



Response of native plants to elevated soil nitrogen in the sand dunes of Lake Michigan, USA



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ABSTRACT

Atmospheric deposition of nitrogen (N) has been reported to reduce the diversity of plant species in N-limited soil. The sand dunes along the southern shore of Lake Michigan have been N-limited historically but receive substantial amount of N from the atmosphere currently. We investigated the effect of N-addition to soil on seed germination rates and species composition of nine native plants. In the greenhouse, the ambient addition (15 kg N ha⁻¹ yr⁻¹) enhanced the germination of *Elymus canadensis* and *Echinacea purpurea*, while the 9× ambient N addition reduced seed germination of *Dalea purpurea* and *Elymus*. However, regardless the results from greenhouse, these species exhibited no or poor emergence in the field plots. *Panicum virgatum* was the only species whose germination was promoted significantly by the ambient addition in the greenhouse and also emerged in the field plots in the early years (2010–2012), but its dominance diminished during 2013–2014. The decline of *Panicum* suggests a failure of establishment and reproduction after germination. Such failure has likely led to reduction or exhaustion of viable seeds in soil. Meanwhile, the species that showed relatively low germination rates (<20%) in the greenhouse, such as *Lupinus perennis*, *Monarda punctata* and *Schizachyrium scoparium*, established substantially in the field plots. Also in the field plots, soil with elevated-N (3×, 5× and 9× ambient) appeared to favor grass over forb species. Dominance of grass over forb species has led to a reduction in species diversity and divergence of species composition between the ambient and elevated-N plots.

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1. Introduction

The global nitrogen (N) cycle has been altered drastically by various human activities such as application of agricultural fertilizers, combustion of fossil fuels, and cultivation of N-fixing crops (e.g., legumes). These activities add excessive amounts of N in the atmosphere and thus cause increased deposition of N from the atmosphere to terrestrial ecosystems (Vitousek et al., 1997; Driscoll et al., 2003; Galloway et al., 2003; Bobbink et al., 2010; Greaver et al., 2012). Deposition of reactive N (mainly nitrate NO₃⁻ and ammonium NH₄⁺) from the atmosphere is a threat to terrestrial plants (e.g., Choi et al., 2008; Bobbink et al., 2010; De Schrijver et al., 2011; Field et al., 2014).

Atmospheric N-deposition causes soil enrichment as well as acidification. Soil acidification, caused by nitrate deposition, often leads to loss of plant nutrients and mobilization of toxic metals, resulting in a decline of plant health and vigor (Driscoll et al., 2003; Bobbink et al., 2010). Elevated level of nitrate and ammonium in soil has been reported as a cause for the enhanced growth and dominance of certain plant species (e.g., grasses), displacement of the species that have evolved in N-

limited soil (Jones et al., 2004; Stevens et al., 2006; Bobbink et al., 2010; Payne et al., 2013), promotion of seed germination accompanied by failure of the seedling establishment, depletion of soil, seed bank (Plassmann et al., 2008; Basto et al., 2015), and ultimately reduction in plant species diversity (Stevens et al., 2006; Bobbink et al., 2010; Henrys et al., 2011; Clark et al., 2013).

The effect of atmospheric N-deposition on plant diversity has been studied in diverse landscapes, including arctic and alpine tundra, temperate forests, shrub-lands, acid and calcareous grasslands, and oceanic coastal sand dunes and slacks (e.g., Niu et al., 2008; Bobbink et al., 2010; Phoenix et al., 2012; Sparrius et al., 2012). However, no such study has been reported from freshwater-created sand dunes under continental climate in North America. The soils of freshwater Lake Michigan sand dunes have historically been N-limited (Olson, 1958; Choi and Pavlovic, 1998; Wilcox et al., 2005; Chun and Choi, 2012), but now receive substantial amounts of reactive N from the atmosphere (NADP, 2013). Therefore, the native plants of Lake Michigan sand dunes, which evolved on the N-limited sand, are very likely sensitive to the N-deposition (Wilcox et al., 2005; Chun and Choi, 2012).

We investigated the effects of N-addition to soil on seed germination and species composition of native plants on Lake Michigan sand dunes over 5 years. In this study, we hypothesized that (1) ambient level N-addition promotes seed germination for certain species, (2) promoted

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Table 1

Number of seeds placed for each of nine species in each pot (15 cm in diameter) for germination experiment in greenhouse, and estimated number of seeds sown for each species in each field plot in each of spring and fall 2010.

Species	Common name	Number of seeds	
		Greenhouse pot	Field plot (estimated)
<i>Lupinus perennis</i> L.	Wild lupine	20	100
<i>Elymus canadensis</i> L.	Canadian rye	100	450
<i>Schizachyrium scoparium</i> (Michx.) Nash.	Little bluestem	100	500
<i>Sorghastrum nutans</i> (L.) Nash.	Indian grass	100	500
<i>Echinacea purpurea</i> L.	Purple coneflower	100	500
<i>Dalea purpurea</i> Vent.	Purple prairie-clover	100	500
<i>Panicum virgatum</i> L.	Switchgrass	200	500
<i>Monarda punctata</i> L.	Horsemint	200	1500
<i>Rudbeckia hirta</i> L.	Black-eyed Susan	200	1500

germination leads to reduction or exhaustion of viable seeds in soil if such species fail to establish, mature or reproduce after germination, and (3) N-enriched soil favors grass over forb species, and leads to the reduction in species diversity and thus divergence of species composition over time.

2. Methods

2.1. Description of the study area

Our study area (87°11'20"W 41°37'56"N) is located in the Indiana Dunes National Lakeshore on the southern shore of Lake Michigan near Gary, Indiana. It is a part of the Tolleston Dune system formed 1000–3500 BP during the successive retreats of the lake's shorelines in the past 14,000 years after the Wisconsin glaciation. The sand dunes along the southern shore of Lake Michigan are among the largest freshwater-dune complexes in the world (Thompson, 1992).

From 1980 to 2009, the mean annual precipitation was 93 cm, and the mean January and July temperatures were -4.2 °C and 23 °C, respectively, according to the climate data reported by a nearby weather station in South Bend, Indiana (Horstmeyer, 2011). The predominant soil is Oakville Series, well-drained fine sands with water table deeper than 2 m below ground surface and no defined soil horizons (Soil Conservation Service, 1992). Due to its sandy nature, the soil is considered N-limited (total N < 0.025%) with very little organic matter (<0.5%) (Choi and Pavlovic, 1998), (Wilcox et al., 2005, Chun and Choi, 2012, our preliminary soil analysis in Appendix 1). However, it has been enriched by deposition of N from the atmosphere (14 – 23 kg ha⁻¹ yr⁻¹ as NO₃⁻ and NH₄⁺ in wet deposition) during recent decades (NADP, 2013).

The vegetation of sand dune is best characterized by *Quercus velutina* Lam. (black oak) savannas on these dunes and sand prairies in the open

flat areas. *Schizachyrium scoparium* Nash. (little bluestem), *Panicum virgatum* L. (switch grass) are the grasses and *Lupinus perennis* L. (wild lupine) and *Monarda punctata* L. (horsemint) are the forbs commonly found in the ground layers of oak-savannas and sand prairies (Wilhelm, 1990; Wilcox et al., 2005; Young et al., 2009).

2.2. Greenhouse experiment for seed germination

Seeds of four grass and five forb species native to the North American prairies (Table 1) were obtained from a local nursery. This nursery collected local variety of seeds, germinated and grew them to seed production for harvest. Equal number of the seeds of each species were placed in twenty-one plastic pots (15 cm in diameter) that were filled with the sand from Lake Michigan dunes. Twenty-one pots of each species were divided randomly into three nitrogen treatment groups, thus each group has seven replicates.

Our treatment for ambient level of N-addition was based on the lower-side estimate of wet N-deposition on Lake Michigan sand dunes. The first treatment group was a control and thus received no ammonium nitrate (NH₄NO₃), the second group received ammonium nitrate at a rate of 15 kg ha⁻¹ yr⁻¹ emulating the condition of ambient deposition of nitrogen, and the third group received ammonium nitrate at the rate of 135 kg ha⁻¹ yr⁻¹ (9 × ambient), emulating a scenario of very high level of N-deposition. All pots were placed in Purdue University Northwest greenhouse and irrigated equally (30 mL H₂O pot⁻¹ wk⁻¹). Germination rates were determined after four to eight weeks.

For each of the nine species, differences in seed germination (%) among the three treatment groups were tested using one-way analysis of variance (ANOVA) followed by Tukey's HSD pairwise mean comparison at $\alpha = 0.05$ with the software STATISTIX (Analytical Software, 2008).

2.3. Field experiment for plant species composition and diversity

A total of twenty plots were established in a sand prairie site at the western end of Tolleston Dunes (see Appendix 2). Each plot, sized 2 m × 2 m, was separated by inserting landscape fabric to 50 cm depth vertically from ground surface on the borders all sides with 1-m space between the borders. The plots were also fenced with plastic nettings on the borders to prevent intrusion and damage by herbivores. All existing plants in each plot were sprayed with herbicide (2% glyphosate) in the fall 2009, followed by mechanical removal of dead plants (clipping of all standing shoots and excavation of roots and rhizomes) and leveling of ground surface in the spring 2010. Identical seed mixes of nine plant species native to the Lake Michigan sand prairies were sown in April after the site preparation and in October 2010 (Table 1).

The twenty plots were divided randomly into four groups of ammonium nitrate treatment (ambient, 3 ×, 5 × and 9 × ambient groups); each group consisted of 5 replicates. Ambient plots were assumed to receive reactive N from the atmosphere at a rate of 15 kg N ha⁻¹ yr⁻¹; thus no ammonium nitrate was added. Each plot of the 3 ×, 5 × or 9 × ambient

Table 2

Mean (± standard error) germination rate (%) of the seeds of nine plant species, native to the Lake Michigan sand dunes, at three levels of ammonium nitrate (NH₄NO₃) addition. Each treatment group consisted of seven pots, the ambient and the 9 × ambient pots received ammonium nitrate at the rates of 15 and 135 kg ha⁻¹ yr⁻¹, respectively. No ammonium nitrate was given to the control pots. The values that share a same alphabet letter are not different statistically at $\alpha = 0.05$ for each species in Tukey's HSD pair-wise mean comparison.

Species	Control	Ambient	9 × ambient	p ^a
<i>Dalea purpurea</i> Vent.	92.1 ^A ± 2.0	90.9 ^A ± 2.1	77.3 ^B ± 3.7	0.04
<i>Elymus canadensis</i> L.	42.0 ^A ± 3.8	76.8 ^B ± 6.6	27.7 ^C ± 4.2	0.03
<i>Echinacea purpurea</i> L.	7.1 ^A ± 1.4	59.6 ^B ± 5.1	18.1 ^A ± 6.1	<0.01
<i>Panicum virgatum</i> L.	21.9 ^A ± 6.7	55.5 ^B ± 3.2	15.8 ^A ± 3.2	0.02
<i>Rudbeckia hirta</i> L.	37.7 ^A ± 7.0	24.8 ^A ± 9.3	20.7 ^A ± 5.0	0.39
<i>Lupinus perennis</i> L.	4.3 ^A ± 1.3	16.4 ^B ± 4.2	1.4 ^A ± 0.9	0.04
<i>Sorghastrum nutans</i> (L.) Nash.	0.1 ^A ± 0.1	11.8 ^B ± 2.4	3.3 ^A ± 1.2	0.01
<i>Monarda punctata</i> L.	1.9 ^A ± 0.3	4.1 ^B ± 1.3	1.1 ^A ± 0.5	0.03
<i>Schizachyrium scoparium</i> (Michx.) Nash.	1.4 ^A ± 0.4	3.7 ^B ± 1.1	0	0.04

^a p: probability of type I error in ANOVA.

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