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DO TREE SPECIES IN A BORNEAN MIXED DIPTEROCARP FOREST DISPLAY
PREFERENTIAL UPTAKE OF DIFFERENT NITROGEN FORMS?

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Abstract:

Lambir Hills National Park in Malaysian Borneo is composed of dipterocarp tree species which specialize on different soil types. Although the mechanisms contributing to this distribution of tree species are unknown, one hypothesis is that tree species at Lambir differ in their preferences for different nitrogen forms. In this study we investigated (1) whether clay soil and sandy loam soil types at Lambir differ in the availability of ammonium and nitrate and (2) whether tree species specializing on either clay soil or sandy loam soil at Lambir have differing preferences or capacities to take up ammonium, nitrate, or glycine (organic nitrogen). We expected sandy loam specialists to show a greater capacity to absorb ammonium, relative to clay specialists, and clay specialists to exhibit greater capacity to absorb nitrate, relative to sandy loam specialists. Generalist species were expected to have no preference for different nitrogen forms. We had no a priori expectations with regard to the expected uptake of glycine. An anion and cation exchange resin experiment revealed that as expected, clay soil consisted of significantly more nitrate than ammonium. However, contrary to predictions, sandy loam soil did not have significantly more ammonium than nitrate. We conducted a ^{15}N tracer experiment by injecting ^{15}N labeled solutions of nitrate, ammonium, or glycine in the soil of potted seedlings with different soil type specialization. ^{15}N and ^{13}C analysis of leaf tissue from treated seedlings did not support our hypotheses that sandy loam specialists would have significantly greater uptake of ammonium over nitrate, and that clay specialists would have significantly greater uptake of nitrate over ammonium. For a majority of the species, uptake of ammonium, nitrate, and glycine was similar. This indicates that these species have the ability to take up organic nitrogen in the form of the simple amino acid, glycine. It appears that nitrogen form preference is not likely to be a mechanism in the distribution of tree species at Lambir.

Introduction:

Many abiotic and biotic factors contribute to the maintenance of tropical tree species diversity, such as niche differences, host-specific pests which reduce recruitment near reproductive adults (the Janzen-Connell effect), and negative density-dependent growth (Wright 2000). The edaphic environment of tropical plant communities is especially important in the diversity and distribution of tropical tree species on local (Baltzer et al. 2005) and regional (Fine et al. 2004) spatial scales. In some tropical ecosystems, plant species are found highly aggregated on certain soil types, which can be described as soil-type specialization (Davies et al. 2005, Ashton 1964). Soil type specialization occurs due to differences in soil characteristics such as soil nutrient availability, hydrological status, and texture, as well as due to biotic interactions between different organisms in the soil (Chapin et al. 2002). Another hypothesis, which we will focus on in this study, is that tree species differ in their ability to take up and use different limiting nutrients.

Many ecosystems have displayed soil type specialization of plants due to preferential uptake of certain nutrient forms in the soil, such as the often-limiting soil nutrient nitrogen (N) (Chapin et al. 2002). All plants require nitrogen for cellular and metabolic activity. The availability of N-forms varies between different soil types due to microbial immobilization-mineralization dynamics and cation exchange capacity (Chapin et al. 2002). Nitrogen exists in three forms in soil that are available for plant uptake: organic N, ammonium (NH_4^+), and nitrate (NO_3^-). Organic N in soil organic matter (SOM) is mineralized by microorganisms to convert SOM to ammonium, NH_4^+ , which is subsequently converted to nitrate, NO_3^- . Immobilization is the process by which NH_4^+ and NO_3^- are taken up by microorganisms or plants and converted back to organic N (Söderlund and Svensson 1976). Plants take up inorganic N-forms for use in

proteins and enzymes, such as Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the enzyme essential in plant photosynthesis (Spreitzer and Salvucci 2002) .

The classical view with regard to N uptake is that plants take up only inorganic N (NH_4^+ and NO_3^-) and not organic N (Schimel and Bennett 2004). However, recent evidence suggests that some plant species have the capacity to take up organic N, especially in N-limited environments (Harrison et al. 2007). Uptake of organic N is usually in the form of the simple amino acids, such as glycine, aspartic acid, alanine, and glutamic acid (Nasholm 2000). Although evidence exists of organic N uptake in some plant species, this is assumed to vary widely between different habitats and species because plants often take up N-forms that are the most readily available in the soil (von Wiren et al. 1997, Chapin et al. 2002). Competition at the root level for different N-forms may affect the growth and survival of plants, and therefore their distributions among soils with different supply rates of N-forms. Although plant species often absorb the most abundant inorganic N-form within their habitat, they may alternatively preferentially absorb a particular N-form as an adaptive mechanism, in turn leading to differences in competitive dominance along edaphic gradients.

Several plant communities display species distributions based on preferences for different N-forms. An interesting example concerns failed reforestation efforts for late-successional conifer species on disturbed soils of boreal and subalpine environments, and the subsequent take-over of early-successional species. Kronzucker et al. (1997) found that the changing species distribution after disturbances such as clear cutting was due to the different compositions of N-forms in pre and post-disturbance soil. Undisturbed soil underlying late-successional forests is enriched in NH_4^+ , whereas disturbed soil is enriched in NO_3^- . Late-successional conifer species

have a greater capacity to absorb NH_4^+ over NO_3^- , and therefore are out-competed on high NO_3^- soil by species that take up NO_3^- more efficiently, such as early-successional conifers.

Although some plant species may always prefer one form of N, other species have been shown to alter N-form uptake in the presence of different competitor plant species nearby. Some alpine tundra species display such plastic N preferences: they are able to absorb all N-forms, but alter N-form preference when competing with other species for limited space and resources (Miller et al. 2007). In the alpine tundra N strongly limits plant growth, which Miller et al. specify as the driving factor in variation among species for N-form uptake. In N-limited environments, plasticity in N-form preference may be adaptive when competing with other species.

Plant species may not only compete with neighbors for N, but also with microorganisms in soil. With growing awareness that some plants are able to utilize dissolved organic N in the form of amino acids, the role of organic N in plant species competition and distribution in N-limited environments has become a topic of interest. A recent study of temperate grassland plant species found that although grasses took up inorganic N at a higher rate than organic N, they were able to compete with microorganisms for amino acids of varying size (Harrison et al. 2007).

The capacity to take up different N-forms should be adaptive in N-limited environments, assuming that costs of such plasticity are not high. The ability of certain species to preferentially absorb a certain N-form may lead to niche partitioning across an edaphic gradient, as seen in the above examples of boreal, alpine tundra, and grassland ecosystems. Although this hypothesis has not been tested in tropical environments, it is possible that such a mechanism of species distribution is at play in N-limited tropical forests as well. We would be most likely to see N-

form preference as a mechanism contributing to tree species distribution in the tropical forests where tree species aggregate on certain soil types. This type of plant species distribution is seen at Lambir Hills National Park in Malaysian Borneo, in which many dipterocarp tree species specialize on either clay or sandy loam soil (Davies et al. 2005).

The mechanisms causing tree species to specialize on different soil types at Lambir are unknown. One hypothesis to explain soil-correlated tree species distributions is that species have varying preferences, or capacities to take up different N-forms. The purpose of this study was to investigate (1) whether clay soil and sandy loam soil types at Lambir differ in the availability of NH_4^+ and NO_3^- and (2) whether tree species specializing on either clay soil or sandy loam soil at Lambir have differing preferences or capacities to take up NH_4^+ , NO_3^- , or organic N.

A study from a nearby site in Sabah, Borneo, in which tree species also show distinct soil type preference, found that alluvial soils in valleys had significantly higher NO_3^- concentration, whereas sandstone soils on ridges had significantly higher NH_4^+ concentration (Baltzer et al. 2005). These observations led us to hypothesize that soil type specialization at Lambir may partially arise due to preferences for different N-forms. We expected clay and sandy loam soil at Lambir to differ in N-form content in parallel with soils in Sabah. We also expected sandy loam specialists to show a greater capacity to absorb NH_4^+ , relative to clay specialists, and clay specialists to exhibit greater capacity to absorb NO_3^- , relative to sandy loam specialists. Generalist tree species, which are similarly abundant on both soils, were expected to have no preference in their absorption of either NO_3^- or NH_4^+ . We had no a priori predictions regarding organic N, and our goal was to identify whether these Bornean species displayed any capacity for taking up organic N in the form of glycine.

Methods:***Study Area:***

Lambir Hills National Park (4° 11' N, 114° 01' E) in Northern Sarawak, Malaysian Borneo, consists of 6,952 ha of lowland mixed dipterocarp rainforest, and has the highest tree species richness recorded in the Paleotropics (Lee et al. 2002). Lambir receives 3000 mm of rainfall per year, with greater than 100 mm of rain in all months (Watson 1985). This study was conducted in the summer of 2010 near and within a 52-ha research plot at Lambir established by the Center for Tropical Forest Science in 1991. The research plot consists of tall, slim-boled and high-buttressed trees, and a dense canopy at 40-50 m. There are approximately 1200 species of trees within the plot, Dipterocarpaceae being the dominant family and the focus of this study (Lee et al. 2009).

Soils at Lambir are sandstone or shale-derived. Sandstone-derived soils, which are found on ridges and slopes, are humult utisols or sandy haplic Acrisols with a raw humus surface and low nutrient and water retention. Shale-derived soils, found in low-lying gullies, are relatively fertile clay-rich utisols (Bailie et al. 2006). Four soil types (sandy loam, loam, fine loam, and clay) have been described based on differences in soil nutrients (C, N and P and exchangeable K, Ca and Mg) and elevation (Davies et al. 2005). Davies et al. (2005) found that of the more abundant species at Lambir, 85% had distributions significantly aggregated based on soil chemistry and topography, indicating that most tree species at Lambir specialize on one of these four soil types. Here we focus on two soil types, clay and sandy loam, at the extremes of this gradient.

Quantification of NH_4^+ and NO_3^- supply rates:

Anion and cation exchange resins were used to quantify NO_3^- and NH_4^+ nutrient supply rates on each soil type within the 52-ha plot at Lambir. Three grams dry weight of cation (for NH_4^+) or anion (for NO_3^-) exchange resins (DOWEX 50WX8 and DOWEX 1X8 respectively, Sigma Aldrich) were placed in nylon stocking bags. Bags containing resins were washed three times in 0.5 M NaCl for 10 minutes each to ensure exchange of H^+ for Na^+ on the cation exchange resin and exchange of OH^- for Cl^- on the anion exchange resin, which minimizes the change in pH around the resin bags when buried in the ground.

Within the 52-ha research plot, three resin bags of each type were buried at 10cm depth in 12 sandy loam plots and 12 clay plots in August 2010, and removed five weeks later. Resin bags were rinsed with distilled, deionized water to remove soil, air-dried, and shipped to the laboratory at the University of Nebraska-Lincoln to extract the soil nutrients. Resin from each bag was removed and placed in an extractant solution of 100 ml 1 M KCl. The resin was shaken in the extractant overnight on a reciprocal shaker. The final dry mass of resin was recorded for each bag. Nutrient Concentrations of NH_4^+ and NO_3^- in the KCl solution were determined with a Lachat Quick Chem 8500 (Lachat instruments, Loveland, CO.). Supply rates were expressed as: mg N/g resin-day.

^{15}N Isotope Tracer Experiment:

A ^{15}N stable isotope tracer experiment was conducted in a shade house at Lambir to identify if species specializing on different soil types have different capacities to take up N-forms. Seedlings of twelve dipterocarp species were used, comprising four congeneric pairs specializing on either clay or sandy loam soil, two additional sandy loam specialists, and two generalist species (Table 1). Seeds of these species were collected in and near Lambir during a

masting event in the previous year, and planted in poly bags containing clay forest soil. Seven to eight individuals per species (a total of 343 potted seedlings) were randomly treated with a total of 10 mL of one of four solutions: $\text{K}^{15}\text{NO}_3^-$ (0.509 mM/L ^{15}N), $^{15}\text{NH}_4^+\text{Cl}$ (2.865 mM/L ^{15}N), ^{15}N glycine (0.675 mM/L ^{15}N), or distilled, deionized water (the control). Atom % of each compound was 98% (Sigma Aldrich). The solutions applied ^{15}N at a rate that was approximately twice as concentrated as the reported total available inorganic N at Lambir (Bailie et al. 2006) to allow for enough ^{15}N -tracer signal without inducing a fertilization effect. A 15-ml syringe with a 10-cm needle was used to inject 2 ml of solution through a uniform depth range of 0-7 cm at each of five injection points in the soil per pot. After 8 h of incubation, each pot was watered with 10 ml of distilled, deionized water to reduce microbial transformation of the applied N-forms. One leaf per plant was harvested at both 24 and 48 h, and then scanned and analyzed to estimate lamina area using Image J software (Rasband, W.S., ImageJ). All seedlings were harvested immediately following the 48 h leaf harvest, and separated into below and above ground tissue. Roots were washed with tap water to remove adhering soil. All seedling tissue was dried at 60° C for two weeks and then shipped to the laboratory at the University of Nebraska-Lincoln. Leaf samples were weighed, ground, and packed in tin capsules for stable ^{13}C and ^{15}N isotopic analysis with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

Statistical Analysis:

All statistical analyses were performed with R statistical software (The R Core Development Team 2006). To determine if there was a difference in NH_4^+ and NO_3^- supply rates on clay and sandy loam soil, the mg N/g resin-day for NH_4^+ and NO_3^- were compared with a one-way analysis of variance (ANOVA) with soil type as the factor.

Only leaves harvested at 48 h were used for statistical analysis due to the low ^{15}N recovery of leaves harvested at 24 h. Uptake into leaves of the ^{15}N labeled solutions was calculated from data on N content, ^{15}N atom percent in excess of natural abundance, and leaf biomass. The following formula was used to determine the μg of leaf N that was derived from the tracer for each species: $F = (N*(A - C))/98$, where N is the total nitrogen in the treated sample, $A = ^{15}\text{N}$ atom % in the sample minus the natural abundance of ^{15}N (0.3663%), C is the average ^{15}N atom % in the control samples minus 0.3663, and 98 represents the atom % of the added isotope (Hauck and Bremner 1976). Uptake rate, U ($\mu\text{g mg}^{-2}$ leaf dry mass h^{-1}), was calculated by taking the μg of leaf N derived from the tracer divided by the mass of the sample used in the ^{13}C and ^{15}N analysis and the incubation time, as seen in the following equation: $U = (F/(M*48))*1000$, where F is the μg of N derived from the tracer found in the harvested leaf, M is the mass of the sample, and 48 represents the hours of incubation before harvesting the leaves.

In order to correct for differences in ^{15}N addition between NO_3^- , NH_4^+ , and glycine treatments, relative uptake rates for each sample were calculated by dividing the absolute uptake rate, U , ($\mu\text{g mg}^{-2}$ leaf dry mass h^{-1}) as calculated above, by the total amount of ^{15}N added for that treatment. Relative uptake rates for each species were analyzed using a generalized least squares linear model, with treatment group as a fixed factor and including a fitted error variance for each group, due to heteroscedasticity (*gls* function). To identify whether soil specialists showed similar N-uptake strategies, we used a principle components analysis on species' relative uptake rates, grouping species by soil specialization. Differences between soil specialists (clay and sandy loam) and generalists were tested with multivariate analysis of variance (*adonis* function).

Results:

Soil type differences in NH_4^+ and NO_3^- supply rates

Consistent with our prediction, NO_3^- was significantly more abundant on clay than sandy loam soil ($p = 0.001$). Contrary to our prediction, NH_4^+ was not significantly more abundant on sandy loam than clay soil ($p = 0.093$; Figure 1), although NH_4^+ tended to have a greater supply rate on sandy loam.

Differences in N-form uptake rates between soil specialists:

Contrary to expectations, sandy loam specialists did not show significantly greater relative uptake of NH_4^+ over NO_3^- (Figure 2). Four of the six sandy loam specialists showed no significant differences in relative uptake rates of any N-forms, which indicates that these species have some capacity to take up glycine. Two of the six sandy loam specialists, *Vatica nitens* and *Hopea beccariana*, showed significantly more relative uptake of NH_4^+ over glycine ($p = 0.0347$ for *V. nitens*, $p = 0.0033$ for *H. beccariana*), but no significant difference between the relative uptake of NH_4^+ and NO_3^- ($p = 0.9235$ for *V. nitens*, $p = 0.5017$ for *H. beccariana*). Both *V. nitens* and *H. beccariana* had significantly greater relative uptake of NO_3^- over glycine, but for *V. nitens* this difference was only marginally significant ($p = 0.0515$ for *V. nitens*, $p = 0.0243$ for *H. beccariana*). No sandy loam specialists displayed differences in relative uptake of NH_4^+ and NO_3^- , or greater relative uptake of glycine than inorganic N-forms.

Also contrary to expectations, clay specialists did not have greater relative uptake of NO_3^- over NH_4^+ (Figure 3). Two of the four clay specialists showed no significant differences in relative uptake of any N-forms, indicating the capacity to take up glycine. *Hopea dryobalanoides* showed significantly more relative uptake of NH_4^+ over glycine ($p = 0.0355$), but no significant difference in relative uptake of NH_4^+ and NO_3^- ($p = 0.335$), nor relative uptake of glycine and

NO_3^- ($p = 0.1024$). *Shorea macrophylla* had significantly greater relative uptake of NO_3^- than NH_4^+ ($p = 0.029$), but no difference in relative uptake of glycine and NH_4^+ ($p = 0.2133$) nor of glycine and NO_3^- ($p = 0.935$). No clay specialists demonstrated significantly greater relative uptake of glycine over other N-forms, or of NH_4^+ over NO_3^- .

Consistent with our prediction, generalists did not exhibit significant differences in relative uptake of NH_4^+ and NO_3^- (Figure 4A, 4B). *Shorea smithiana* had marginally significantly greater relative uptake of NO_3^- over glycine ($p = 0.0604$), but no difference in relative uptake between glycine and NH_4^+ ($p = 0.3065$) or NH_4^+ and NO_3^- ($p = 0.6877$). *Anisoptera grossivenia* showed no difference in relative uptake between any N-form.

The principle components analysis demonstrated that soil specialists did not have distinct N-uptake strategies. The confidence ellipse of sandy loam specialists overlapped significantly with those for clay specialists, and both encompassed the generalists in all three principle component plots (Figure 5), indicating similar uptake of all N-forms for all soil specialists. In addition, differences between soil specialists in overall relative uptake of N-forms was not shown to be significant using multivariate analysis of variance ($df = 2$, $F = 1.1161$, $p = 0.369$). When generalists were excluded from the multivariate analysis of variance, differences between soil specialists in overall relative uptake of N-forms was still not significant.

Discussion:

Although clay soil had significantly more NO_3^- than sandy loam soil, sandy loam soil did not have significantly more NH_4^+ than clay soil, which was only partially consistent with our initial hypothesis that NO_3^- would have a greater supply rate on clay soil, and NH_4^+ would have a greater supply rate on sandy loam soil. Despite the significant difference in inorganic N-form abundance on clay soil, the results of our ^{15}N tracer experiment showed little support for our

hypothesis that soil specialists should have different preferences for specific N-forms. Principle components analysis and multivariate analysis of variance further support that soil type specialists did not have distinct N-form uptake strategies, but instead showed similar uptake of all N-forms. N-form preference is therefore unlikely to be an important mechanism in the distribution of tree species at Lambir among different soil habitats.

Our hypothesis that sandy loam specialists would show significantly higher uptake of NH_4^+ over NO_3^- was disproven because relative uptake of NH_4^+ and NO_3^- was similar. Although we had no a priori expectations with regard to uptake of organic N, the higher uptake of inorganic N over organic N (glycine) in two of the sandy loam specialists was not surprising, as plants are known to take up inorganic N more readily than organic N. However, the similar relative uptake of glycine and inorganic N-forms for four of the sandy loam specialists indicates that most sandy loam specialists have no preference for different N-forms, and are able to take up simple forms of organic N, such as glycine.

The higher amount of NO_3^- in clay compared to sandy loam soil led to the expectation that clay soil specialists should prefer NO_3^- over NH_4^+ ; however, this was also not supported. Just as sandy loam specialists did not have significantly higher uptake of NH_4^+ over NO_3^- , a majority of clay specialists (three out of four) did not have significantly higher uptake of NO_3^- over NH_4^+ . Only one clay specialist, *S. macrophylla*, had higher uptake of NO_3^- than NH_4^+ , which did not support our hypothesis that all clay specialists would show a trend of higher relative uptake of NO_3^- . An even greater percentage of clay specialists (75%) had similar uptake rates of inorganic and organic N compared to sandy loam specialists, which is again an intriguing result of this study.

As expected, the generalist species had no difference in uptake of inorganic N-forms. *A. grossivenia* showed no difference in uptake of all N-forms, however, *S. smithiana* had higher uptake of NO_3^- over glycine, but no difference in uptake between glycine and NH_4^- . This was expected due to the even distribution of generalists on both clay and sandy loam soils, and thus the predicted ability of generalists to take up different inorganic N-forms equally. The ability of take up organic N in similar proportion to inorganic N was also seen in generalists.

One interesting finding of this study was the pattern of similar uptake rates of organic N (glycine) and inorganic N-forms among these Bornean tree species: seven of twelve species showed similar uptake of glycine, NH_4^+ , and NO_3^- , and ten of twelve species showed similar uptake of glycine with at least one inorganic N-form. This is unexpected due to the widely-held, but relatively untested view that plants more readily take up inorganic over organic N (Schimel and Bennett 2004). However, our findings are consistent with other recent studies that have similarly found that some plant species do have the ability to take up organic N in the form of simple amino acids (Nasholm 2000, Harrison et al. 1997). Due to the relatively equal uptake rates of all N-forms by clay and sandy loam specialists, it appears that dipterocarp tree species have flexible strategies of N-uptake in this Bornean rainforest. These findings may shed new light on our understanding of N cycling and plant use of organic N in tropical ecosystems.

N-form preference does not appear to be the underlying mechanism in the distribution of tree species on clay and sandy loam soil types at Lambir, indicating that other mechanisms determine niche partitioning. Other soil nutrients may determine soil-type specialization, such as phosphorous, another often-limiting terrestrial nutrient, especially in tropical systems (Elser et al. 2007). Water and light availability may also play a role in the distribution of dipterocarp tree species at Lambir, as well as possible interspecific interactions such as competition for N

between plants and microorganism, as seen in grasslands (Harrison et al. 2007). There are many possibilities in terms of mechanisms affecting distribution of species along an edaphic gradient at Lambir, but these mechanisms are not yet understood.

Conclusions:

In summary, N-form preference does not appear to be a dominant mechanism causing tree species to specialize on different soil types in this Bornean rainforest. This was surprising due to higher abundance of NO_3^- on clay soil than sandy loam soil. The relatively equal uptake of inorganic N and glycine on clay and sandy loam soil is an indication that dipterocarp tree species are able to take up organic N in the form of glycine just as readily as inorganic N-forms, which contradicts the dominant, but untested, view that plants more readily take up inorganic N forms over organic N. The overall equal relative uptake of N-forms for clay and sandy loam specialists indicates that dipterocarp tree species have flexible strategies of N-uptake. We conclude that other mechanisms in relation to soil chemistry, hydrology, or topography may be more important contributors to niche partitioning of dipterocarp species along the edaphic gradient at Lambir.

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Table 1: Soil specialization of dipterocarp tree species with species abbreviations in parentheses.

Clay	Sandy Loam	Generalist
<i>Dryobalanops lanceolata</i> (Dryola)	<i>Dryobalanops aromatica</i> (Dryoar)	<i>Shorea smithiana</i> (Shorsm)
<i>Hopea dryobalanoides</i> (Hopedr)	<i>Hopea beccariana</i> (Hopebe)	<i>Anisoptera grossivenia</i> (Ani2gr)
<i>Shorea macrophylla</i> (Shorml)	<i>Shorea beccariana</i> (Shorbe)	
<i>Shorea xanthophylla</i> (Shorxa)	<i>Shorea laxa</i> (Shorla)	
	<i>Vatica nitens</i> (Vatint)	
	<i>Dipterocarpus globosus</i> (Diptgl)	

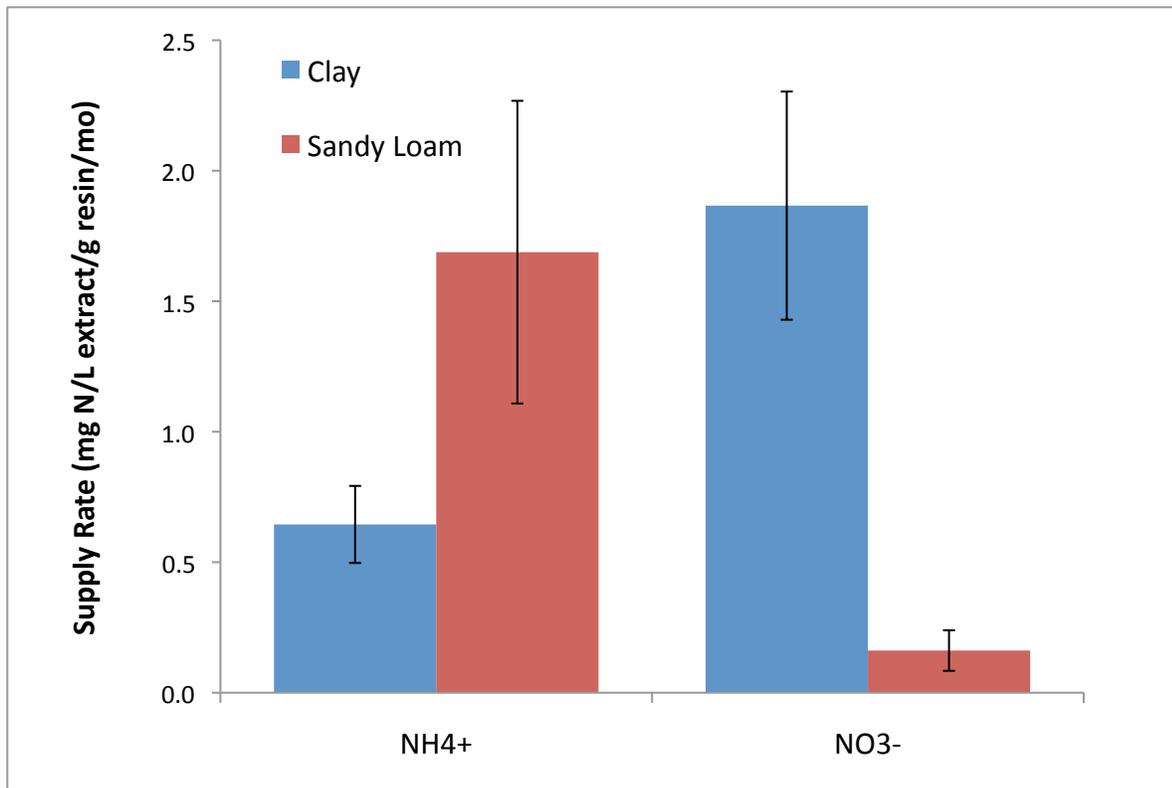


Figure 1: Nutrient supply rates (mg/L extractant /g resin/mo) for ammonium and nitrate in clay and sandy loam soil. Differences between soil types were significant for NO₃⁻ ($p = 0.001$), but not for NH₄⁺ ($p = 0.093$).

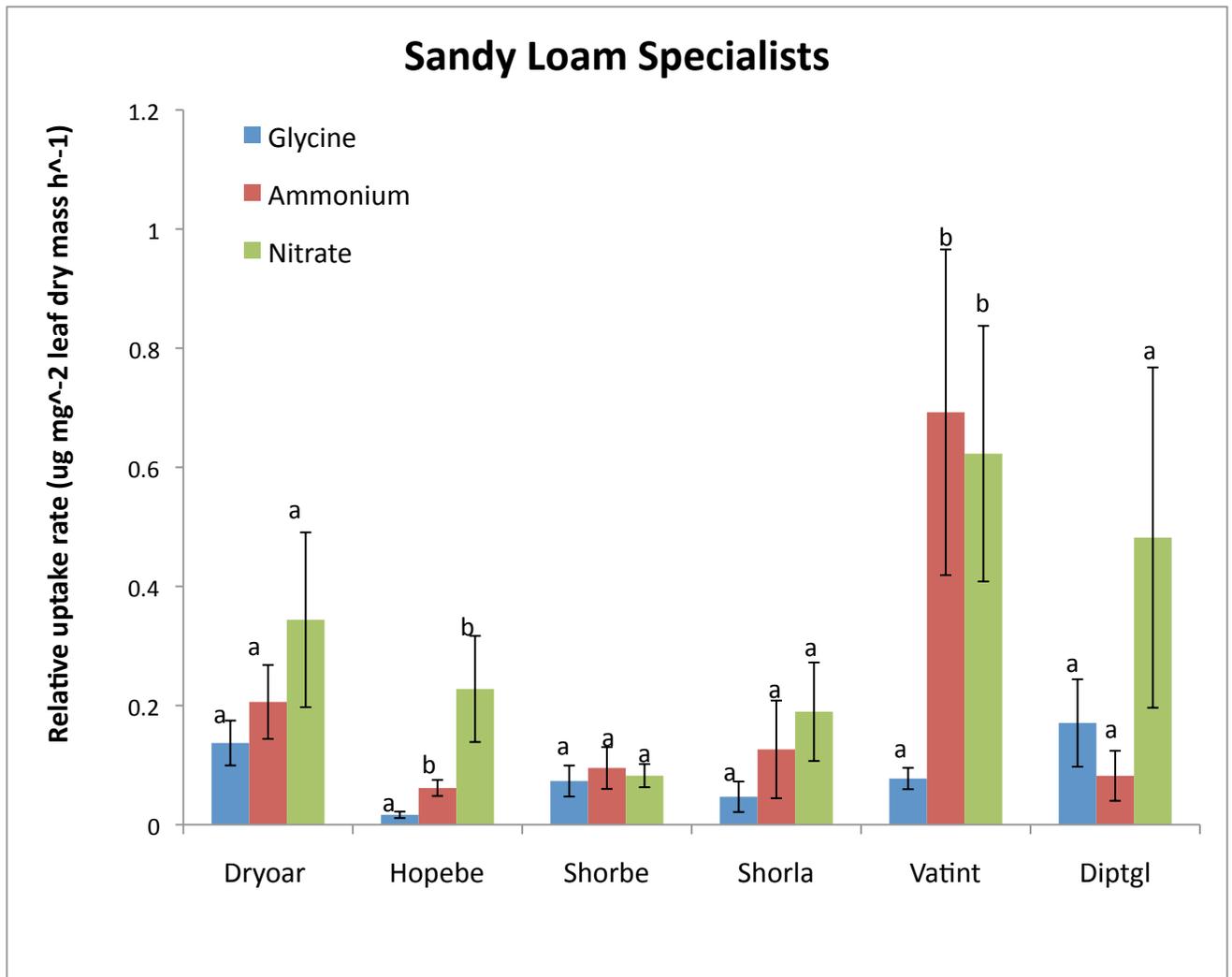


Figure 2: Leaf ¹⁵N relative uptake for sandy loam specialists after 48 hours. Lower case letters represent significant differences among treatment means for each species. Species codes are listed in Table 1. Error bars are standard errors.

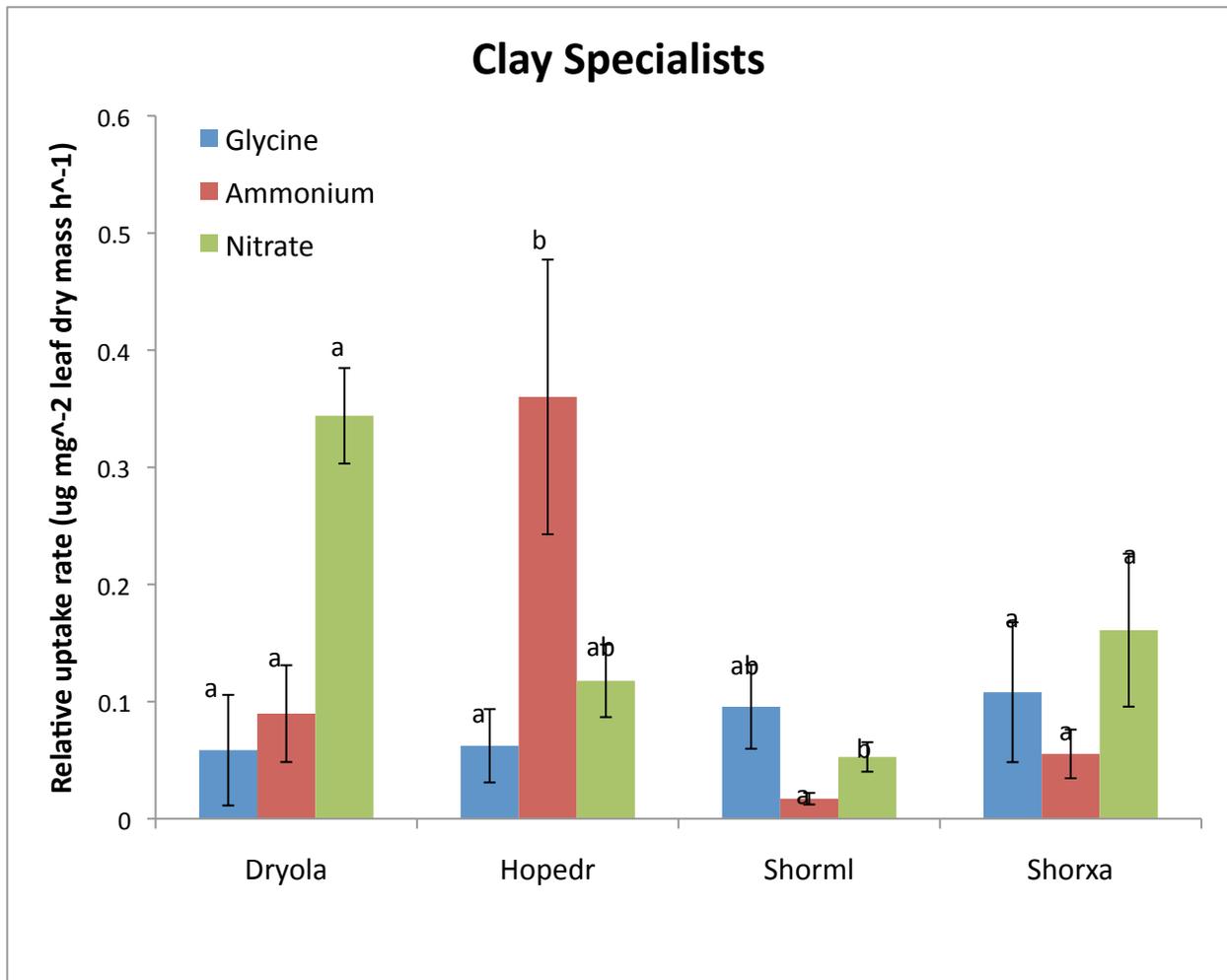


Figure 3: Leaf ^{15}N relative uptake for clay specialists after 48 hours. Lower case letters represent significant differences among treatment means for each species. Species codes are listed in Table 1. Error bars are standard errors.

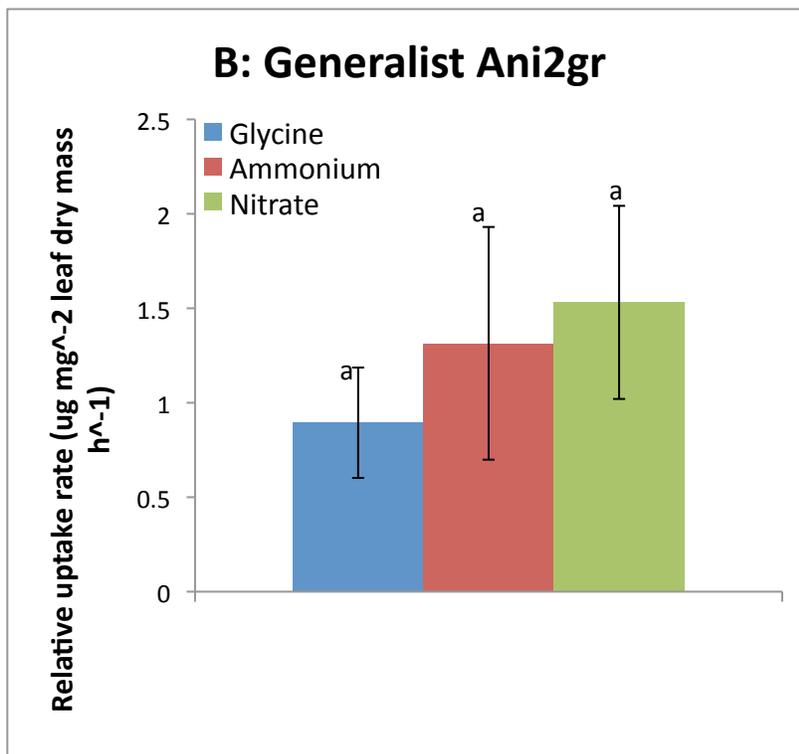
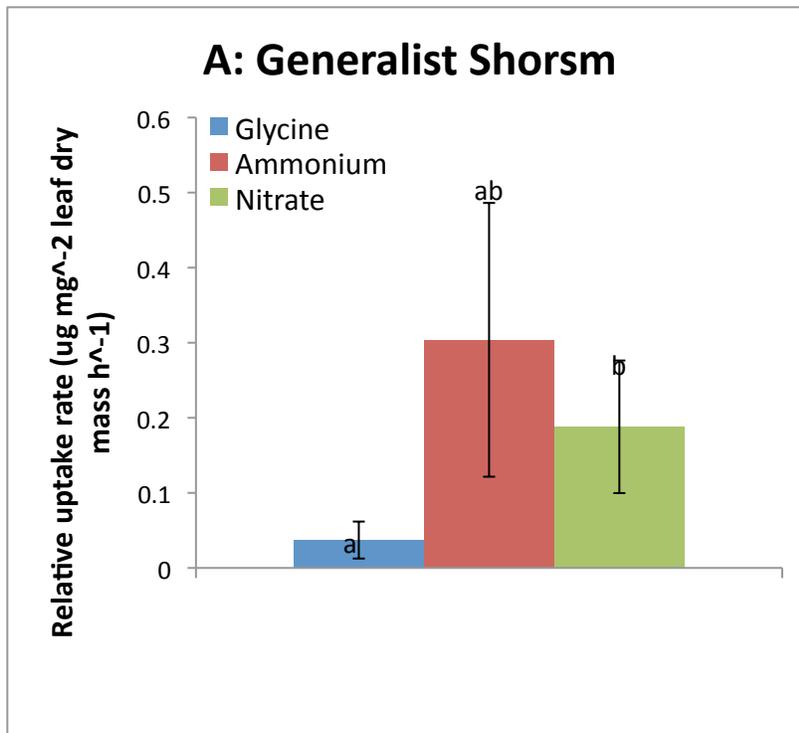


Figure 4A, 4B: Leaf ¹⁵N relative uptake for the generalist species Shorsm (3A) and Ani2gr (3B) after 48 hours. Lower case letters represent significant differences among treatment means for each species. Species codes are listed in Table 1. Error bars are standard errors.

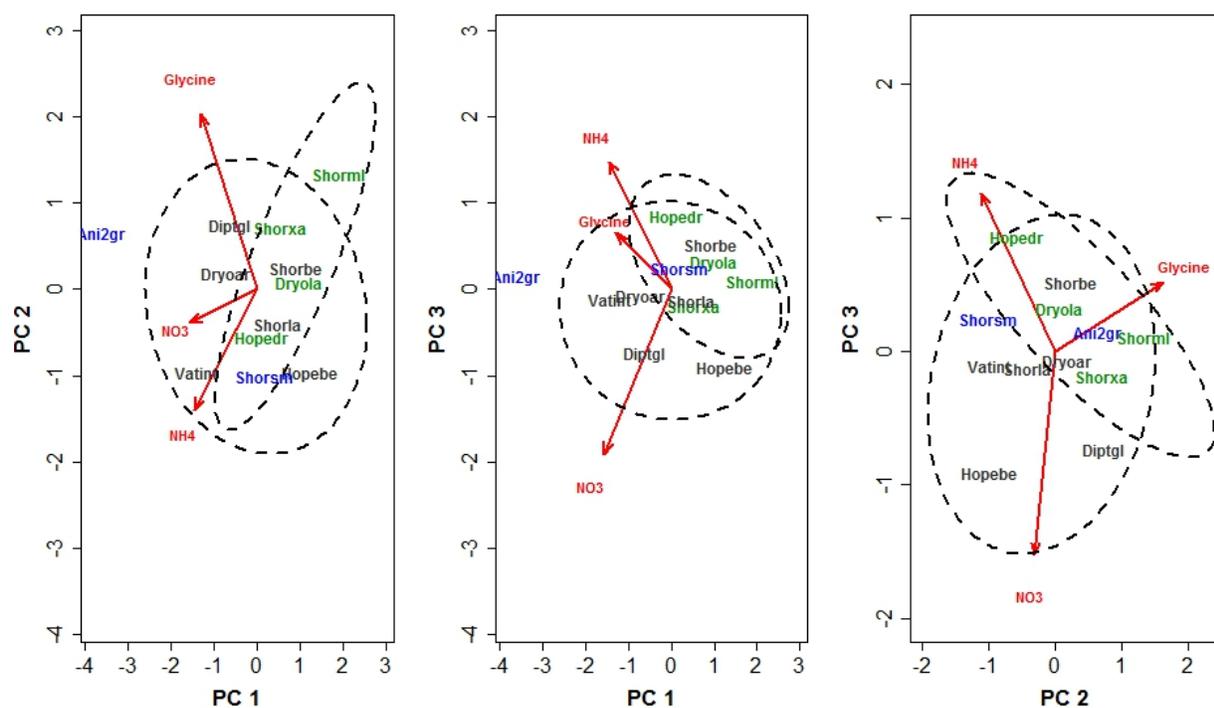


Figure 5: Plots of the first three principle components (PC), with blue indicating generalists, green indicating clay specialists, and grey indicating sandy loam specialists. The first three PC's explained 72%, 20%, and 8% of the total variation, respectively. Species codes are listed in Table 1. Ninety-five percent confidence ellipses are plotted for sandy loam (grey) and clay (green) specialists. Red arrows indicate the correlations between different N-forms (NO₃⁻, NH₄⁺, and glycine) and the principle components.