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Nitrogen Fixing Shrubs Create Soil N Fertility Patches in Native Sand Dune and Tallgrass-Prairie Communities of Central North America

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ABSTRACT

In sand dune ecosystems, native, actinorhizal (*Frankia*-nodulated, N-fixing) speckled alder trees (*Alnus incana* (L.) Moench ssp. rugosa (Du Roi) R.T. Clausen), and the native, N-fixing leguminous shrub leadplant (*Amorpha canascens* Pursh) both had elevated soil amino sugar N concentrations, an indicator of soil N fertility, beneath their canopies. For background comparisons soil adjacent samples were also taken 2 m from the N fixing shrub shrub and at least 4 m from any other N-fixing plant canopies. Elevated soil amino sugar N patches contribute to the compositional and functional diversity of ecosystems. The alder patches had 51 and 62% increases in soil amino sugar N concentrations over respective, background soil levels of 51 and 73 mg kg^{-1} amino sugar N at two sand dune locations with loamy fine sands along Lake Michigan in Wisconsin. Leadplant had soil amino sugar N levels 7% greater than an adjacent background level of 487 mg kg^{-1} in a black-soil-prairie silty clay loam and 46% greater than an adjacent background level of 37 mg kg^{-1} at a sand dune location with a loamy fine sand. Actinorhizal Canada buffaloberry (*Shepherdia canadensis* (L.) Nutt.), New Jersey tea (*Ceanothus americanus* L.) and, at one location, leguminous leadplant did not have different amino sugar N concentrations in soils beneath their crowns than in adjacent soils lacking N-fixing plants. Alder shrubs were larger than other N-fixing plants studied and occurred on mesic, sheltered, lower-dune slopes. Lead-plant, a leguminous shrub widespread in grassland ecosystems, had higher levels of amino sugar N beneath their canopies than levels occurring in background soils in a rich prairie Mollisol. This increase was comparable in amount, but lower in percentage, than the increase that occurred on a sandy, infertile soil. In a second prairie Mollisol, there was no increase in soil amino sugar N under leadplant shrubs. Buffaloberry did not have higher amino sugar N concentrations than surrounding soils in either of two locations where it was found. Buffaloberry occurred on sand dunes, but on drier sites (dune ridges) than alder at the same locations. New Jersey tea occurred in three locations: two with rich black prairie soils and another with coarse, dry sand, but its associated soils did not have elevated levels of amino sugar N. The lack of accretion of soil amino sugar N at some locations probably was a result of high levels of available soil N and dry conditions, both of which can inhibit N fixation. Even though all N-fixing shrubs in this study were nodulated, accretion of fixed nitrogen in soil under these shrubs occurred primarily at sites on lower, sheltered dune slope positions, sites having higher soil moisture holding capacities and where there was lower background soil nitrogen fertility.

Key words: actinorhiza; *Alnus*; *Amorpha*; *Ceanothus*; nitrogen fixation; nitrogen-fixing trees; *Shepherdia*

INTRODUCTION

Actinorhizal (*Frankia*-nodulated) trees can increase the accretion of soil nitrogen (N) through symbiosis as indicated by measured increases of various forms of soil N (Dawson et al. 1983; Friedrich and Dawson 1984; Paschke et al. 1989: Giardina et al. 1995; Hart et al. 1997; Rothe et al. 2002). Measures of actinorhizal and other N-fixing tree and shrub influences on soil N include increases in total soil N concentration, soil N mineralization rates and N cycling (Bormann et al. 1993). The N fixed symbiotically is released to the soil primarily by decomposition of N-enriched litter and sloughed roots. Many methods that are used to estimate soil N contributions of N-fixing trees produce contradictory results and are not useful for estimating soil N fertility. For instance, some forms of N detected in soils are resistant to decomposition and so there is no consequent release of inorganic N compounds necessary for plant uptake. The growth of valuable black walnut trees (*Juglans nigra* L.) in interplantings with actinorhizal *Elareagnus umbellata* L. shrubs in a controlled field experiment was correlated with net annual N mineralization rates estimated using an in-situ buried-bag technique (Paschke et al. 1989). However, *J. nigra* growth was not correlated with total soil N concentrations determined using the classical Kjeldahl total N determination method in the same plots. Hence, even when total organic N is correlated with plant growth, it is not recommended as an index for the capacity of soil to supply N to plants because it oversimplifies N cycling and transformations in the soil (Wang et al. 2001).

Walley et al. (2002) evaluated several soil-available-N indices to examine the size of the N pool available for crop uptake. Most did not account for N accretion in crops and no single index seemed to adequately predict N fertilization requirements. Measurements of net or gross mineralization processes have often been used to estimate the N fertility of a soil. N-mineralization rates can be determined by several methods including ^{15}N natural abundance, ^{15}N tracers, ^{15}N isotope dilution, inorganic-N adsorptive resin cores, buried resin bags, closed-top tubes and aerobic incubations (Hart et al. 1994). Wang et al. (2001) suggested that net N mineralization assays, even in-vivo assays using buried bags, do not represent N mineralization in soils with total accuracy because simultaneous mineral N uptake by plants occurs in nature during the course of mineralization. They used gross N mineralization in laboratory incubations of soil cores as their preferred index.

Numerous studies have emphasized the need to obtain reliable soil N availability indices in order to predict and evaluate soil N fertility in crop production and for recommending fertilization (Bundy and Meisinger 1994; Walley et al. 2002). No accepted standards have yet been formulated for agricultural soils, let alone for soils of complex native plant communities. Methods for assessing N availability in forest soils, particularly through use of an anaerobic incubation method, were reviewed by Keeney (1980). However, incubation methods are time consuming and must be refined to accurately estimate net soil mineralization in the field (Picone et al. 2002). Thus, attempts have been made to develop rapid chemical, rather than biological, methods to estimate potentially-available N in soil. But more rapid and appealing chemical methods likely do not reflect integrated, plant/soil environmental influences over meaningful time intervals. N is subject to active uptake by plant roots, immobilization by soil microbes, and other processes such as leaching that rapidly remove labile N forms from the soil (Schlesinger 1997).

Soil nitrate measurements are considered one of the best options for estimating potentially available soil N (Bundy and Meisinger 1994; Hong et al.1990; Magdoff et al. 1984). However, there is high temporal and spatial variability in plant-available, inorganic forms of N, nitrate and ammonium. Furthermore, soil NO_3 concentrations depend on numerous N-cycle processes (e.g., denitrification, immobilization, leaching, mineralization, nitrification, and plant uptake). These facts limit the applicability of nitrate-based tests for assessing the soil-N contributions of N-fixing trees and shrubs.

Acetylene-reduction assays, in which ethylene evolved from acetylene-incubated plants via symbiotic, bacterial N-fixers in nodules, has been used to estimate nitrogen fixation by N-fixing plants in ecological studies. However, the acetylene-reduction assay for bacterial nitrogenase activity estimates *in-situ* N-fixation rates as a measure of enzyme activity during the time and under the conditions of incubation. Thus, when acetylene-reduction values are extrapolated to estimate annual inputs of N from N-fixing plants into a community, error is likely. Furthermore, the acetylene-reduction assay does not estimate soil N fertility (Sylvia et al. 1997).

According to Mulvaney et al. (2001), an ideal soil test would estimate an organic fraction that supplies the plant through mineralization. They found that the distribution of amino sugar N was higher in agricultural soils non-responsive to N fertilization, such as those that had been manured, than in N-fertilizer-responsive soils, and was useful in estimating soil-N availability. Others have used this amino sugar nitrogen test with success in estimating the N fertility of agricultural soils (Klapwyk and Ketterings 2006; Klapwyk et al. 2006; Ruffo et al. 2006; Williams et al. 2007). Another study (Laboski et al. 2008) refuted the precision of the test and cautioned against its use in precisely adjusting N fertilizer rate recommendations for maize in the North Central Region of the United States. Nonetheless, plantings of actinorhizal *Elaeagnus umbellata* Thunb. and *Alnus glutinosa* (L.) Gaertn. increased the amino sugar N concentration in soils of mine spoils and a fertile Mollisol indicating that this assay has potential for development as a means of indexing N fertility enhancement by N-fixing trees (Wang et al. 2010). On mine spoils there was a negative correlation between amino sugar N concentration and total N. High amino sugar N concentrations with low total N values under actinorhizal plants may have resulted from increased mineralization and loss of N from a recalcitrant soil organic N pool. Overall, the results of published research indicate a potential role for the use of amino sugar N values in estimating soil N fertility in a rapid and direct manner.

Amino sugar N is strongly associated with microbial activity, commonly limited by high carbon to nitrogen ratios in soils. These sugars primarily occur in cell wall material produced by bacteria, actinomycetes, and fungi (Parsons 1981; Stevenson 1982), not in plant cells. The addition of labile N to soil speeds the decomposition of organic matter and the mineralization of organic N in soils. This is analogous to acceleration of composting vegetable matter with the addition of fertilizer N. Under conditions that favor the breakdown of C in soils with a high C:N ratio (i.e. the addition of N available to decomposers), micro-organisms become a major sink for N as organic matter decomposition, including N mineralization, intensifies, dominating soil microbial processes. In accordance with this model, the addition of the N-enriched leaves, litter and sloughed roots of actinorhizal shrubs may increase the microbial biomass of soil. Correspondingly, the amount of living and dead microbial cell wall material containing amino sugar N will accumulate and serve as the basis of an indicator of soil N fertility.

We hypothesized that amino sugar N concentrations in soils would be higher under N-fixing plants than in adjacent soils away from the leaf canopies of N-fixing plants. We further hypothesized that the increases in average soil amino sugar N would be less under N-fixing plants in fertile soils with high background concentrations of amino sugar N than in infertile soils with low background concentrations (high levels of available N inhibit N fixation).

MATERIALS AND METHODS

Study locations: We selected six natural areas in the upper Midwestern United States (Figure 1) having communities containing the actinorhizal trees and shrubs speckled alder [*Alnus incana* (L.) Moench ssp. rugosa (Du Roi) R.T. Clausen], Canada buffaloberry (*Shepherdia canadensis* (L.) Nutt.), New Jersey tea (*Ceanothus americanus* L.) and the native, leguminous shrub, leadplant (*Amorpha canascens* Pursh) (Table 1). All of the study species were found to be nodulated at their respective sites. Their areas and geographic coordinates are as follows:

Sand dune communities:

1. Ridges Sanctuary WI (647 ha) 45°4'19"N 87°7'13"W
2. Whitefish Dunes State Park WI (350 ha) 44°55'13"N 87°12'16"W
3. Illinois Beach State Park IL (1,683 ha) 42° 25'2" N 87°48'42"W
4. Henry Allan Gleason Sand Prairie IL (44.5 ha) 40°24'41"N 89°51'58"W

Black soil prairies:

5. Loda Cemetery Prairie Nature Preserve IL (1.4 ha) 40°26'47"N 88°08'23"W
6. Prospect Cemetery Prairie Nature Preserve IL (2 ha) 40°26'43"N 88° 05'50"W

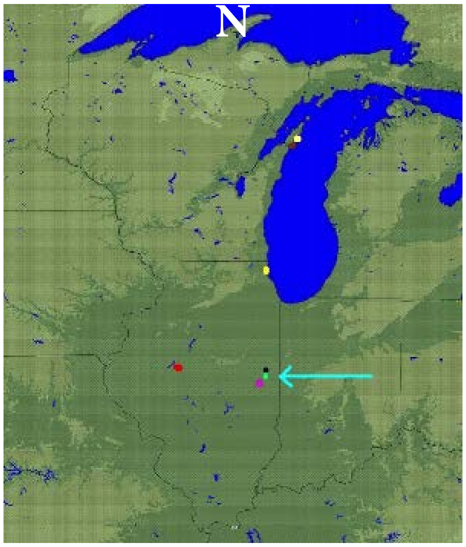

Figure 1. Arrow indicates the location of the two black soil prairie sites, Prospect Cemetery Prairie and Loda Prairie, and the University of Illinois (S). The other dots, from N to S, are the Ridges Sanctuary, Whitefish Dunes State Park, Illinois Beach State Park, all located on the shores of Lake Michigan in either Wisconsin (2-N) or Illinois (1-S), and Henry Allan Gleason Sand Prairie in Illinois.

Table 1. Native species and types of N-fixing shrub symbioses at the study locations.

SITE	SPECIES	COMMON NAME	SYMBIOSIS
IL Beach State Park	*Ceanothus americanus*	New Jersey tea	actinorhizal
Whitefish Dunes	*Alnus incana*	speckled alder	actinorhizal
	Shepherdia canadensis	Canada buffaloberry	actinorhizal
Ridges Sanctuary	*Alnus incana*	speckled alder	actinorhizal
	Shepherdia canadensis	Canada buffaloberry	actinorhizal
HAG Sand Prairie	*Amorpha canescens*	lead plant	rhizobial
Loda Prairie	*Amorpha canescens*	lead plant	rhizobial
	Ceanothus americanus	New Jersey tea	actinorhizal
Prospect Prairie	*Amorpha canescens*	lead plant	rhizobial
	Ceanothus americanus	New Jersey tea	actinorhizal

Soil sampling: Soil samples at each study location were collected within 1-ha areas containing the N-fixing shrubs. Samples were taken around plants that occurred within 1 m of randomly selected points on a m^2 grid overlaying a site map, and which had canopies separated by at least 4 m from any other N fixing plant cover. Sample points under the canopy of-, and 2 m away from, the N-fixing plant canopy, were sampled along radial vectors that were randomly oriented using a table containing a set of 360 degree coordinates. Ten or fifteen paired soil samples were taken, under canopy and 2 m away from canopy, according to the number of available, randomly-selected shrubs that met sampling criteria on a 1-ha plot. Adjacent samples were located along the same vector and at least 2 m away from the canopy, edge of the study, and any other, N-fixing plant. Individual soil samples for N-fixing plants were taken at a radial midpoint under the canopy. A soil probe with a 2-cm internal diameter was used to collect each soil sample to a depth of 30 cm. The samples were collected once for each location during June or July 2003. Samples were dried the same day as sampled for 24 h at 40°C. Each soil sample was then ground to pass through a 2-mm sieve prior to chemical analysis.

Chemical analysis of soils: The samples were analyzed using the technique described by Khan et al. (2001) employing the direct alkalization of soil rather than using the soil hydrolysate for amino sugar acid determination. Alkaline decomposition of soil organic matter was accomplished by heating with a strong base to liberate amino sugar N as gaseous NH$_3$ at a temperature carefully maintained at 48-49°C to obtain a reliable estimate of amino sugar N. One gram of ground, air-dried soil was treated in a Mason jar with 10 mL of 2 M NaOH. A 5-cm-diameter Petri dish containing 5 mL H$_3$BO$_3$ indicator solution was suspended from the lid of the container. The sealed jars were heated for 5 h at 48-49°C. After 5 h of ammonia diffusion, the indicator solution was titrated with 0.01 M H$_2$SO$_4$ to determine the quantity of ammonium from amino sugar and ammonium N in the soil samples captured. For each subsample, triplicates were analyzed to ensure consistency. An artificial soil with a known amino sugar N concentration (Khan et al. 2001) was used in each incubation analysis to determine the accuracy of the results. Soil ammonium is also a component of N in the amino sugar N analysis we employed. In aerobic soils, ammonium is rapidly oxidized to nitrate by nitrification and is typically found in soils at concentrations of only a few mg kg^{-2} (Barker and Pilbeam 2007). Our results are referred to as amino sugar N values for the sake of simplicity, even though a small percentage of the N is likely from ammonium in the soil samples.

Statistical analysis: Each site was a unique natural area with distinctive topography and soils, so the study is treated as a series of individual cases studies. Average values were calculated for amino sugar nitrogen in soil beneath and beyond plant canopies for each species at each location. Paired t-tests for all pair combinations at each site were performed. A probability level of 90% (α = 0.10) was selected because of the inherent variability of soil ecosystems.

RESULTS

Sand dunes: At Ridges Sanctuary, average amino sugar N concentration of soil beneath speckled alder was greater than both the adjacent and Canada buffaloberry soil averages for amino sugar N concentrations (Table 2). The background and Canada buffaloberry averages for soil amino sugar N concentration did not differ from one another. At neighboring Whitefish Dunes State Park amino sugar N concentration average of soil beneath speckled alder, was greater than the background average but not the Canada buffaloberry average at the same locale for soil amino sugar N concentration (Table 2). The backgound and Canada buffaloberry averages for soil amino sugar N concentration did not differ from one another at Whitefish Dunes State Park. At Illinois Beach State Park amino sugar N concentration average of soil beneath New Jersey tea was identical to that of the adjacent background soils. At Henry Alan Gleason Sand Prairies leadplant soil amino sugar N concentration was greater than the background soil average (Table 2).

Black soil prairie: Average soil amino sugar N concentration beneath leguminous leadplant shrubs at Prospect Cemetery was greater than in adjacent soils 2 m distant from its canopies as well as the New Jersey tea soil average. However, leadplant shrub values for soil amino sugar N concentrations did not differ from either background

Table 2. Soil properties, associated vegetation and average amino Sugar-N under N-fixing shrubs for samples underneath and 2 m away from the edge of the shrub canopy in sand dune and black soil prairies. The number of values per average = n.

SITE Source of Soil	Vegetation	Amino Sugar N (mg kg^{-1})	% change w/r to background	Soil Type	Soil Texture
Henry Allan Gleason Sand Prairie		**(n=10)**			
Amorpha	sand prairie & post oak sav.	54.5a	46	sandy, mixed Entic Hapludoll	loamy fine sand
Away		37.4b			
Whitefish Dunes State Park		**(n=15)**			
Alnus	mixed conifers & hardwoods w. pine, beech	76.9a	51	mixed, frigid, Typic Udipsamment	loamy fine sand
Shepherdia		60.8ab	19		
Away		50.9b			
Ridges Sanctuary		**(n=15)**			
Alnus	boreal confirs & hardwoods w. spruce, beech	118.4a	62	mixed, frigid Typic Psammaquent	loamy fine sand
Shepherdia		62.5b	-14		
Away		73.1b			
IL Beach State Park		**(n=10)**			
Ceanothus	sand prairie, black oak sav.	87.0	-1	mised, mesic Typic Udipsamment	loamy coarse sand
Away		87.5			
Prospect Cemetery Prairie		**(n=15)**			
Amorpha	mesic black soil prairie	486.6a	7.1	fine, mixed, active mesic Aquic Arguidoll	silty clay loam
Ceanothus		428.6b	-5.6		
Away		454.2b			
Loda Cemetery Prairie		**(n=15)**			
Amorpha	mesic black soil prairie	549.9z	6.8	fine, illitic, mesic Aquic Arguiudol	silty clay loam
Ceanothus		520.7a	1.1		
Away		514.8			

*Means with the same letter within a column for a given location are not significantly different (t-test $\alpha = 0.10$). Note: the N fertilizer non-response level of amino sugar N is 235 mg kg^{-1}, the level above which no additional fertilizer is needed to maximize maize growth.

soils or soils beneath actinorhizal New Jersey tea shrubs at Loda Cemetery Prairie (Table 2). At Prospect Cemetery Prairie the New Jersey tea soil and adjacent soil average values did not differ from one another, while at Loda Cemetery Prairie there were no differences among average soil amino sugar N concentrations of leadplant, New Jersey tea or the background soils 2 m away from the respective N-fixing plants.

DISCUSSION

Soils under speckled alder at the northernmost study locations of Ridges Sanctuary and Whitefish Dunes State Park, Wisconsin exhibited the greatest increase in amino sugar N over adjacent background soils compared with all other N-fixing plants in this study. Speckled alder finds its niche at our study sites on lower, moister dune slopes compared to the drier site niches of other N-fixing plants examined. Alder occurs inland from lake shores in dune swales which have moderated wind exposure and are open to sunlight. N-fixation is positively correlated with leaf area and photosynthesis in alder (Dawson and Gordon 1979). Photosynthesis in actinorhizal plants is promoted by high light intensity (Cote et al. 1988). Nitrogenase activity in actinorhizal plant nodules is limited by high levels of plant-available soil N (Arnone et al. 1994) and inadequate soil moisture (Uliassi and Ruess 2002)). At our study locations, alder occurred on mesic soils with some wind protection and high light intensities. The alder shrubs were larger than other N-fixing shrubs (multi-stemmed alder were up to 6 m in height) and had the highest leaf areas per plant and greatest size. Thus, it is likely that alder had greater photosynthetic rates and consequent energy-demanding N fixation rates per plant. Furthermore, soil N fertility at these dune sites was not likely high enough to limit N fixation, having average amino sugar N values well below the point of 235 mg kg^{-2} amino sugar N at which N fertilization ceases to benefit crop growth (Khan et al. 2001). This could account for the increase over background soils in amino sugar N under alder because larger quantities of N-enriched leaf, litter and root tissue would be incorporated into the associated soil each year.

At Illinois Illinois Beach State Park the coarse, sandy soil had low fertility and extremely-low water holding capacity. At this location, New Jersey tea shrubs were small (< 1m height) and did not accrete greater concentrations of soil amino sugar N than adjacent soils not influenced by N-fixing plants (Table 2). This is consistent with the idea that limitations of photosynthesis inhibited growth, N fixation and N deposition by shrubs in soil due to xeric conditions and deficiencies of soil nutrients other than N.

Buffaloberry-associated soils did not differ in average concentrations of soil amino sugar N from nearby soils unaffected by symbiotic, N-fixing plants. A possible explanation for this is that buffaloberry shrubs were small (< 2m in height) relative to alder trees at the same location and occurred on wind-exposed, dry dune ridge tops and upper slopes rather than on moister lower slopes and swales where alder occurred. Thus, similarly to New Jersey tea growing on a coarse sand at Illinois Beach State Park, dry soil conditions might have limited photosynthesis and consequent N fixation and deposition in soil.

Leadplant patches had greater levels of soil amino sugar N than adjacent soils at both the dry, sandy Harry Alan Gleason Sand Prairie and at one of the two mesic, N-fertile Mollisols, Prospect Cemetery Prairie. Possibly this small (< 1m in height) shrub species is better able to carry on N-fixation and contribute to soil N accumulation under a wider range of adverse soil conditions compared with sympatric actinorhizal shrubs. Apparently, high levels of substrate N fertility in a prairie Mollisol did not totally inhibit N fixation and consequent accretion in soil of amino sugar N for this species, nor did it inhibit European alder N fixation and soil accretion in a planting on a similar soil nearby in an Illinois arboretum (Wang et al. 2010). This raises the possibility of genetic differences among N-fixing tree species in their ability to carry on N fixation and related physiological processes under a range of environmental conditions.

There were not any increases in soil amino sugar N at any location associated with New Jersey tea plants. Patches of New Jersey tea plants have been shown to influence C3 vs. C4 composition of associated grasses in native prairies (Taft and Dawson 2011), but this influence may be due to factors such as shade rather than differences in soil N fertility. It is possible that we were not able to detect inputs of mineralizable N due to rapid N movements in the biologically complex, root-dense soils of the prairie. It is also possible that high N-fertility of the black soil prairie Mollisol inhibited N fixation and N deposition in soil by the native New Jersey tea. Perhaps N fixed was efficiently retained within *Ceanothus* tissue due to physiological adaptations that lessen its need to compete for soil N with grasses and other prairie plants.

CONCLUSION

Even though all N-fixing trees and shrubs in this study were nodulated, increases in our index of soil N fertility, amino sugar N accretion, associated with nitrogen fixing shrubs occurred primarily in soil beneath N fixers where environmental factors such as lower slope position, higher soil moisture holding capacity and lower background soil N fertility occurred. Soil amino sugar nitrogen determinations suggest that N-fixing plants can create patches of N fertility that likely influence the diversity, integrity and function of organisms in prairie and sand dune ecosystems.

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