Correlation of Soil Nutrient Characteristics and Reed Canarygrass (Phalaris arundinacea: Poaceae) Abundance in Northern Illinois (USA)

JASON P. MARTINA¹ AND CARL N. VON ENDE

Department of Biological Sciences, Northern Illinois University, Dekalb 60115

ABSTRACT.—Phalaris arundinacea L. (reed canarygrass) is an aggressive graminoid species that invades wetlands in much of the northern United States. In areas previously used for agriculture and other recently disturbed habitats, P. arundinacea out-competes the native flora and creates monocultures, which reduce biodiversity and alter ecosystem functioning. Much research has focused on the growth response of P. arundinacea to varying abiotic and biotic conditions in the lab or under controlled field conditions, but few studies have examined if these results are congruent with what is observed in natural settings. We examined the relationship between P. arundinacea abundance and soil nutrient characteristics at Glacial Park, USA, a conservation area in northeastern Illinois. We found significant positive relationships between P. arundinacea abundance and total inorganic nitrogen, calcium and cation exchange capacity in the soil. These results are consistent with controlled experiments showing increased P. arundinacea growth in nitrogen-rich soil, and also suggest that calcium may influence P. arundinacea abundance in restored areas in the Midwest.

Introduction

Phalaris arundinacea L. (Poaceae), reed canarygrass, is an aggressive C3 perennial grass species with both native and exotic genotypes known throughout the United States (Merigliano and Lesica, 1998; Lavergne and Molofsky, 2007). Recent work has shown that intentional repeated introductions (for forage, bank stabilization and phytoremediation) into the United States since the mid-19th Century have contributed to its invasion success by yielding a number of novel genotypes (Lavergne and Molofsky, 2004; Lockwood et al., 2005; Lavergne and Molofsky, 2007). Phalaris arundinacea primarily invades wetlands and its invasive range spans most of the northern United States. It can produce very high levels of standing crop biomass when experimentally grown in nitrogen-rich soil, which is consistent with it being considered a pest species in areas of N-runoff (Green and Galatowitsch, 2002). Phalaris arundinacea is phenotypically plastic: biomass allocation can vary significantly under different environmental conditions in controlled experiments (Lavergne and Molofsky, 2004; Martina, 2006), which likely increases its ability to invade diverse habitats (Zedler and Kercher, 2004).

Many studies have concluded that increasing nitrogen levels lead to increased biomass production in *Phalaris arundinacea* (Katterer and Andren, 1999; Green and Galatowitsch, 2001, 2002; Maurer and Zedler, 2002; Mahaney *et al.*, 2004; Perry *et al.*, 2004; Gusewell, 2005). Green and Galatowitsch (2002) tested the hypothesis that adding nitrogen to a plant community will favor invasive species over natives. They grew 11 native species alone and with *P. arundinacea* in three treatment levels of increasing nitrogen concentrations (0, 12 and 48 g m⁻² y⁻¹). *Phalaris arundinacea* suppressed the biomass of the native community at all treatment levels, but native biomass was most severely reduced (by half) at the highest addition of nitrogen. In an experiment with another invasive species, *Typha* × *glauca* Godr.,

¹Present address: Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824; Telephone: (517) 353-2953; e-mail: marti993@msu.edu

Green and Galatowitsch (2001) found again that greater biomass production by P. arundinacea suppressed the native community in nutrient-enriched treatments. $Typha \times glauca$ did not significantly increase growth in the nitrogen-addition treatments, although it is known to invade a number of wetland types (Green and Galatowitsch, 2001).

Whereas one can directly test the effects of abiotic factors on plant growth and development with experiments in a controlled environment, observational studies are necessary to examine the robustness of the conclusions in a natural setting. This is particularly true for greenhouse studies designed to assist restoration efforts, because if results are not confirmed in the field, time and money can be wasted on ineffective management practices. For example, although studies have shown that *Phalaris arundinacea* has a competitive advantage over native species in N-enriched soil (Green and Galatowitsch, 2001, 2002; Maurer and Zedler, 2002), it has yet to be shown that nitrogen enrichment is positively correlated with *P. arundinacea* abundance in a natural setting. If this relationship can be verified, then restoration techniques that reduce the amount of available soil N might be warranted. Observational studies are also a good way to identify other factors worthy of study in a controlled setting, or to assess the importance of one factor relative to others that may vary in the field.

We surveyed 12 sites in Glacial Park, USA, a conservation area in northeastern Illinois, to investigate the relationship between soil nutrient characteristics and *Phalaris arundinacea* abundance. Because Glacial Park has a well-documented history of restoration, it was ideal for conducting a field study of this type. *Phalaris arundinacea* has invaded nearly all restored wetlands and waterways within the park and is expanding its range annually (J. Martina, pers. obs.), although the extent of invasion varies among sites. We hypothesized that *P. arundinacea* abundance would be positively correlated with soil nitrogen concentration, but have little or no correlation with concentrations of other plant nutrients, such as calcium, magnesium, phosphorus and potassium.

Materials and Methods

STUDY SITES

The study sites were located on the McHenry County Conservation District property known as Glacial Park (Ringwood Township, N: 42°25.166′ W: 88°19.400′). The park is approximately 1300 ha in area and was established as a county park in 1975. Glacial Park is located in the Nippersink-Boone Outwash Physiographic System in the ecological classification of McHenry County Soils, which is described as well-sorted outwash deposit (stratified sand and gravel) associated with glaciation (Hotchkiss, 2006). The dominant soil types found in the park include poorly drained silty clay loam and clay loam texture with a thick organic-rich A horizon.

The abundance of *Phalaris arundinacea* was estimated at 12 sites that varied in *P. arundinacea* dominance. Sites were selected that represented a monotonic gradient of *P. arundinacea* dominance and included most *P. arundinacea* populations at Glacial Park restored between 1994 and 1996. Initially, these sites were ranked by simple observation from least to greatest percent cover of *P. arundinacea*, ranging from the absence of *P. arundinacea* to a monoculture of *P. arundinacea*. Common species found at sites that were not monocultures of *P. arundinacea* were as follow: *Agropyron repens* L. (quack grass), *Typha latifolia* L. (broadleaf cattail), *Solidago* spp. L. (goldenrod), and *Cirsium arvense* L. (canada thistle). Each site was approximately 2–3 ha in area with most sites separated by less than 500 m. Sites were comparable in topography and hydrology as they were areas of low elevation classified as wet prairie or marsh, except for one site (PWN), which was the

backslope of an elevation gradient. All 12 sites were restored between 1994 and 1996. For restoration, aboveground vegetation was removed, the soil surface tilled and a similar mixture of seeds of native species was broadcast on the mostly bare ground (T. Simpson, pers. comm.). The sites used in this study were representative of grassland and wetland habitats found in northern Illinois, especially on restored sites where the majority of the species are invasive.

FIELD SAMPLING

Sampling at the 12 sites was done by the restricted random sampling technique (Elzinga \it{et} $\it{al.}$, 2001). Macroplots (9 × 30 m) were placed randomly within each site from 9 Aug. to 12 Aug. 2005. Each macroplot was divided into nine 3 × 10 m subplots. Within each of these subplots, a quadrat (0.2 × 1 m) was randomly placed at one of the 150 possible locations. Within each macroplot, a total of nine quadrats were sampled. Preliminary sampling analysis indicated a minimum of nine quadrats was needed to reliably estimate $\it{Phalaris}$ $\it{arundinacea}$ abundance (Elzinga \it{et} $\it{al.}$, 2001). The percent cover of $\it{P.}$ $\it{arundinacea}$ was estimated within each quadrat and assigned to a cover class from 1 to 6 (1: 0–5% cover; 2: 6–25%; 3: 26–50%; 4: 51–75%; 5: 76–95%; 6: 96–100%). All $\it{P.}$ $\it{arundinacea}$ stems within each quadrat were counted, clipped at the soil surface and returned to the lab for drying (60 C for 72 h) and weighing. The number of tillers with inflorescences was also counted in each quadrat.

After all *Phalaris arundinacea* stems were clipped and removed from a quadrat, a soil core was collected with a long-handled bulb planter (9 cm diam, 25 cm deep). Soil samples were individually placed in Ziploc bags in the field, returned to the lab the same day and stored in an environmental chamber at 5 C. On 17 Aug. 2005, the nine soil samples collected in each macroplot were pooled and homogenized. A 450 g subsample was taken from the homogenized mixture for chemical analysis (A&L Great Lakes Laboratories, Incorporated, Fort Wayne, IN 46808). Percent organic matter, phosphorus, potassium, magnesium, calcium, pH, cation exchange capacity, nitrate and ammonium were estimated for each sample.

STATISTICAL ANALYSIS

A simple parametric (Pearson) correlation matrix was constructed using Statistica 7.1 (StatSoft, Inc., 2005) to analyze the bivariate relationships of all soil nutrient variables (total inorganic N, percent organic matter, phosphorus, potassium, magnesium, calcium and cation exchange capacity) with each biological variable (total biomass, total tillers, biomass per tiller, inflorescence number and cover class). Nitrate and ammonium data were combined and reported as total inorganic soil-N. Biomass per quadrat data were not collected at one site (BPF) site because the high abundance of native species present made it difficult to sample without injuring the native species. Cation concentrations from another site (RSM) were excluded from the analysis because the high acidity of the soil at that site altered its cation exchange capacity.

Multiple hypothesis testing has been a frequent topic of discussion for ecologists (Garcia, 2004). Likewise it has become an active area of statistical investigation more recently with the production of large data sets of genomic microarray data (Pounds, 2006; Cheng and Pounds, 2007). Traditionally the p-value has been used for performing a single significance test. The p-value of a test measures the minimum *false positive rate* that is incurred when declaring that test significant. Classically, multiple hypotheses have been addressed in terms of the *familywise error rate* (FWER) (Storey, 2002). Benjamini and Hockberg (1995) introduced the concept of *false discovery rate* (FDR), which ecologists have begun to use (Garcia, 2004). Whereas the *false positive rate* measures the proportion of true null hypotheses that are (incorrectly) called significant, the *false discovery rate* (FDR) measures the proportion of alternative hypotheses that

TABLE 1.—Correlation matrix among all soil nutrient variables (total soil-N, percent organic matter, phosphorus, potassium, magnesium, calcium and cation exchange capacity [CEC]) and each biological variable (total biomass, biomass per tiller, total tillers, inflorescence number and cover class). *See* Methods for explanation of Q values

		Total-N	% OM	Phosphorus	Potassium	Magnesium	Calcium	CEC
Total biomass	r	0.665	0.488	-0.403	-0.494	0.148	0.734	0.730
	P-value	0.026**	0.128	0.219	0.141	0.664	0.016**	0.017**
	Q-value	0.023	0.057	0.073	0.060	0.155	0.023	0.023
Biomass/tiller	r	0.635	0.271	-0.231	-0.187	-0.032	0.714	0.689
	P-value	0.027**	0.420	0.495	0.562	0.890	0.014**	0.019**
	Q-value	0.023	0.114	0.126	0.135	0.198	0.023	0.023
Total tillers	r	0.418	0.456	-0.309	-0.480	0.193	0.602	0.601
	P-value	0.201	0.159	0.355	0.154	0.569	0.066*	0.066*
	Q-value	0.071	0.064	0.102	0.063	0.136	0.039	0.039
Inflorescence	r	0.400	0.125	-0.281	-0.436	-0.198	0.755	0.706
	P-value	0.223	0.714	0.403	0.177	0.560	0.007**	0.015**
	Q-value	0.074	0.165	0.111	0.067	0.135	0.023	0.023
Cover class	r	0.518	0.550	-0.245	-0.427	0.200	0.646	0.659
	P-value	0.085*	0.063*	0.442	0.167	0.534	0.032**	0.027**
	Q-value	0.045	0.038	0.118	0.065	0.131	0.024	0.023

^{**} P < 0.05

are (incorrectly) called significant. The *positive false discovery rate* (pFDR) has been proposed as an error rate for multiple testing in microarray data, and the "q-value" as an error measurement (in a Bayesian framework) related to pFDR for each of the many tests performed simultaneously (Storey, 2002, 2003). The q-value measures the minimum *false discovery rate* that is incurred when calling that test significant (according to the p-value), *i.e.*, the expected proportion of false positives among all tests as, or more extreme, than the observed test. It is more useful than p-values when many tests are being done in exploratory studies (Storey and Tibshirani, 2003). We estimated q-values for each p-value calculated for the correlation matrix using the R (R Development Core Team, 2007) package "fdrtool," in which the q-value is the tail area-based FDR (="Fdr") (Strimmer, 2008). Alpha was set at 0.05 for p-values (p-values < 0.10 were considered marginally significant and noted in Table 1). In an exploratory study such as this, results should be considered preliminary and followed by more detailed investigations.

RESULTS

The variability in total inorganic soil-N concentrations among sites was primarily due to differences in concentrations of nitrate rather than ammonium. Nitrate concentrations ranged from 3 to 13 mg kg⁻¹. Ammonium concentrations were less than 4 mg kg⁻¹ at all sites except RSM (5 mg kg⁻¹). Calcium concentrations ranged from 1250 to 9000 mg kg⁻¹, phosphorus concentrations ranged from 7 to 74 mg kg⁻¹, potassium concentrations ranged between 35 and 298 mg kg⁻¹ and magnesium concentrations ranged from 170 to 1095 mg kg⁻¹. pH was slightly alkaline at most sites, but acidic at the RSM site (5.2). The lowest total inorganic soil-N concentration (5 mg kg⁻¹) was found at the two sites where *Phalaris arundinacea* was absent.

Total *Phalaris arundinacea* biomass was positively correlated with total inorganic soil-N (Fig. 1; P = 0.026, Q = 0.023, Table 1), Ca (Fig. 1; P = 0.016, Q = 0.023, Table 1) and cation

^{*} P < 0.10

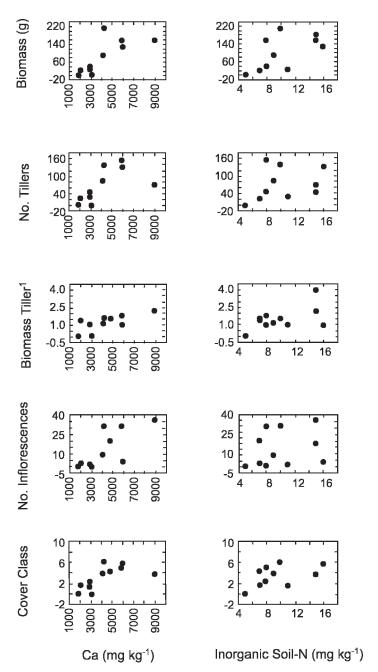


Fig. 1.—Correlation matrix for each biological variable (total biomass, total tillers, biomass per tiller, inflorescence number and cover class) against calcium and total inorganic soil-N. Biomass data are reported in grams and soil nutrient concentrations are reported in mg ${\rm kg}^{-1}$

exchange capacity (CEC) (P = 0.017, Q = 0.023, Table 1). The total number of tillers was marginally correlated with CEC (P = 0.066, Q = 0.039, Table 1) and Ca (Fig. 1; P = 0.066, Q = 0.039, Table 1). There was a significant positive relationship between biomass per tiller and total inorganic soil-N (Fig. 1; P = 0.027, Q = 0.023, Table 1), Ca (Fig. 1; P = 0.014, Q = 0.023, Table 1) and CEC (P = 0.019, Q = 0.023, Table 1). Inflorescence number was positively correlated with both Ca (Fig. 1; P = 0.007, Q = 0.023, Table 1) and CEC (P = 0.015, Q = 0.0150.023, Table 1). The cover class of P. arundinacea was positively correlated with Ca (P = 0.032, Q = 0.024, Table 1) and CEC (P = 0.027, Q = 0.023, Table 1), and marginally correlated with total inorganic soil-N (P = 0.085, Q = 0.045, Table 1) and soil organic matter (P = 0.063, Q =0.038, Table 1). Some correlations may be nonlinear (Fig. 1) but more samples would be needed to fully support a nonlinear relationship. Percent organic matter, phosphorus, potassium and magnesium were not significantly, nor marginally significantly, correlated with any measure of P. arundinacea abundance (Table 1). Although P and K were not significantly correlated with any biotic variable, each biotic variable showed a negative relationship with increasing P and K concentrations in the soil. Due to the correlation of total inorganic soil-N and calcium with many of the biological parameters, a separate correlation analysis between inorganic soil-N and calcium was included. There was a positive relationship between soil-N and calcium (r = 0.752, P = 0.008), which could be caused by rapid nitrogen mineralization in calcium-rich soil (Larcher, 2003). In addition, there was a significant correlation between Ca and CEC (r = 0.990, P < 0.001).

DISCUSSION

Nitrogen is required for the cellular production of amino acids, nucleic acids and other essential organic compounds and is widely considered the most limiting nutrient in most terrestrial ecosystems (Chapin *et al.*, 2004). As N availability increases due to agricultural runoff and N deposition, ecosystems can become more vulnerable to invasion as some invasive plants respond more positively than natives to N-enrichment (Zedler and Kercher, 2004). The positive correlation between total biomass and inorganic soil-N supports controlled studies indicating *Phalaris arundinacea* responds positively to high levels of soil-N (Katterer and Andren, 1999; Green and Galatowitsch, 2001; Green and Galatowitsch, 2002; Maurer and Zedler, 2002; Mahaney *et al.*, 2004; Perry *et al.*, 2004; Gusewell, 2005) and confirms that these studies were observing an interaction between inorganic soil-N and *P. arundinacea* growth actually found in nature. Inorganic soil-N was also positively correlated with biomass per tiller, implying that in high-N environments *P. arundinacea* has increased ability to compete for light because more robust stems are better able to avoid being blown down by wind (J. Martina and C. von Ende, pers. obs.).

The positive correlation of Ca and cation exchange capacity (CEC) with total biomass, biomass per tiller, inflorescence number and percent cover, and marginal correlation with total tillers, justifies future experiments examining the effects of Ca on *Phalaris arundinacea* productivity. It is likely that the correlation between *P. arundinacea* abundance and CEC was an effect of calcium's large percentage of the soil CEC (63.6% to 87.6% base saturation), which is supported by the positive correlation between Ca and CEC. It is more reasonable to assume that Ca, rather than CEC, had the overriding influence on *P. arundinacea* abundance and productivity. Calcium is involved in multiple aspects of normal plant function such as membrane integrity, stomatal regulation, enzyme activation, carbohydrate metabolism, chemical defense and cold hardiness (McLaughlin and Wimmer, 1999). If invasive plants are able to utilize Ca more efficiently than the native flora, they may be able to successfully

colonize and spread into an area with high soil Ca concentrations. More studies are needed to investigate this potential aspect of *P. arundinacea* invasion.

As discussed above, nitrogen and calcium are known to play a vital role in plant growth, especially in invasive plants. In a nitrogen addition experiment in the Mojave Desert, Brooks (2003) showed that the density and biomass of exotic annual plants increased with increasing N levels while the density, biomass and species richness of the native species decreased. Howard *et al.* (2004) found that calcium and nitrogen were positively correlated with the abundance of woody invasive species in the hardwood forest fragments of eastern New York. High levels of leaf nitrogen have been linked with a high relative growth rate (Cornelissen *et al.*, 1997), and high foliar calcium can increase photosynthetic rate (McLaughlin and Wimmer, 1999). Calcium can also stimulate fine root production, which can act as a positive feedback by increasing the uptake of nitrogen. In particular, invasive species that respond positively to high levels of calcium and nitrogen can cause serious problems in nutrient-enriched restored areas. It seems plausible that high soil Ca is facilitating *Phalaris arundinacea* dominance, but more experimental evidence is needed before Ca levels in the soil should be monitored during grassland and wetland restoration.

The positive correlation found between inorganic soil-N and *Phalaris arundinacea* abundance suggests that high nutrient levels in restored sites can be problematic. Adding carbon (such as sucrose or sawdust) to immobilize plant-available N could be a useful management technique to reduce *P. arundinacea* invasion into newly restored areas (Blumenthal *et al.*, 2003). It was shown in a greenhouse study that adding carbon to nitrogen-enriched soil to reduce the amount of plant-available N decreased the competitive ability of *P. arundinacea* when grown with *Carex hystericina* Muhl. ex Willd., a native sedge (Perry *et al.*, 2004). This technique will only be useful for newly restored areas because already established populations of *P. arundinacea* will be resistant to sudden alterations in soil-N availability. Adding C to reduce the amount of plant-available N will likely have to be used in conjunction with other management practices, such as herbicide application, burning, mowing and plowing, to control established populations of *P. arundinacea*.

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