute Nitrogen Uptake Rate

For closed-canopy forest stands, canopy tree nitrogen uptake rate (U) in units of gN m^{-2} y^{-1} can be calculated as the sum of nitrogen uptake into foliage (U_F), fine roots (U_R), live wood (including branch, bole, and coarse roots, U_W), and reproductive tissues (U_S):

$$U \approx U_F + U_R + U_W + U_S \quad (1)$$

To be clear, ''uptake'' in this context is mediated by fine roots, which initially bring nitrogen into the tree before it is transported to a given organ for ''uptake'' (but see Guerrieri and others 2021). Estimating each of these components requires its own assumptions and field techniques, which we describe below.

U_F, U_R, and U_S share a common general mathematical expression for a stand whose foliage, fine root, or reproductive components are approximately in dynamic equilibrium:

$$U_x \approx B_x T_x N_x (1 - Q_x),\ \text{where } x \in (\mathrm{F},\ \mathrm{R},\ \mathrm{S}) \quad (2)$$

B_x is the biomass of the tissue in units of g m^{-2}. T_x is the turnover rate in units of y^{-1}. N_x is the nitrogen concentration of the tissue in units of gN g^{-1}. Finally, Q_x is the unitless fraction of nitrogen that is retranslocated prior to tissue senescence or dispersal. Taken together, the expression states that nitrogen uptake into component X is equal to the *new* biomass produced ($B_x T_x$) multiplied by the *new* nitrogen it requires ($N_x(1 - Q_x)$). Foliage mass and fine root mass are either approximately in dynamic equilibrium in closed-canopy forests or change very slowly relative to the yearly timescale necessary for this assumption (Covington and Aber 1980; Claus and George 2011; Jagodzinski and Kalucka 2011; Dybzinski and others 2015; Jagodzinski and others 2016).

In the case of foliage or reproductive tissues, it is often methodologically expedient to measure the rate at which senesced tissues are lost, which avoids the need to measure turnover rates or, if also measuring senesced tissue nitrogen concentration, the retranslocation fraction. Again, assuming the foliage or reproductive components are approximately in dynamic equilibrium, the nitrogen lost in the senesced tissues must be approximately equal to the nitrogen taken up to replace that loss. Thus,

$$U_x \approx D_x N_x (1 - Q_x) \text{ or } U_x \approx D_x N_{D,x},\ \text{where } x \in (\mathrm{F},\ \mathrm{S}) \quad (3)$$

D_x is the rate of senesced tissue loss in units of g m^{-2} y^{-1}, and $N_{D,x}$ is the nitrogen concentration of the senesced tissue.

Unlike foliage, fine root, and reproductive structures, wood growth likely increases for decades or centuries after canopy closure (Dybzinski and others 2015, their Figure 6). Moreover, even in an old growth forest where wood biomass truly is in dynamic equilibrium, it is difficult to make good methodological use of that fact given the spatially and temporally heterogeneous nature of wood growth and loss. Hence, an alternative way to estimate U_W uses basal area and wood growth increments:

$$U_W \approx G_W N_W (1 - Q_W) \quad (4)$$

G_W is the net primary productivity of wood in units of g m^{-2} y^{-1}, N_W is the nitrogen concentration of living sapwood, and Q_W is the retranslocation of nitrogen prior to sapwood conversion to heartwood. G_W is conventionally estimated as $G_W \approx \left(\frac{1}{A}\sum_{i=1}^{n} I_{i,t} - I_{i,t-1}\right)$, where $I_{i,t}$ is the wood biomass of tree I in the measurement year, $I_{(i,t-1)}$ is the wood biomass of tree i in the year prior to the measurement year, and n is the number of trees measured within area A. In addition to being time consuming and difficult, directly measuring tree biomass is wildly destructive, so we estimate $I_{i,t}$ and $I_{i,\ t-1}$ using allometric equations keyed to diameter, $I_{i,t} \approx H(dbh_{i,t})$ and $I_{i,t-1} \approx H(dbh_{i,t-1})$. $H()$ is an empirically determined power law function of diameter at breast height, *dbh*.

As in the case of senesced reproductive tissues and foliage, U_W may be simplified by measuring heartwood nitrogen concentration, $N_{D,W}$, which effectively includes retranslocation without having to measure it. Hence,

$$U_W \approx G_W N_{D,W}. \quad (5)$$

Description of the Morton Arboretum Plots

The new in situ measurements occurred in monodominant forestry plots at the Morton Arboretum (41.81° N, 88.05° S) in Lisle, Illinois, USA, primarily from June to August 2019. The region has a continental climate, where average temperatures range from − 6 °C in January to 22 °C in July, and mean annual precipitation totals 800–1000 mm

(Midgley and Sims 2020). The arboretum's forestry plots range from 0.05 to 0.8 hectares in area, were established beginning in 1922, and remain strongly monodominant (Midgley and Sims 2020). Eighteen of these forestry plots were used, which represent data from 13 different tree species (five species are replicated twice) (Table 1). The species are approximately evenly split between angiosperms and gymnosperms, and species within each of those taxonomic groups are approximately evenly split between those with ectomycorrhizal and arbuscular mycorrhizal associations (Table 1). Understories are populated by short-statured herbaceous species and are generally open and walkable. Given the nature and sizes of the plots, inferences and generalizations about small-scale, monodominant stands are warranted. We describe the methods used to measure in situ foliage production, fine root mass, wood production, and tissue nitrogen concentrations in the Supplemental Online Material.

Description of FACE Data

Data on pool size, flux, and turnover of foliage, wood, and fine roots were assembled by Finzi and others (2007) on four forest FACE sites: Duke Forest (Hendrey and others 1999), Rhinelander (Karnosky and others 1999, 2005), Oak Ridge National Lab (ORNL, Norby and others 2001), and Pop-Euro (Miglietta and others 2001). Their dominant species, mycorrhizal associations, and other details are presented in Table 1. We display and analyze the replicate plots within each FACE site, which provide an indication of site-level variability. Given the nature and sizes of the plots, inferences and generalizations about small-scale, monodominant stands are warranted. Although data were separately available for elevated CO_2 and ambient CO_2 plots, their within-site differences were small compared to across-site differences. Thus, to simplify the presentation, we ignored the CO_2 treatment of a forest FACE plot. In addition, we omitted pre-treatment data.

Description of Data Base Values

TRY

Trait data were requested from the TRY database (Kattge and others 2011) on September 18, 2020, and we received data from 330 families covering fresh foliage [*N*] (TRY trait #14, n = 120,306), foliage turnover rate (#12, n = 4808), fine root [*N*] (#2035 & #475, n = 4574), fine root turnover rate (#2065 & #1955, n = 695), and stem [*N*] (#3453, & #1229, n = 22,332). The records we used reflected the following adjustments: Duplicate records were removed using the ''ObservationID'' field. Outlier values (greater than 245 mg g^{-1}) were omitted from fresh foliage [*N*], as were all data labeled as from ''Dataset 170'' because they contained a large number of outlier and suspicious values. All values were converted to fractions. Foliage turnover rates were calculated as the inverse of reported leaf lifespan in months multiplied by 12 months y^{-1}. Values recorded as 0 months (that is, infinite turnover) were removed. Fine root [*N*] were converted to fractions. Fine root turnover data erroneously labeled with units mg g^{-1} were omitted, and fine root turnover data reported in units of days (that is, longevity) were converted to turnover by multiplying their inverse by 365 d y^{-1}. Stem [*N*] records were filtered to include only those for which the ''PlantGrowthForm'' field equaled ''tree,'' and data expressed in mg g^{-1} were converted to fractions.

FluxNet

The ''1_Site_Information'' and ''3_Estimate_NPP'' tables from the FluxNet database (Luyssaert and others 2007) were merged and filtered to include only data for which the ''Climatic.region'' field equaled ''Temperate Humid.'' We converted FluxNet's units of g C to g biomass by dividing values by 0.5 (that is, assuming g C = 0.5 g biomass).

Analysis Scenarios

As detailed in Table 2, we considered six broad approaches to calculating nitrogen uptake rate (labeled *a* through *f*) with specific scenarios nested within each broad approach (labeled with subscript numbers). The first of these scenarios, a_1, represents our best in situ estimate of nitrogen uptake, including uptake into foliage, fine roots, and wood. Uptake into foliage is calculated using Eq. 3 with in situ litter production and litter [*N*] values, sidestepping any need for retranslocation values. Uptake into fine roots is calculated using Eq. 2 with in situ fine root biomass measurements and their [*N*] together with fine root turnover rates taken from the TRY database to lowest available taxonomic order. Importantly, we assume that fine roots do not resorb nitrogen before their death, an assumption that is better supported by data than any other (Gordon and Jackson 2000). Uptake into wood is calculated using Eq. 5 with in situ stem diameters and heartwood [*N*], sidestepping any need for retranslocation values. We use the Jenkins and others (2003) allometries for plant functional types (PFTs) to convert diameter to biomass, including estimates of belowground wood in coarse

Table 1. Summary of Sites and Plots

Location	Overstory species	Family	Mycorrhizal association	Taxonomic group	Leaf habit	Wood type	Age	Soil classification	Soil texture	Size (ha)	Subplot radii (m)	Mean N uptake
Morton Arb	*Aesculus glabra*	Sapindaceae	AM	Angiosperm	Deciduous	Diffuse	94	Udollic Epiaqualfs	Silty clay loam	0.05	5	8.92
Morton Arb	*Asimina triloba*	Annonaceae	AM	Angiosperm	Deciduous	Ring	71	Cumulic Endoaquolls	Silty clay loam	0.07	2	9.93
Morton Arb	*Asimina triloba*	Annonaceae	AM	Angiosperm	Deciduous	Ring	73	Oxyaquic Hapludalfs	Silt loam	0.11	1.5	20.69
Morton Arb	*Carya ovata*	Juglandaceae	ECM	Angiosperm	Deciduous	Ring	88	Oxyaquic Hapludalfs	Silt loam	0.10	7.5	6.35
Morton Arb	*Chamaecyparis pisifera*	Cupressaceae	AM	Gymnosperm	Evergreen	Tracheid	92	Oxyaquic Hapludalfs	Silt loam	0.31	4	8.34
Morton Arb	*Juniperus chinensis*	Cupressaceae	AM	Gymnosperm	Evergreen	Tracheid	89	Oxyaquic Hapludalfs	Silt loam	0.11	4	4.53
Morton Arb	*Picea abies*	Pinaceae	ECM	Gymnosperm	Evergreen	Tracheid	95	Oxyaquic Hapludalfs	Silt loam	0.80	7.5	4.16
Morton Arb	*Pinus strobus*	Pinaceae	ECM	Gymnosperm	Evergreen	Tracheid	79	Oxyaquic Hapludalfs	Silt loam	0.10	5, 7.5	4.92
Morton Arb	*Pinus strobus*	Pinaceae	ECM	Gymnosperm	Evergreen	Tracheid	94	Udollic Epiaqualfs	Silty clay loam	0.66	7.5	5.25
Morton Arb	*Platanus occidentalis*	Platanaceae	AM	Angiosperm	Deciduous	Diffuse	78	Typic Endoaquolls	Silty clay loam	0.16	7.5	6.65
Morton Arb	*Quercus alba*	Fagaceae	ECM	Angiosperm	Deciduous	Ring	93	Oxyaquic Hapludalfs	Silt loam	0.12	7.5	6.64
Morton Arb	*Quercus bicolor*	Fagaceae	ECM	Angiosperm	Deciduous	Ring	90	Cumulic Endoaquolls	Silty clay loam	0.12	5	5.74
Morton Arb	*Quercus bicolor*	Fagaceae	ECM	Angiosperm	Deciduous	Ring	90	Typic Endoaquolls	Silty clay loam	0.41	7.5	5.94
Morton Arb	*Robinia pseudoacacia*	Fabaceae	AM	Angiosperm	Deciduous	Ring	≥ 38	Oxyaquic Hapludalfs	Silt loam	0.06	5	10.04
Morton Arb	*Thuja occidentalis*	Cupressaceae	AM	Gymnosperm	Evergreen	Tracheid	97	Oxyaquic Hapludalfs	Silt loam	0.18	5	9.39
Morton Arb	*Thuja occidentalis*	Cupressaceae	AM	Gymnosperm	Evergreen	Tracheid	≥ 53	Cumulic Endoaquolls	Silty clay loam	0.03	3	13.70
Morton Arb	*Tsuga canadensis*	Pinaceae	ECM	Gymnosperm	Evergreen	Tracheid	97	Oxyaquic Hapludalfs	Silt loam	0.05	3	21.46

Table 1. continued

Location	Overstory species	Family	Mycorrhizal association	Taxonomic group	Leaf habit	Wood type	Age	Soil classification	Soil texture	Size (ha)	Subplot radii (m)	Mean *N* uptake
Morton Arb	*Tsuga canadensis*	Pinaceae	ECM	Gymnosperm	Evergreen	Tracheid	≥ 92	Typic Endoaquolls	Silty clay loam	0.39	5	9.81
Duke FACE (6 plots)	*Pinus taeda*	Pinaceae	ECM	Gymnosperm	Evergreen	Tracheid	17	Ultic Hapludalf	Clay loam	0.05	NA	5.35
Rhinelander FACE (12 plots)	*Populus tremuloides, Acer saccharum, Betula papyrifera*	Salicaceae	ECM, AM	Angiosperm	Deciduous	Diffuse	5	Alfic Haplorthod	Sandy loam	0.07	NA	4.92
ORNL FACE (5 plots)	*Liquidambar styraciflua*	Hammamelidaceae	AM	Angiosperm	Deciduous	Diffuse	14	Aquic Hapludult	Silty clay loam	0.05	NA	11.35
POP-EURO FACE (18 plots)	*Populus alba, Populus nigra, Populus x euramericana*	Salicaceae	ECM	Angiosperm	Deciduous	Diffuse	1.5	Pachic Xerumbrept	Loam and silt loam	0.04	NA	27.29

Mean N uptake in units of g N m^{-2} y^{-1} using the baseline scenario, a_1

Table 2. Overview of the Scenarios Used to Estimate Nitrogen Uptake Rate

Rationale	ID	U_F foliage N uptake	U_R fine root N uptake	U_W wood N uptake	U_S	Comment
Are foliage, fine root, and wood nitrogen uptake measurements all needed?	a_1	Equation 3: D_F, $N_{D,F}$ in situ	Equation 2: B_R, N_R in situ; Q_R = 0; T_R from TRY to lowest taxa	Equation 5: A, dbh, $N_{D,W}$ in situ; $H()$ from Jenkins et al. (2003) to PFT	0	Considered the baseline measurement with the most in situ measurements and the most trusted data sources for the balance
	a_2	0	As in a_1	As in a_1	0	Similar to baseline except omitting foliage
	a_3	As in a_1	0	As in a_1	0	Similar to baseline except omitting roots
	a_4	As in a_1	As in a_1	0	0	Similar to baseline except omitting wood
Are in situ nitrogen concentrations needed or can trait database values be substituted? If trait database values are used, what is the best taxonomic level?	b_1	As in a_1 except N_F from TRY to PFT level; Q_F = 0.62	As in a_1 except N_R from TRY to PFT level	As in a_1 except N_W from TRY to PFT level; Q_W = 0.24	0	Similar to baseline except that all nutrient concentrations are taken from databases at the PFT level
	b_2	As in a_1 except N_F from TRY to family level; Q_F = 0.62	As in a_1 except N_R from TRY to family level	As in a_1 except N_W from TRY to family level; Q_W = 0.24	0	Similar to baseline except that all nutrient concentrations are taken from databases at the family level where family level is not possible, taken at PFT
	b_3	As in a_1 except N_F from TRY to genus level; Q_F = 0.62	As in a_1 except N_R from TRY to genus level	As in a_1 except N_W from TRY to genus level; Q_W = 0.24	0	Similar to baseline except that all nutrient concentrations are taken from databases at the genus level where genus level is not possible, taken at family or PFT
	b_4	As in a_1 except N_F from TRY to species level; Q_F = 0.62	As in a_1 except N_R from TRY to species level	As in a_1 except N_W from TRY to species level; Q_W = 0.24	0	Similar to baseline except that all nutrient concentrations are taken from databases at the species level where species level is not possible, taken at genus, family, or PFT
	b_5	As in a_1 except N_F from TRY to PFT level; Q_F = 0.62	As in a_1	As in a_1	0	Similar to baseline except that all foliage nutrient concentrations are taken from databases at the PFT level
	b_6	As in a_1 except N_F from TRY to family level; Q_F = 0.62	As in a_1	As in a_1	0	Similar to baseline except that all foliage nutrient concentrations are taken from databases at the family level where family level is not possible, taken at PFT

Table 2. continued

Rationale	ID	U_F foliage N uptake	U_R fine root N uptake	U_W wood N uptake	U_S	Comment
	b_7	As in a_1 except N_F from TRY to genus level; Q_F = 0.62	As in a_1	As in a_1	0	Similar to baseline except that all foliage nutrient concentrations are taken from databases at the genus level where genus level is not possible, taken at family or PFT
	b_8	As in a_1 except N_F from TRY to species level; Q_F = 0.62	As in a_1	As in a_1	0	Similar to baseline except that all foliage nutrient concentrations are taken from databases at the species level. Where species level is not possible, taken at genus, family, or PFT
	b_9	As in a_1	As in a_1 except N_R from TRY to PFT level	As in a_1	0	Similar to baseline except that all fine root nutrient concentrations are taken from databases at the PFT level
	b_{10}	As in a_1	As in a_1 except N_R from TRY to family level	As in a_1	0	Similar to baseline except that all fine root nutrient concentrations are taken from databases at the family level where family level is not possible, taken at PFT
	b_{11}	As in a_1	As in a_1 except N_R from TRY to genus level	As in a_1	0	Similar to baseline except that all fine root nutrient concentrations are taken from databases at the genus level where genus level is not possible, taken at family or PFT
	b_{12}	As in a_1	As in a_1 except N_R from TRY to species level	As in a_1	0	Similar to baseline except that all fine root nutrient concentrations are taken from databases at the species level where species level is not possible, taken at genus, family, or PFT
	b_{13}	As in a_1	As in a_1	As in a_1 except N_W from TRY to PFT level; Q_W = 0.24	0	Similar to baseline except that all wood nutrient concentrations are taken from databases at the PFT level
	b_{14}	As in a_1	As in a_1	As in a_1 except N_W from TRY to family level; Q_W = 0.24	0	Similar to baseline except that all wood nutrient concentrations are taken from databases at the family level where family level is not possible, taken at PFT
	b_{15}	As in a_1	As in a_1	As in a_1 except N_W from TRY to genus level; Q_W = 0.24	0	Similar to baseline except that all wood nutrient concentrations are taken from databases at the genus level where genus level is not possible, taken at family or PFT
	b_{16}	As in a_1	As in a_1	As in a_1 except N_W from TRY to species level; Q_W = 0.24	0	Similar to baseline except that all wood nutrient concentrations are taken from databases at the species level where species level is not possible, taken at genus, family, or PFT

Table 2. continued

Rationale	ID	U_F foliage N uptake	U_R fine root N uptake	U_W wood N uptake	U_S	Comment
Can allometric relationships or stand-level database values replace the need for in situ leaf litter production measurements?	c_1	Equation 2; B_F = Lambert et al. (2005) foliage allometry; T_F = TRY to lowest taxa; $N_F(1-Q_F)$ = in situ senesced foliage [N]	As in a_1	As in a_1	0	Similar to baseline, except that foliage mass is calculated via *dbh* allometry and summed across trees within a known ground area
	c_2	Equation 3:D_F from FluxNet foliage NPP to PFT; $N_{D,F}$ in situ	As in a_1	As in a_1	0	Similar to baseline, except that foliage NPP is taken from FluxNet. Taxonomic levels below PFT were not available
Can allometric relationships or stand-level database values replace the need for in situ fine root production measurements? How much do assumptions about fine root turnover rates matter to the total nitrogen uptake estimate and/or the ranking of sites by total nitrogen uptake?	d_1	As in a_1	Equation 3:D_R from FluxNet fine root NPP to PFT; $N_{D,R}$ in situ	As in a_1	0	Similar to baseline, except that fine root NPP is taken from FluxNet. Taxonomic levels below PFT were not available
	d_2	As in a_1	As in a_1 except T_R is the mean turnover from TRY (1.34 per yr)	As in a_1	0	Similar to baseline, except that simple assumptions are made about fine root turnover
	d_3	As in a_1	As in a_1 except T_R is 1 for all roots	As in a_1	0	Similar to baseline except that turnover rate is equal to 1 for all roots
	d_4	As in a_1	As in a_1 except T_R is .5 for $<$ 1 mm roots and .1 for 1–2 mm roots. N_R separated into value associated with $<$ 1 mm and 1–2 mm roots	As in a_1	0	Similar to baseline except that turnover rate is equal to .5 for roots $<$ 1 mm in diameter and .1 for roots 1–2 mm in diameter. Specific nitrogen concentrations associated with
	d_5	As in a_1	As in a_1 except T_R is 1 for $<$ 1 mm roots and .2 for 1–2 mm roots. N_R separated into value associated with $<$ 1 mm and 1–2 mm roots	As in a_1	0	Similar to baseline except that turnover rate is equal to 1 for roots $<$ 1 mm in diameter and .2 for roots 1–2 mm in diameter
	d_6	As in a_1	As in a_1 except T_R is 2 for $<$ 1 mm roots and .5 for 1–2 mm roots. N_R separated into value associated with $<$ 1 mm and 1–2 mm roots	As in a_1	0	Similar to baseline except that turnover rate is equal to 2 for roots $<$ 1 mm in diameter and .5 for roots 1–2 mm in diameter

Table 2. continued

Rationale	ID	U_F foliage N uptake	U_R fine root N uptake	U_W wood N uptake	U_S	Comment
Can allometric relationships or stand-level database values replace the need for in situ wood production measurements?	e_1	As in a_1	As in a_1	As in a_1 except $H()$ from Lambert et al. (2005) to hardwood/softwood	0	Similar to baseline except using a different allometry
	e_2	As in a_1	As in a_1	As in a_1 except $H()$ from Lambert et al. (2005) with no distinction btwn spp	0	Similar to baseline except using a different allometry
	e_3	As in a_1	As in a_1	Equation 5: $N_{D,W}$ in situ; G_W from FluxNet to PFT	0	Similar to baseline except using FluxNet wood NPP
Is careful sorting of fine roots and leaf litter needed, and is it necessary to include nitrogen uptake into reproductive structures?	f_1	As in a_1	As in a_1 except B_R includes all fine roots collected	As in a_1	0	Similar to baseline except that root biomass includes all fine roots collected, not only those of a plot's target species
	f_2	As in a_1 except B_F includes all foliage collected	As in a_1	As in a_1	0	Similar to baseline except that foliage biomass includes all foliage collected, not only those of a plot's target species
	f_3	As in a_1 except B_F includes all foliage collected	As in a_1 except B_R includes all fine roots collected	As in a_1	0	Similar to baseline except that root and foliage biomass includes all fine roots and foliage collected, not only those of a plot's target species
	f_4	As in a_1	As in a_1	As in a_1	Equation 3: D_S, $N_{D,S}$ in situ	Baseline with in situ reproductive structures included

U_F, U_R, U_W, and U_S are defined in Eq. 1.

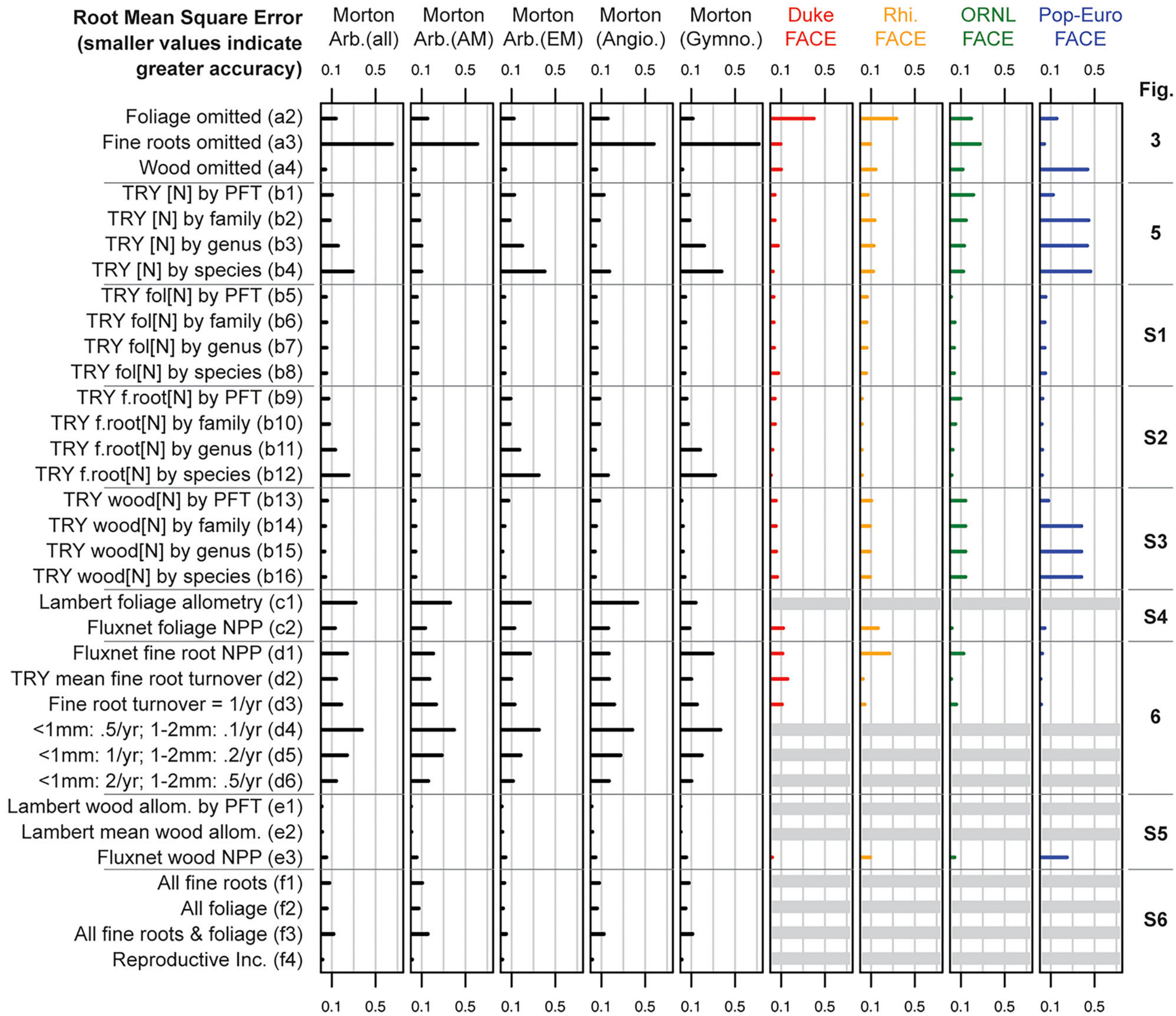


Figure 1. The accuracy (RMSE) of different simplified nitrogen uptake calculation scenarios as compared with the baseline scenario with all available in situ measurements. See Table 2 for descriptions of each scenario and Table S1 for a table of these values. The nature of the FACE data did not permit calculation of some scenarios as indicated by gray bars.

roots. In keeping with convention (for example, Zaehle and others 2014) and in recognition of the complications of dispersal and the basket method for collecting aboveground litter, we omit nitrogen uptake into reproduction in scenario a_1 but include it in scenario f_4. We submit that the a_1 scenario represents the most defensible estimate with the minimum of simplifications. Thus, we compare nitrogen uptake calculations from all other scenarios with those of a_1. Scenarios a_2, a_3, and a_4 are identical to a_1 except that either foliage uptake, fine root uptake, or wood uptake are omitted, representing possible simplifications and reductions in time required to reasonably estimate stand-level nitrogen uptake.

In the second major labor- and time-saving approach to estimating nitrogen uptake, we replace some or all in situ tissue $[N]$ values with taxa means from TRY (Table 2). Scenarios b_1 through b_4 replace all in situ tissue $[N]$ with TRY data aggregated at the PFT (b_1), the family (or PFT if family-level data are unavailable, b_2), the genus (or next-highest available level, b_3), or the species (or next-highest available level, b_4). Because available foliage $[N]$ data are on fresh (that is, not senesced) foliage, we used an average retranslocation fraction, $Q_F = 0.62$ (Vergutz and others 2012, their Figure 4), to approximate the $[N]$ in senesced foliage. Similarly, we used the average retranslocation fraction, $Q_W = 0.24$ (Meerts 2002), to approximate

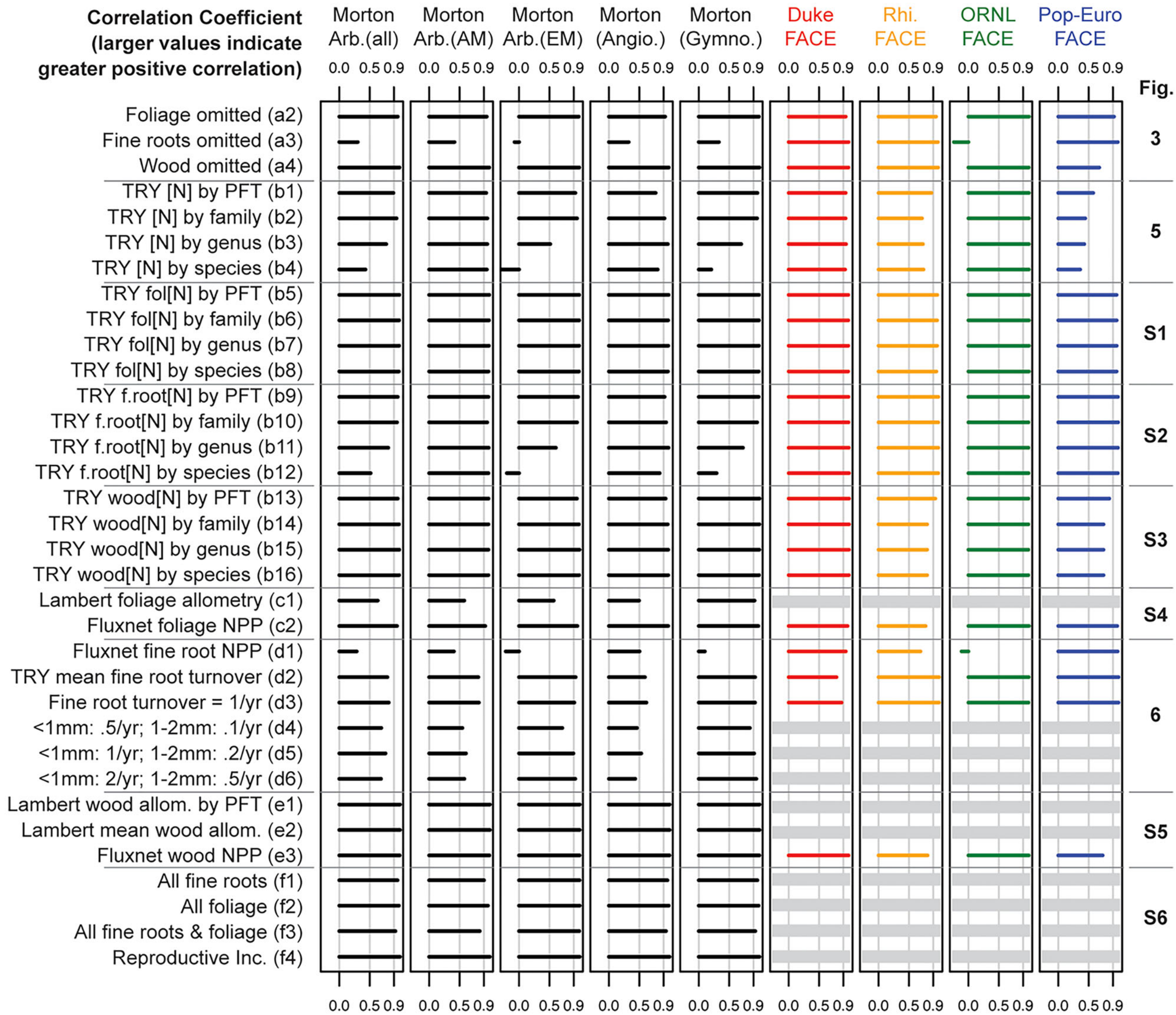


Figure 2. The correlation (Pearson's r) of different simplified nitrogen uptake calculation scenarios as compared with the baseline scenario with all available in situ measurements. See Table 2 for descriptions of each scenario and Table S2 for a table of these values. The nature of the FACE data did not permit calculation of some scenarios as indicated by gray bars.

the [*N*] in heartwood. The remaining *b* scenarios focus on individual organs. Scenarios b_5 through b_8 replace only foliage tissue [*N*] values with taxa means from TRY; scenarios b_9 through b_{12} replace only fine root tissue [*N*] values with taxa means from TRY; and scenarios b_{13} through b_{16} replace only wood tissue [*N*] values with taxa means from TRY. Within each set of four, the same taxonomic hierarchy is explored (that is, PFT, family, genus, species).

Scenarios c_1 and c_2 explore alternative labor- and time-saving ways to estimate foliage nitrogen uptake (Table 2). Scenario c_1 uses Lambert and others (2005) allometries separated by angiosperm and gymnosperm PFTs with stem diameter to estimate foliage biomass. We combine those estimates with foliage turnover from TRY to the lowest available taxa and in situ measures of senesced foliage [*N*]. Scenario c_2 uses FluxNet estimates of foliage NPP to PFT (which integrates biomass and turnover) and in situ measures of senesced foliage [*N*].

Scenarios d_1 through d_6 explore alternative labor- and time-saving ways to estimate fine root nitrogen uptake and the plausibility of making different assumptions about fine root turnover rates (Table 2). Analogous to scenario c_2, scenario d_1 uses FluxNet estimates of fine root NPP to PFT (which integrates biomass and turnover) and in situ measures of fine root [*N*]. Scenario d_3 uses the TRY mean fine root turnover (1.34 y^{-1}), and

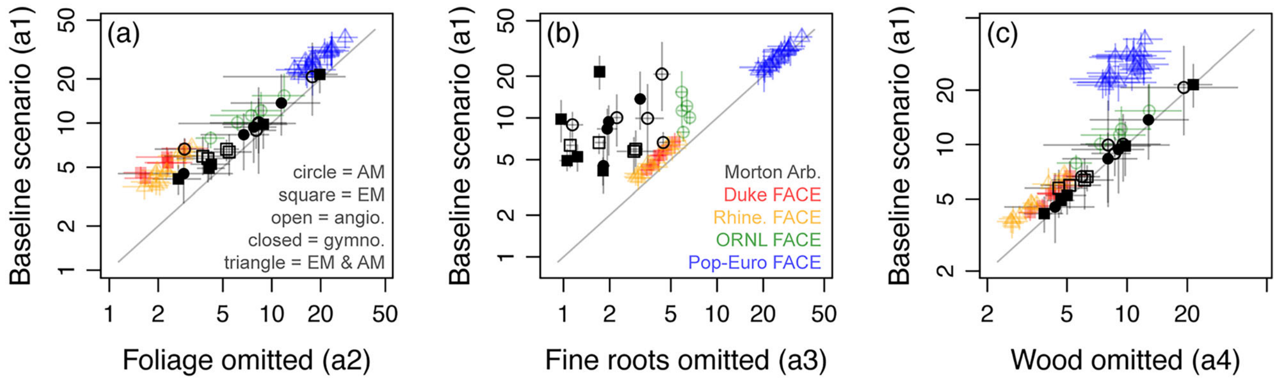


Figure 3. Nitrogen uptake rates (g N m^{-2} y^{-1}) calculated via the baseline scenario (that is, as many in situ measurements as are available) versus calculations with foliage uptake omitted (**a**), fine root uptake omitted (**b**), and wood uptake omitted (**c**). Scenarios are explained in Table 2. Statistics for accuracy (RMSE) and correlation (r) are presented in Figures 1 and 2 and in Tables S1 and S2. Bars indicate 95% confidence intervals of the mean via bootstrap; gray lines indicate 1:1. Black symbols indicate data from the Morton Arboretum. Color symbols indicate published data from forest FACE sites: red = Duke, orange = Rhinelander, green = Oak Ridge, blue = Pop-Euro. Open symbols indicate angiosperms; closed symbols indicate gymnosperms. Squares indicate EM associations; circles indicate AM associations; and triangles indicate AM and EM associations. Note log scale.

scenario d_4 uses a value of 1 y^{-1} for fine root turnover. Scenarios d_4 through d_6 make separate assumptions about turnover rates of fine roots less than 1 mm and those between 1 and 2 mm (Table 2), being careful to associate the correct in situ [N] with each size class.

Scenarios e_1 through e_3 explore alternative approaches to estimating wood productivity (Table 2). Scenarios e_1 and e_2 use Lambert and others (2005) allometries separated by angiosperm and gymnosperm PFTs or not separated by angiosperm and gymnosperm PFTs, respectively. Scenario e_3 uses FluxNet estimates of wood NPP to PFT (which integrates biomass and turnover) and in situ measures of hardwood [N].

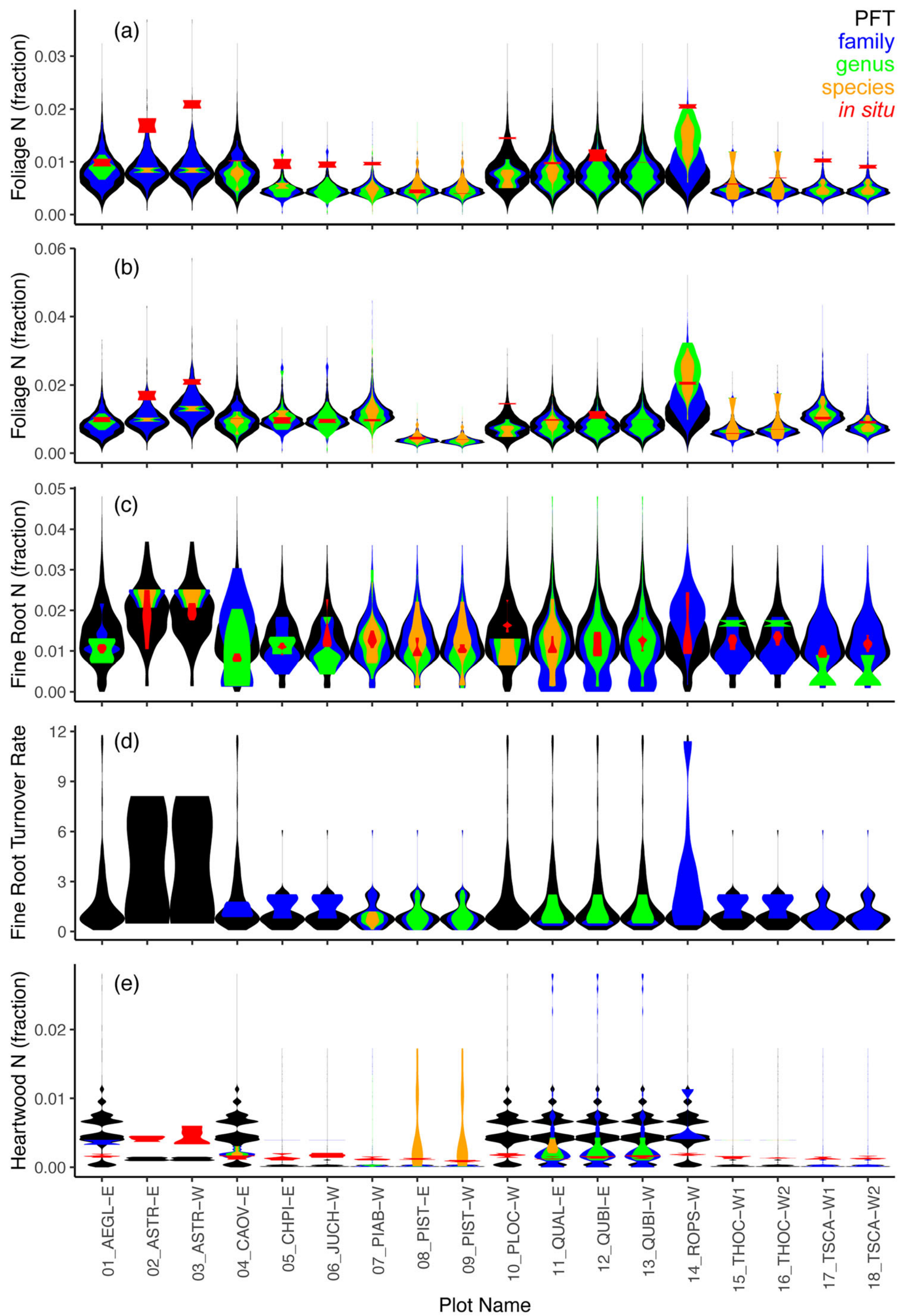
Finally, scenarios f_1 through f_4 determine the impact of alternative labor- and time-saving approaches for in situ measurements at the Morton Arboretum (Table 2). Scenario f_1 includes all of the fine roots that were collected, including fine roots that were obviously not those of a given plot's monodominant species. Similarly, scenario f_2 includes all of the foliage that was collected, including foliage that was obviously not that of a given plot's monodominant species. Scenario f_3 combines f_1 and f_2 and thus uses all fine roots and foliage collected. Scenario f_4 includes uptake into reproductive structures by using their collected dry mass per ground area and measured [N] (Eq. 3).

We present additional methodological details in the Supplemental Online Materials but summarize them briefly here. First, error is propagated in all estimates by bootstrapping over all available measurements, replicates, or subsamples 100 times. The error bars on all figures represent the approximate 95% confidence interval derived from that process. Second, database values that are unavailable for a particular species at a given taxonomic level are taken from the next higher taxonomic level that does have representative data. Third, we quantify the *accuracy* and *correlation* of a given scenario compared with the baseline scenario by measuring the root mean square error (RMSE) and correlation coefficient (respectively) between them. Smaller values of RMSE represent a more accurate scenario, whereas larger values of the correlation coefficient represent better correlation.

Results

Are Foliage, Fine Root, and Wood Nitrogen Uptake Measurements all Needed?

Omitting foliage nitrogen uptake from calculations consistently reduced accuracy across sites and taxa but preserved correlations (Figures 1, 2, 3a). The accuracy was especially poor at Duke FACE and Rhinelander FACE. Omitting fine root nitrogen uptake from calculations had divergent results at different sites. At Morton Arboretum and Oak Ridge FACE, omitting fine roots dramatically reduced both accuracy and correlations across taxa, whereas the other FACE sites retained both accuracy and correlation (Figures 1, 2, 3b). Omitting wood nitrogen uptake from calculations largely retained accuracy and correlation at every site and



(a)
(b)
(c)
(d)
(e)
PFT
family
genus
species
in situ
Foliage N (fraction)
Fine Root N (fraction)
Fine Root Turnover Rate
Heartwood N (fraction)
01_AEGL–E
02_ASTR–E
03_ASTR–W
04_CAOV–E
05_CHPI–E
06_JUCH–W
07_PIAB–W
08_PIST–E
09_PIST–W
10_PLOC–W
11_QUAL–E
12_QUBI–E
13_QUBI–W
14_ROPS–W
15_THOC–W1
16_THOC–W2
17_TSCA–W1
18_TSCA–W2
Plot Name

◀**Figure 4.** Distributions of trait values by plot for senesced foliage nitrogen concentration using fresh foliage nitrogen concentration data from TRY and applying a single retranslocation factor for all taxa (**a**), senesced foliage nitrogen concentration applying in situ retranslocation values to TRY data (**b**), fine root nitrogen concentration (**c**), fine root turnover rate (per year) (**d**), and heartwood nitrogen concentration assuming a single retranslocation value for TRY data (**e**). Color indicates the specific data source and taxonomic resolution with database data aggregated at the functional group (black), family level (blue), genus level (green), and species level (orange), as well as in situ measurements (red). The width of violins is scaled to allow nested data to be visualized and thus does not permit comparisons of sample sizes between taxonomic levels. Missing colors indicate missing data at a particular level. For (**a**), TRY data are on fresh foliage and thus are multiplied by (1–0.62) to adjust for retranslocation. For (**d**), TRY data are on sapwood and thus are multiplied by (1–0.24) to adjust for retranslocation. Note, there are no in situ fine root turnover measurements because minirhizotron tubes are, at the time of writing, still establishing. Plot names indicate monodominant species: AEGL = *Aesculus glabra*, ASTR = *Asimina triloba*, CAOV = *Carya ovata*, CHPI = *Chamaecyparis pisifera*, JUCH = *Juniperus chinensis*, PIAB = *Picea abies*, PIST = *Pinus strobus*, PLOC = *Platanus occidentalis*, QUAL = *Quercus alba*, QUBI = *Quercus bicolor*, ROPS = *Robinia pseudoacacia*, THOC = *Thuja occidentalis*, and TSCA = *Tsuga canadensis*. ''W'' and ''E'' refer to the plot's location (west or east) on the Morton Arboretum grounds.

across all taxa except for the coppiced system, Pop-Euro FACE, where it dramatically decreased both measures (Figures 1, 2, 3c).

Are In Situ Nitrogen Concentrations Needed or Can Trait Database Values Be Substituted? If Trait Database Values are Used, What is the Best Taxonomic Level?

We measured senesced foliage nitrogen concentration in situ at the Morton Arboretum, which helpfully sidesteps the need to measure retranslocation, but the vast majority of TRY database foliage nitrogen concentrations are on fresh foliage. Using a published general retranslocation fraction to adjust the TRY data showed that although our in situ measurements fell within the distribution of adjusted TRY data, the in situ measurements tended to fall toward the upper extreme (Figure 4a). Using taxa-specific in situ retranslocation values from the Morton Arboretum together with the TRY data generally placed the in situ measurements closer to the center of each species' distribution (Figure 4b). However, using in situ retranslocation values together with trait database nitrogen concentrations is not a practical way to simplify nitrogen uptake calculations because if a site has in situ retranslocation values, then it necessarily has in situ senesced foliage nitrogen concentrations, obviating the need for database values. Our in situ fine root nitrogen concentration measurements fell largely within the center of the TRY database distributions (Figure 4c). Similar to foliage nitrogen retranslocation adjustments, we adjusted TRY database sapwood nitrogen concentrations using a published general retranslocation fraction to approximate heartwood nitrogen concentrations. Our in situ heartwood nitrogen concentration measurements largely fell within the adjusted TRY database distributions, but those distributions are far from normally distributed and are generally multimodal (Figure 4e). Due to the multi-year time course required to accurately assess fine root turnover, we were unable to derive species-specific estimates for taxa at the Morton Arboretum, and the availability of database estimates remains sparse.

Using trait database nitrogen concentration values had divergent effects on accuracy and correlation across sites and taxa and across different taxonomic levels of database aggregation (Figure 5). First we consider the Morton Arboretum data. Using database nitrogen concentrations was generally accurate and highly correlated for AM-associating species and, to a slightly lesser extent, angiosperms (Figures 1, 2, 5). For EM-associating species and gymnosperms, accuracy and correlation were high when tissue nitrogen concentrations were aggregated at the PFT or family level, but they became progressively worse when traits were aggregated at the genus or species level (Figures 1, 2, 5). This is largely driven by root nitrogen concentrations in EM-associating gymnosperm *Tsuga canadensis*, where in situ values are near the center of the trait database distributions at the PFT and family levels but which are entirely outside of the distributions at lower taxonomic levels (inspect Figure 4c for plots 17 and 18). Indeed, isolating foliage, fine root, and wood database nitrogen concentrations for Morton Arboretum data indicates that foliage and wood values are highly accurate and correlated (Figures 1, 2, S1, S3), whereas fine root values drive the patterns described above (Figures 1, 2, S2). Trait database nitrogen concentrations used for Duke FACE and Rhinelander FACE were quite accurate and well-correlated across tissues and taxonomic aggregation (Figures 1, 2, 5, S1, S2, S3). Trait database nitrogen concentrations used for Oak Ridge FACE were

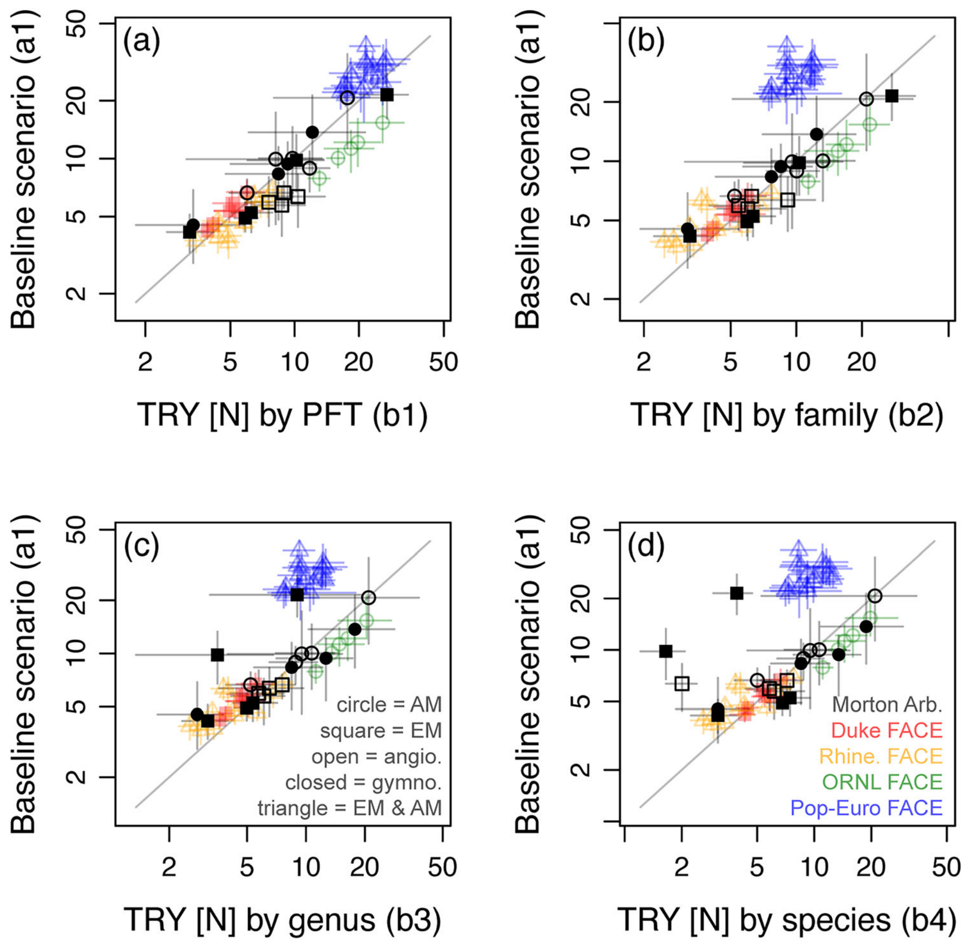


Figure 5. Nitrogen uptake rates (g N m^{-2} y^{-1}) calculated via the baseline scenario (that is, as many in situ measurements as are available) versus calculations that use TRY tissue nitrogen concentration data aggregated at the level of PFT (**a**), family (**b**), genus (**c**), and species (**d**). For plots without data available down to the specified taxonomic level, a higher available taxonomic level is substituted. Scenarios are explained in Table 2. Statistics for accuracy (RMSE) and correlation (*r*) are presented in Figures 1 and 2 and in Tables S1 and S2. Other details are explained in the Figure 3 legend. Note log scale.

highly correlated but suffered from reduced accuracy, especially at higher taxonomic levels as a consequence of mismatches in wood nitrogen concentration (Figures 1, 2, 5, S1, S2, S3). Also driven by mismatches in wood nitrogen concentration, Pop-Euro FACE exhibited the worst accuracy and correlation of all the sites (Figures 1, 2, 5, S1, S2, S3). Like the Morton Arboretum but unlike Oak Ridge FACE, the accuracy of Pop-Euro FACE declined at lower taxonomic levels.

Can Allometric Relationships or Stand-Level Database Values Replace the Need for In Situ Leaf Litter Production Measurements?

Using Lambert and others (2005) stem diameter-based foliage allometry to approximate foliage production at Morton Arboretum was far less accurate or correlated with in situ measures than simply omitting foliage altogether (Figures 1, 2, S4a). Using PFT-level foliage production values from FluxNet sites produced estimates of nitrogen uptake that were highly correlated at all the sites and across all the taxa (Figures 2, S4b). However, only at Oak Ridge FACE and Pop-Euro FACE were the values using FluxNet foliage production accurate (Figure 1). At the Morton Arboretum, estimates using FluxNet foliage production were comparable to the accuracy of omitting foliage altogether (Figure 1). The accuracy at Duke FACE and Rhinelander FACE was comparable to that at Morton Arboretum (Figure 1).

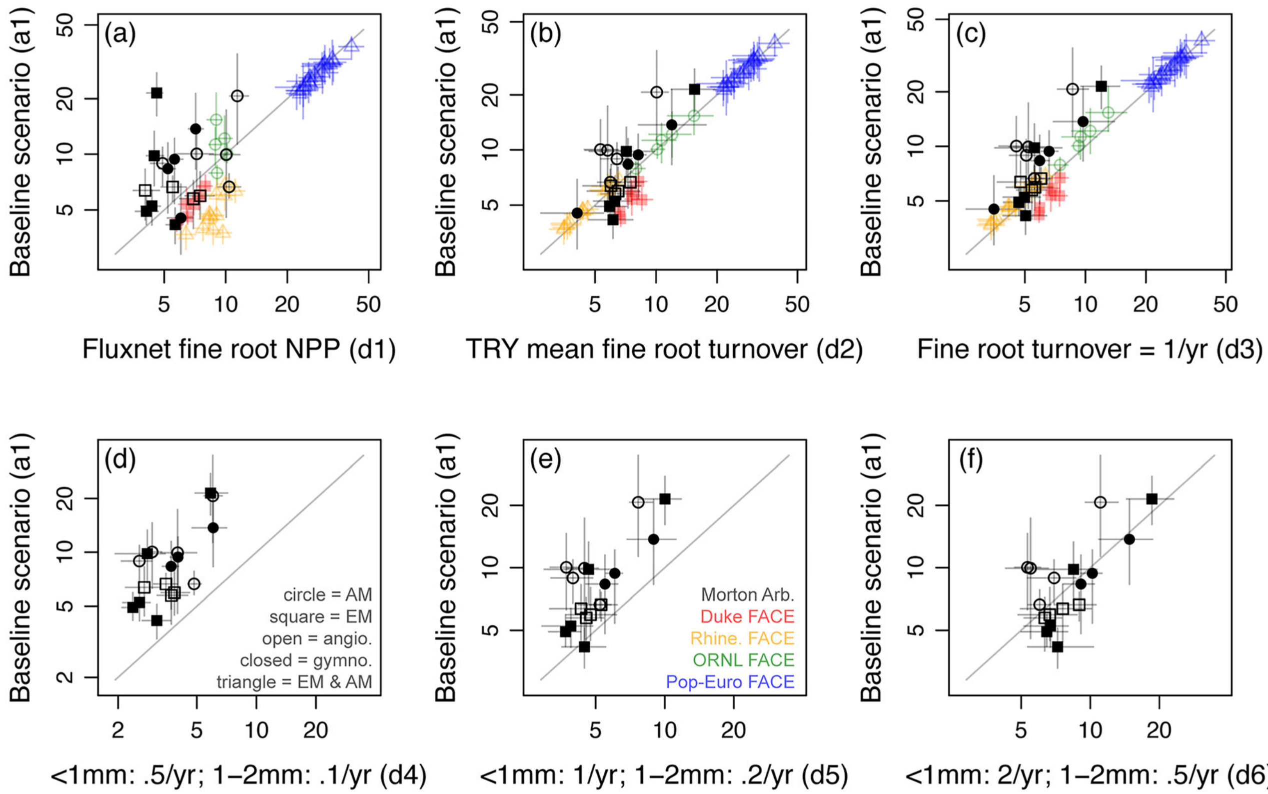


Figure 6. Nitrogen uptake rates (g N m^{-2} y^{-1}) calculated via the baseline scenario (that is, as many in situ measurements as are available) versus calculations using Fluxnet fine root NPP data to PFT (Luyssaert et al. 2007) (**a**) the grand mean fine root turnover rate from TRY data (1.338 y^{-1}) (**b**), fine root turnover rate equal to 1 y^{-1} (**c**), fine root turnover equal to 0.5 y^{-1} for roots < 1 mm and 0.1 y^{-1} for roots between 1 and 2 mm (**d**), fine root turnover equal to 1 y^{-1} for roots < 1 mm and 0.2 y^{-1} for roots between 1 and 2 mm (**e**), and fine root turnover equal to 2 y^{-1} for roots < 1 mm and 0.5 y^{-1} for roots between 1 and 2 mm (**f**). Appropriate FACE data were unavailable for (**d**, **e**). Scenarios are explained in Table 2. Statistics for accuracy (RMSE) and correlation (*r*) are presented in Figures 1 and 2 and in Tables S1 and S2. Other details are explained in the Fig. 3 legend. Note log scale.

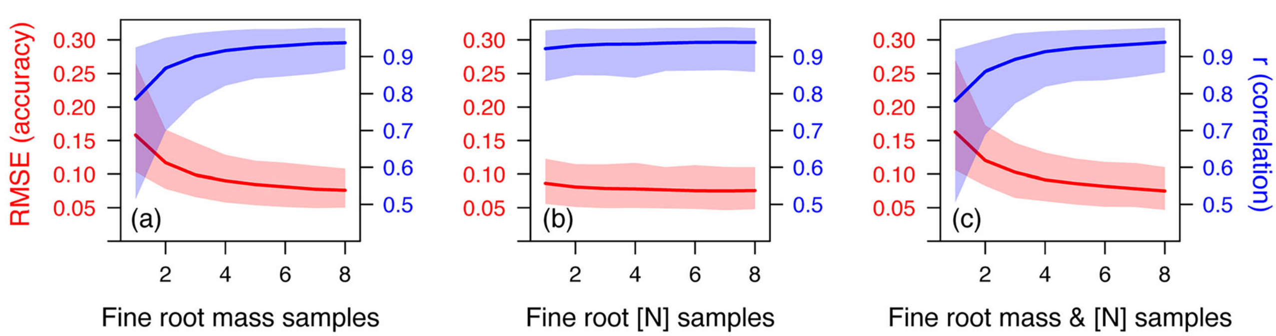


Figure 7. Power analysis of sample sizes per plot for the 18 Morton Arboretum plots: fine root biomass (**a**), fine root nitrogen concentration (**b**), or both (**c**). Values were randomly chosen (with replacement) from existing data 1000 times per plot at each sample size. In comparison with estimates using the full data set (that is, baseline scenario a_1), smaller values of RMSE (red) indicate greater accuracy and larger values of *r* (blue) indicate greater correlation. Shaded bands show 95% confidence intervals.

Can Allometric Relationships or Stand-Level Database Values Replace the Need for In Situ Fine Root Production Measurements? How Much do Assumptions About Fine Root Turnover Rates Matter to the Total Nitrogen Uptake Estimate and/or the Ranking of Sites by Total Nitrogen Uptake?

Using FluxNet PFT-level fine root production values led to highly inaccurate and poorly correlated nitrogen uptake estimates across all taxa at the Morton Arboretum, Rhinelander FACE, and Oak Ridge FACE (Figures 1, 2, 6a). Accuracy and correlations at Duke FACE and Pop-Euro FACE were better (Figures 1, 2, 6a). At the Morton Arboretum, using mean TRY fine root turnover (Figure 6b), turnover of once per year (Figure 6c), or three reasonable assumptions about differential fine root turnover rates for different fine root size classes (Figure 6c–e) all generated estimates of nitrogen uptake that were inaccurate and poorly correlated with the in situ measurements irrespective of taxa (Figures 1, 2). In contrast, the FACE sites generated accurate and well-correlated estimates of nitrogen uptake (Figures 1, 2) using mean TRY fine root turnover (Figure 6b) or turnover of once per year (Figure 6c), although Duke FACE was slightly less accurate or well-correlated.

Calculations of absolute nitrogen uptake rate using as few as two in situ measures of fine root nitrogen concentration per plot were accurate and well correlated with the default calculations using all eight measures per plot (Figure 7b). In contrast, we found that calculations of absolute nitrogen uptake rate required at least five in situ measures of fine root biomass per plot to approach acceptable accuracy and correlation with the default calculations using all eight measures per plot (Figure 7a, c). That said, there were still detectable improvements using six, seven, or eight measures of fine root biomass per plot (Figure 7a, c).

Can Allometric Relationships or Stand-Level Database Values Replace the Need for In Situ Wood Production Measurements?

At Morton Arboretum, using Lambert and others (2005) stem diameter-based allometries, either at the PFT level (Figure S5a) or averaged across all taxa (Figure S5b) generated nitrogen uptake estimates that were very similar to our default Jenkins and others (2003) allometries and thus accuracy and correlation were nearly perfect (Figures 1, 2, S5a, b). Using FluxNet PFT-level wood production values generated nitrogen uptake estimates that were accurate and well-correlated across all taxa and at every site except Pop-Euro FACE (Figures 1, 2, S5c). However, the accuracy and correlation at the Morton Arboretum was not greater than it would have been by omitting wood altogether (Figure 1).

Is Careful Sorting of Fine Roots and Leaf Litter Needed, and is it Necessary to Include Nitrogen Uptake into Reproductive Structures?

With the exception of the plots of two species, the AM-associating gymnosperm *Juniperus chinensis* and the AM-associating angiosperm *Asimina triloba*, the Morton Arboretum nitrogen uptake estimates were very similar (Figures 1, 2) irrespective of whether fine roots (Figure S6a), foliage (Figure S6b), or fine roots and foliage (Figure S6c) were sorted to target species. In addition, including nitrogen uptake into reproductive structures had negligible effects on nitrogen uptake estimates (Figures 1, 2, S6).

Discussion

Calculating the absolute nitrogen uptake rate of forests under natural conditions provides insights into a range of basic and applied ecological questions, most notably questions concerning forest carbon sequestration in prevalent nitrogen-limited conditions (Fisher and others 2012; Brzostek and others 2014). However, the standard methods required to measure absolute forest nitrogen uptake are data and labor intensive. Here, we found ways in which those methods could be simplified with a minimum loss of fidelity.

The Importance of Uptake into Foliage, Fine Roots, and Wood

Using PFT-level estimates of foliage and wood production produced similar correlations and maintained or improved accuracy relative to scenarios in which these pools were omitted from total nitrogen uptake estimates, indicating that in situ measurements of foliage and wood production may not be necessary for estimating total nitrogen uptake or assessing relative uptake rates within and across sites. Across plots and taxa, omitting foliage nitrogen uptake rate or wood nitrogen uptake rate largely preserved relative rankings of stands within a given site (Figures 2, 3a, c) but had modest (the Morton Arboretum) to severe (FACE sites) impacts on accuracy (Figures 1, 3a, c). The relative rankings are preserved because a similar fraction of nitrogen is allocated to foliage and a similar fraction of nitrogen is allocated to wood at a given site. Thus, omitting these fractions does not affect the plots' relative rankings. However, the sites differed in the absolute amount of nitrogen allocated to foliage or wood, and thus measures of accuracy suffered in proportion to the magnitude of allocation. Specifically, foliage nitrogen uptake was well correlated with total nitrogen uptake across sites, so although omitting this component reduced total nitrogen uptake rate estimate accuracy (Figures 1, 3a), it maintained plot ranking (Figures 2, 3a). Replacing in situ measurements of foliage biomass production rates with FluxNet NPP values at the PFT level increased or maintained accuracy relative to omissions and produced comparable correlations (Figures 1, 2, 3a, S4b). Similarly, when wood nitrogen uptake was a major component of total nitrogen uptake, FluxNet wood NPP values also improved nitrogen uptake estimates relative to omitting wood entirely (Figures 1, 2, 3c, S5c), although they tended to underestimate total nitrogen uptake at Pop-Euro FACE.

Relatively low accuracy and correlations among several fine root turnover scenarios suggest that collecting plot and species-specific fine root turnover rate data is critical for accurately estimating total nitrogen uptake rates. Because fine root nitrogen uptake does not appear to be correlated with aboveground nitrogen uptake, omitting roots dramatically decreased accuracy in and correlations with total nitrogen uptake estimates (Figures 1, 2, 3b). Simplifications involving fine root nitrogen uptake had a large impact on both accuracy and ranking at Oak Ridge FACE and across all taxa at the Morton Arboretum (Figures 1, 2, 3b, 6). Omitting fine root nitrogen uptake there would have made any ranking of plots impossible (correlations ranged from 0.42 at best to − 0.24 at worst). Using different simplifying assumptions about fine root turnover rates was generally better than omitting fine root nitrogen uptake entirely, but accuracy and correlations were still quite poor, especially at Duke FACE and the Morton Arboretum (Figures 1, 2, 6b–f). Collecting fine root biomass data in situ and applying a uniform fine root turnover rate (for example, Whittaker and others 1979) was an improvement over omitting fine roots entirely.

Using Trait Database Values

Tissue nitrogen concentrations may be an area where useful simplifications can be made using database values when in situ measurements are unavailable. Further, data aggregation at the PFT level, where many data exist, would be a better approach than using data aggregated at lower taxonomic levels, where fewer data exist. At the Morton Arboretum, accuracy and correlations were generally good when the tissue nitrogen data were aggregated at the PFT level but became progressively worse when they were aggregated at the family, genus, and species levels (Figures 1, 2, 5, S1, S2, S3). Pop-Euro FACE exhibited a similar pattern. Duke FACE and Rhinelander FACE were similarly accurate and well-correlated when using tissue nitrogen data aggregated at any taxonomic level, and Oak Ridge FACE accuracy and correlation improved slightly at lower taxonomic levels (Figures 1, 2, 5, S1, S2, S3). Taken together however, any presumed benefit of species-specific tissue nitrogen traits evidently does not outweigh the negative effects of smaller species-specific sample sizes or idiosyncratic trait database or site-specific values.

Differences Among Taxa and Mycorrhizal Association

The accuracy and correlation of root nitrogen concentration and turnover parameterization simplifications depended somewhat on tree mycorrhizal associations and taxonomy. For EM and gymnosperm species, nitrogen uptake accuracy and correlations were best when root nitrogen concentrations were taken at the family or PFT level. This pattern appears to be driven by two species in particular, *T. canadensis* and *Quercus alba*. TRY did not contain species-level fine root nitrogen concentrations for *T. canadensis* and *Tsuga* genus values underestimated *T. canadensis* fine root nitrogen concentrations. *Quercus alba* estimates were also improved when higher-level nitrogen concentrations values were used despite the availability of species-level root nitrogen concentration values in databases. Similarly, family-level wood nitrogen values led to underestimations of *Populus* wood nitrogen concentrations at Pop-Euro FACE that were corrected when values were taken at the PFT level. In contrast, while all root turnover choices reduced the accuracy of nitrogen uptake rate calculations, EM and gymnosperm stands maintained their ranks whereas AM and angiosperm species did not. Further studies are needed to determine whether these mycorrhizal association and plant taxonomic patterns were driven by a few species that happened to be in our dataset or if these are general patterns.

Caveats

We have attempted to provide accurate in situ estimates of absolute nitrogen uptake rate for comparison with a comprehensive collection of alternative estimation scenarios. However, we have no epistemic insight into the *actual* accuracy of our in situ estimates, and there are several aspects of our measurements that remain uncertain. First, although we did measure stem diameter and stem diameter growth rates in situ, we converted those measurements into wood productivity via allometric equations developed elsewhere (Jenkins and others 2003). Nevertheless, nitrogen uptake into wood was much smaller than uptake into foliage or fine roots at the Morton Arboretum (Figure 3), and even if it increased by several factors, it would remain the smallest component.

Second, estimates of fine root nitrogen uptake, in contrast to wood uptake, played a huge role in determining total nitrogen uptake rates at the Morton Arboretum, and we assumed that nitrogen retranslocation from fine roots is zero, a position best supported by data (Gordon and Jackson 2000) but nearly impossible to verify (Kunkle and others 2009). Additionally, our estimate of fine root nitrogen uptake depended on database values for fine root turnover, which may differ from in situ measurements. Finally, we treated all roots < 2 mm as ''fine roots,'' a classification routinely made in the literature (McCormack and others 2015). However, any single size cutoff—especially across taxa—is now known to be a coarse and somewhat arbitrary cutoff on a gradient between the smallest roots (which are responsible for acquisition and interaction with the rhizosphere) and larger roots (which are responsible for support and transport) (McCormack and others 2015). Beyond these considerations, belowground measurements are simply more difficult that aboveground measurements; however, our power analysis of fine root biomass sampling (Figure 7) suggests that our sample size for the Morton Arboretum plots (8 replicates) was likely adequate.

A third more general caveat relates to the nature of trait database values that are drawn from a wide and not necessarily representative collection across ecological gradients (Kattge and others 2011), such as the TRY database values we use here. Although most of the variation across all of the TRY traits is between species, up to 40% of the variation may be within species (Kattge and others 2011). In light of this, we recommend, whenever possible, using trait data collected from plants growing in similar ecological conditions to those of the study plots.

A fourth and final general caveat relates to the relatively small number of sites from which we draw data and their inevitably idiosyncratic nature. For example, the POP-Euro FACE site was evidently not nitrogen limited (Finzi and others 2007), but any affect that might have had on nitrogen uptake rate simplifications is conflated with the other idiosyncratic fact that the site was coppiced and thus likely deviated from natural allocation patterns. All five sites utilize plots that are monodominant, which is convenient for linking plant traits to their ecosystem-level consequences but does not necessarily represent diverse forests (for example, Zhang and others 2012). It is possible that interspecific interactions in diverse forests may change nitrogen uptake patterns. Although one may be tempted to weight species-specific traits by basal area, a slightly better approach would be to allometrically approximate crown area as stem diameter raised to the 1.4 power (Dybzinski and others 2011, their Appendix A). All five sites are in the temperate forest biome, limiting the inferences that can be made in other biomes. In addition, all four forest FACE sites were relatively young (Table 1), limiting the inferences that can be made to mature secondary and old growth forests.

Takeaways for Minimal-Effort Absolute Nitrogen Uptake Rate Measurements in Monodominant Stands

- Are foliage, fine root, and wood nitrogen uptake measurements all needed? The answer clearly depended on the site, with different sites exhibiting greater uptake (and thus sensitivity) to different organs. Thus, *we recommend that researchers undertake as complete a set of absolute nitrogen uptake rate measurements as possible on a small subsample of plots and use the information gleaned to possibly omit uptake into low-sensitivity organs on the balance of plots.* Indeed, it would have been possible to identify each of our five sites' greatest sensitivities with no more than three completely sampled plots (inspect Figure 3). With that information at the Morton Arboretum, for example, we could have skipped measurements of nitrogen uptake into wood with practically no loss of accuracy (Figure 1) or rank (Figure 2). Alternatively, many sites will already have measurements of biomass allocation to foliage, wood, and roots that can guide researcher time and effort toward organs with large or variable allocation and away from organs with low or consistent allocation.

- Are in situ nitrogen concentrations needed or can trait database values be substituted? If trait database values are used, what is the best taxonomic level? Using in situ measurements of tissue nitrogen concentrations to calculate absolute nitrogen uptake rates was appreciably better than using tissue nitrogen concentrations from a trait database. However, the negative impact to accuracy (Figure 1) and rank (Figure 2) was not so great, especially when the trait data were drawn at the PFT or family level. Thus, *if limited time or research effort could be better spent elsewhere, we do not see a large disadvantage to using tissue nitrogen concentrations aggregated at high taxonomic levels (PFT or family)*. Moreover, researchers can determine if their species are well-represented or poorly represented in trait databases. Poorly represented species would be more deserving of in situ measurements.
- Can allometric relationships or stand-level database values replace the need for in situ leaf litter, fine root, and/or wood production measurements? At all five sites, using FluxNet foliage, fine root, or wood NPP to PFT to calculate that component of nitrogen uptake had similar accuracy (Figure 1) and rank (Figure 2) compared with omitting foliage, fine root, or wood uptake, respectively. Thus, these NPP substitutions were bad when the uptake calculation was sensitive to the organ in question, and they were of little consequence when the uptake calculation was insensitive to the organ in question. Separately, using stem diameter-related allometric equations to estimate foliage biomass was always much worse than simply omitting foliage. Thus, *we do not advise using stand-level database NPP values or estimating foliage biomass allometrically.*
- How much do assumptions about fine root turnover rates matter to the total nitrogen uptake estimate and/or the ranking of sites by total nitrogen uptake? At sites where total absolute nitrogen uptake rates were sensitive to uptake into fine roots, assumptions about fine root turnover rates mattered a lot (Figures 1, 2). Thus, *we strongly recommend including robust in situ measures of fine root turnover and note that sites that already have established minirhizotron tubes and the person power to collect and analyze their images are well-situated to undertake the other, relatively easier measurements required to calculate absolute nitrogen uptake rates.* If in situ fine root turnover rates are simply unavailable, *we recommend using mean database values to PFT but also recommend noting the considerable uncertainty associated with that approach.*
- Is careful sorting of fine roots and leaf litter needed, and is it necessary to include nitrogen uptake into reproductive structures? Neither the sorting of fine roots and litter, nor inclusion of reproductive structures had much impact on the accuracy (Figure 1) or rank (Figure 2) of absolute nitrogen uptake rate calculations. Thus, *if limited time or research effort could be better spent elsewhere, we do not see a large advantage to sorting fine roots or foliage or for measuring nitrogen uptake into reproductive structures, at least in monodominant stands*. That said, none of our species were masting in the year of measurement; including nitrogen uptake into reproductive structures may matter in a masting year.
- Are the results of any simplifications systematically different for major plant groups, including mycorrhizal associations or plant divisions? Given the recommendations above, *we found no appreciable differences between AM-associating and EM-associating species or between angiosperms and gymnosperms that would recommend any differences in the simplifications used to calculate absolute nitrogen uptake rates* (Figures 1, 2). However, all of our insights were derived from monodominant stands; whether or how these simplifications may be applied in diverse forests is an open question.

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DATA AVAILABILITY

Data and novel source code are available in Dryad at https://doi.org/10.5061/dryad.6hdr7sr66.

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