Comparing Explanatory Variables in the Analysis of Species Composition of a Tallgrass Prairie

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Although the relationship between soil characteristics and plant species composition has been well studied, exploratory analyses have been limited by the cost and/or difficulty of analyses. I used Canonical Correspondence Analysis to determine whether a set of potentially important but difficult to measure (or new) soil variables (total C and N, inorganic N, potential net N-mineralization and net nitrification rates, P fractions, and soil textural classes), explain species composition beyond that explained by a more routinely collected (or old) set. Through forward selection, I chose five environmental variables (total C (C_t), pH, Fe, residual P (P_r), and Zn) that explained a significant ($\alpha = .05$) portion of variation in species composition. However, during a second forward selection using only the old variables, soil organic matter (SOM) and slope were chosen in place of C_t and P_r. The explanatory power of C_t and P_r was not significantly greater than that of SOM and slope. In addition, the large number of significant correlations between C_t and P_r and essential resources suggest that these variables are only indirectly linked to species composition. This study demonstrates that difficult-to-measure variables may be superfluous and that exploratory analyses are likely to choose proxy variables. *© 2004 Oklahoma Academy of Science*

INTRODUCTION

The relationship between soil characteristics and species composition is useful for understanding restoration because the success of maintaining or restoring a specific community depends on how management impacts such characteristics (Critchley et al 2002). Canonical Correspondence Analysis (CCA) is a form of direct gradient analysis (Palmer 1993) that is widely used in plant ecology to model the relationship between plant species composition and measured environmental variables (De'ath 2002, Kenkel et al 2002, Lepš and Šmilauer 2003, Graffelman and Tuft 2004). Thus, it is a potentially useful technique for restoration ecology. However, exploratory analyses of species composition are limited because soil analysis is often expensive or labor intensive. Fortunately, canonical analyses such as CCA can provide statistics that estimate the proportion of variance of the response data that is accounted for by the explanatory variables (Makarenkov and Legendre 2002), and CCA

with variance partitioning allows comparisons between variables or groups of variables (Økland 1994). These properties of CCA allow the comparisons of explanatory variables, and may lead researchers to exclude uninformative or redundant explanatory variables in future analyses.

Nitrogen and P are of particular interest as potential explanatory variables because they are the two most commonly limiting soil nutrients in grasslands (Seastedt et al 1991, Boeye et al 1997, Turner 2003). Nutrient limitation is one of the most important factors affecting plant communities (Grime et al 1997). This might be due to competition for the one most limiting nutrient such as N or differential limitation between species by different nutrients (Koersleman and Meuleman 1996). For example, higher P availability may favor legumes, whereas higher N availability could favor grasses (Janssens et al 1998). The quantity of available nitrogen can have a major influence on species composition and diversity (Mountford et al 1993, Willems et

al 1993), and P can control vegetation type and soil organic matter (Smeck 1973). Ratios of these nutrients with organic C may also have substantial effects on vegetation (Koerselman and Meuleman 1996). For instance, a C:N ratio of 14 has been observed to cause a N-mineralization rate that maximized plant productivity, whereas lower ratios caused nitrate leaching and higher ratios caused litter accumulation (Alvarez et al 1998).

Not all variables are equally useful in explaining plant species composition (Palmer et al 2002). Previous exploratory analyses of tallgrass prairie have included N and P gradients that correlate well with productivity in agronomic systems. However, natural communities occur across a wide range of nutrient regimes, and measurements of highly available nutrient pools might not represent the major sources of plant available N and P in unfertilized systems with coevolved niche differentiation (Critchley et al 2002, Schmidt et al 1996). Such systems may rely heavily on the mineralization of organic N and P through microbial activity. Distinctions between mineralization processes, such as ammonification and nitrification, could provide greater explanatory value because plant competition is affected by the form of available N (Schimel et al 1989, Bloom et al 2003). There is substantial temporal heterogeneity and microbial redistribution of P (Hedley et al 1982, Magid and Nielson 1992). Although P-mineralization is difficult to measure, the total P in soils can be divided into inorganic and organic fractions and can be quantified based on levels of bioavailability (Hedley et al 1982). Agriculture-based P measurements quantify the combined total of immediately soluble P plus portions of the more easily extracted, insoluble fractions (Mehlich 1984); however, biologically active P has been found in several fractions (Nichols 1984, Schmidt et al 1996). Fractionation of total P allows for comparisons of pools of P that may be plant available (Abrams and Jarrell 1992) and recalcitrant P forms that

may explain community structure through their correlation to soil weathering (Smeck 1973).

It is also important to explore relationships between important environmental gradients. Many variables that display high explanatory power in direct gradient analyses may in fact be serving as proxies for one or many variables that have a more direct, causal relationship with plant species composition. The species composition of the plant community is not only controlled by the initial physical environment but also by the modifications to the physical environment imposed by community succession (Odum 1969). As a result, the causal relationships resulting in simple correlations between species composition and environmental variables may be extremely convoluted. For example, P availability may be controlled by the chemical characteristics of the soil parent material or the chemical characteristics of plant litter (Walker and Adams 1958, Walker et al 1959, Nichols 1984). Phosphorus availability may affect species composition directly by favoring legumes (Walker and Adams 1958, Janssens et al 1998), or it could exert indirect control by affecting N-fixation, N-mineralization, and nitrification (Hue and Adams 1984, Janssens et al 1998). There is strong evidence for control of N-mineralization rates by the C:N ratio (Aulakh et al 2000). Textural classes are strongly correlated with P fractions (O'Halloran et al 1987) and soil organic matter (Hook and Burke 2000). Such correlations by proxy may provide useful generalizations, but it is important to demonstrate causality to apply information provided through direct gradient analyses to management.

My objectives for this study were 1) to estimate the potential of several pools of soil C, N, P, and soil texture to improve explanations of plant species composition in tallgrass prairie and 2) to examine proxy relationships between variables with high explanatory value and other potentially important environmental variables in this community.

METHODS

All vascular plant species were recorded in 20 permanent 10 m x 10 m plots in the Nature Conservancy's Tallgrass Prairie Preserve during June of 2002 (Palmer et al 2003). The plots were a random sample of grassland plots from a total of 151 that are located at the intersections of the 1 km x 1 km Universal Transverse Mercator Grid. This grid, adopted by the National Imagery and Mapping Agency, consists of two sets of straight, parallel lines, uniformly spaced, each set perpendicular to the other with coordinates measured north and east in meters. These 20 plots have been resurveyed annually beginning in 1998. Species abundance was quantified by estimating percent cover (Palmer et al 2002). Each plot is one sample in the species data for use in CCA (Ter Braak 1986).

For direct gradient analysis, I used estimates of percent slope, aspect, height of grasses, forbs, and woody plants and percent cover of rock, bare ground, and woody plants. I also collected soil samples from each plot. The samples consisted of four combined cores from the top 10 cm of the soil profile (Palmer 1990). I divided each sample into two portions. At Oklahoma

Figure 1. Sequential extraction procedure and functional significance of extracted soil fractions (P_i: inorganic, P_o: organic; adapted from Tiessen and Moir 1993)

State University, I measured P fractions (Fig. 1; Tiessen and Moir 1993), inorganic N (Maynard and Kalra 1993), potential net N-mineralization and net nitrification rates (Vinton and Burke 1995), total carbon and nitrogen with a LECO CN 2000 combustion analyzer (Leco, St. Joseph, MI), and soil texture (Gavlak et al 2003). The other portions of these samples were sent to Brookside Labs in New Knoxville, Ohio, to be analyzed for cation exchange capacity, pH, percent soil organic matter (SOM), estimated N-release, soluble S, exchangeable Ca, Mg, K, and Na , and Mehlich III extractable P, Mn, Zn, B, Cu, Fe, and Al (Mehlich 1984). Unlike potential net N-mineralization, estimated N-release is calculated as a function of SOM. I log transformed all variables, excluding pH, that were derived from these soil analyses (Palmer 1990). In addition, I included easting, northing, and sampling date for each plot sampled in the analysis. For the purposes of discussion I will refer to total C and N, inorganic N, mineralization and nitrification rates, P fractions, and soils textural classes as the new environmental variables. All other environmental data constitute the old variables.

Direct gradient analysis (Palmer 1993) and variance partitioning (Borcard et al 1992, Økland 1994, 2003) with the environmental variables and species data, were performed using CCA through CANOCO for Windows software (Ter Braak and Šmilauer 1998). I chose to square-root transform the species data in order to reduce the effects of dominant species and down weight rare species prior to analysis. Because the number of environmental variables collected was greater than the number of samples, stepwise forward selection was used to choose the environmental variables from the full set that explained the greatest amount of variation in plant species composition within the samples (Ter Braak 1988b, Hallgren et al 1999). Stepwise forward selection is a semi-automated procedure performed through CANOCO. Environmental variables are added, one at a time, until
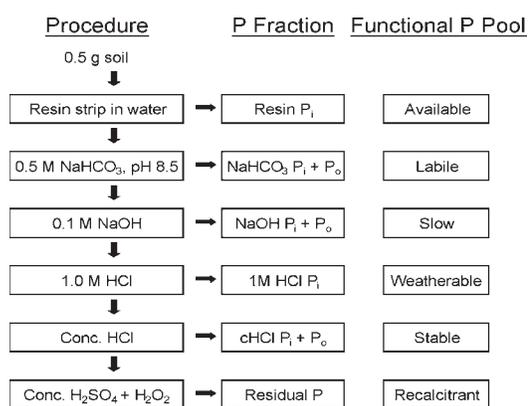
no other variables significantly explain residual variation in species composition. However, the user is allowed to make choices about inclusion of variables. In addition, I used stepwise forward selection to choose environmental variables from only the old set of variables to detect those variables that are potentially interchangeable with new variables. Variables with P values less than 0.05 derived through Monte-Carlo permutations tests with 999 permutations were chosen for further analyses.

I used variance partitioning (Økland 2003) to evaluate the redundancy in explanatory value of a set of old (O) and two new (N_1 and N_2) variables chosen through forward selection. The CCA of all selected variables measures the total inertia (TI) of the variation in plant species composition and the inertia explained by the union of the 3 sets ($N_1 \cup N_2 \cup O$; n = 3). Inertia is analogous to the variance in a data set (Palmer 2004). I divided the TI explained by $N_1 \cup N_2 \cup O$ into $2^n - 1 = 2^3 - 1 = 7$ components in order to determine the relative importance of the three sets of variables, separately and jointly. I quantified the inertia uniquely explained by each set ($N_1 | N_2 \cup O$, $N_2 | N_1 \cup O$, and $O | N_1 \cup N_2$) with three partial CCAs in which I entered one set as environmental variables and the two remaining sets as covariables. A partial CCA is a CCA in which the effects of certain environmental variables (covariables) are removed. For example $N_1 | N_2 \cup O$ represents the variation explained by N_1 not included in $N_2 \cup O$. The redundant portions of two or more data sets are called the intersections. I quantified the intersections between all three sets ($N_1 \cap N_2 \cap O$) and each pair of sets ($N_1 \cap N_2 | O$, $N_1 \cap O | N_2$, and $N_2 \cap O | N_1$) indirectly. For example, $N_1 \cap N_2 | O$ is the difference between $N_1 \cup N_2 | O$ and the sum of $N_1 | N_2 \cup O$ and $N_2 | N_1 \cup O$, and $N_1 \cap N_2 \cap O$ is the difference between $N_1 \cup N_2 \cup O$ and the sum of $N_1 | N_2 \cup O$, $N_2 | N_1 \cup O$, $O | N_1 \cup N_2$, $N_1 \cup N_2 | O$, $N_2 \cup N_1 | O$, and $O \cup N_1 | N_2$. I used variance partitioning to test the null hypothesis: the new environmental variables do not explain variation in plant species beyond that which is explained by the old environmental variables (Ter Braak 1986, 1987, 1988a).

In addition to CCA, I compared all environmental variables by using Pearson correlations with SPSS (2001). As I displayed these correlation coefficients to assess the strength, rather than the significance of these relationships, I did not correct for the multiple correlation (Legendre and Legendre 1998).

RESULTS

Forward selection chose environmental variables in the order total C (C_t) ($P = 0.001$), Mehlich III extractable Fe (Fe) ($P = 0.001$), pH ($P = 0.002$), residual P (P_r) ($P = 0.031$), and Mehlich III extractable Zn (Zn) ($P = 0.041$). The remaining variation in plant species composition could not be significantly explained ($\alpha = 0.05$) with the available set of environmental variables. The selected variables explained 41% of the total inertia of the species data. C_t and P_r were chosen from the new set of variables. Forward selection from only the old variables set resulted in the following selection: SOM ($P = 0.001$), Fe ($P = 0.001$), pH ($P = 0.001$), slope ($P = 0.044$), and Zn ($P = 0.044$). These variables also explained 41% of the total inertia of the species data.

Variance partitioning shows that 37.9% of the variation explained by C_t, Fe, pH, P_r, and Zn was uniquely explained by the new variables C_t and P_r (Fig. 2). C_t uniquely accounts for 20.1% of the explained variation, and P_r accounts for 15.0% of the explained variation. I do not display variance partitioning between the selected new variables and the alternate old variables (SOM and slope) because the partial CCAs necessary to produce N | O and O | N had P values of 0.16 and 0.21, respectively ($\alpha = 0.05$).

When testing with two-tailed tests of significance, C_t, Fe, pH, P_r, and Zn were significantly correlated ($\alpha = 0.05$) with 25, 12, 18, 17, and 4, respectively, of the unused environmental variables in the data set.
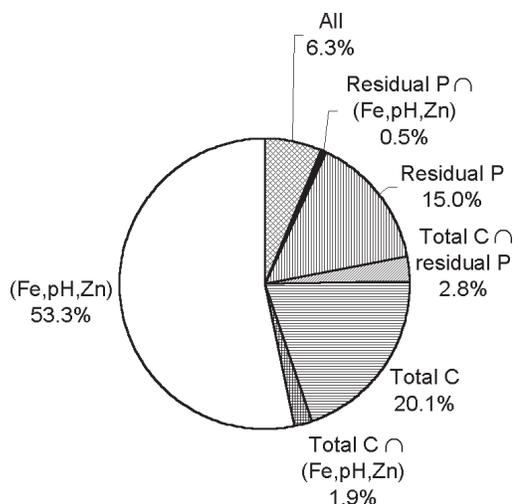
Figure 2. Partitioning of variation in plant species composition explained by the soil variables total C, Mehlich III extractable Fe, pH, residual P, and Mehlich III extractable Zn. Variation explained by Fe, pH, and Zn is grouped as one unit. ∩ = intersection.

Table 1. Pearson correlation coefficients between total C, residual P, and soil nutrients, soil texture, and site characteristics.

	Total C	Residual P
Total N	_0.977**	_0.679**
NO_3	_0.464*	−0.017
NH_4	_0.534*	_0.179
Resin P_i	_0.664**	_0.353
$NaHCO_3$ P_i	_0.455*	_0.240
NaOH P_i	_0.512*	_0.392
1M HCl P_i	_0.542*	_0.485*
cHCl P_i	_0.866**	_0.781**
$NaHCO_3$ P_o	−0.361	−0.004
NaOH P_o	_0.398	_0.546*
cHCl P_o	_0.899**	_0.790**
K	_0.583**	_0.551**
SO_4	_0.808**	_0.632**
Ca	_0.868**	_0.633**
Mg	_0.827**	_0.650*
Na	_0.234	_0.186
Sand	−0.835**	−0.778**
Silt	_0.758**	_0.689**
Clay	_0.892**	_0.693**
Soil organic	_0.959**	_0.713**
Bare ground	−0.496*	−0.337
Grass height	_0.588**	_0.259
Forb height	_0.523*	_0.473*

** Significant at the 0.01 level (2-tailed)
*   Significant at the 0.05 level (2-tailed)

Total N was the soil nutrient variable most highly correlated with both C_t and P_r (Table 1). All variables were significantly correlated with C_t except $NaHCO_3$ P_o, NaOH P_o, and Na. Most soil nutrients were significantly correlated with P_r except the labile forms of N and P and Na. C_t was significantly correlated with all variables associated with biomass and soil type. P_r was significantly correlated with all texture variables, SOM, and forb height. C_t was significantly correlated with all inorganic fractions of soil P and organic soil P extracted with concentrated HCl. P_r was significantly correlated with the other recalcitrant forms of soil P (HCl extractable P and NaOH extractable organic P). The correlation coefficient between P_r and slope was 0.438 ($P = 0.053$).

DISCUSSION

Based on the results of variance partitioning, the new environmental variables were unable to explain variance in species composition beyond that explained by the old environmental variables. The low level of redundancy found between C_t, Fe, pH, P_r, and Zn suggests that C_t and P_r could provide additional, significant explanation of species composition. However, partial CCAs comparing C_t and P_r to SOM and slope show that differences between the new variables and alternate old variables are not significant.

The lack of significance is primarily due to the strong correlation between C_t and SOM. C_t represents pools of inorganic C, which may be found in abundance in limestone soils, in addition to the organic C rep-

resented by SOM. However, organic C also tends to be higher in limestone soils. By combining two of the common characteristics of soils forming from limestone parent material, high inorganic C and high organic content, C_t could provide a marginal increase in explanatory power over variables representing organic content and Ca content in plant communities that are highly influenced by soil type such as the boundary between cross-timbers and prairie (Francaviglia 2000). Unfortunately, the small sample size in this study is inadequate for outlining the differences in such highly correlated variables.

P_r was not so highly correlated with any single variable in the available set, and its correlation with slope was only marginally significant. However, interpreting its value in explaining plant species composition is problematic. P_r tends to be correlated, although weakly, with many of the same environmental variables as C_t. This is likely because recalcitrant P is also associated with a limestone parent material (Schlesinger 1997). The explanatory value of P_r beyond that of the other selected variables, though statistically significant, shows no discernable relationship with the ecological traits of the species variables. In addition, P_r almost certainly functions as a proxy variable because the pool of soil P represented by P_r is not bioavailable without extensive weathering. As a proxy variable P_r is likely related to soil type and extent of weathering (Smeck 1973). A stronger causal connection between P_r and species responses is still needed to interpret the role of P_r in controlling species composition. It is also possible that the significant explanatory value of P_r is an artifact of a low sample size. Unfortunately, the high cost of P fractionation suggests that P_r is not likely to play a substantial role in the future of direct gradient analysis.

C_t and P_r are strong examples of the use of proxy variables in direct gradient analysis. Unlike indirect gradient analysis, direct gradient analyses, such as CCA, constrain the scores of the response variables to be linear combinations of explanatory variables. The variation in species composition of the samples is represented in terms of the chosen explanatory variables, but a causal relationship cannot be guaranteed. Environmental gradients, such as C_t, SOM, Ca, and pH, tend to be strongly correlated with patterns in plant species composition, but it is difficult to unravel the causal relationships responsible for this correlation. It is likely that most if not all of these variables serve as proxies for environmental conditions contributing to the spatial arrangement of species within the prairie community. Resources traditionally recognized to limit plant growth include space, light, water, and nutrients. C_t and P_r are correlated with environmental variables associated with the availability of space, light, and water, and C_t is correlated with plant available nutrients (Table 1). The correlation of C_t and P_r with such a large number of potentially influential environmental variables suggests that the relationships between C_t and P_r and plant species composition are probably not directly causal.

It is not surprising that proxy variables representing multiple factors affecting species composition were chosen through stepwise forward selection because I intentionally chose variables that explain the greatest amount of variation in the species data. Future research intended to identify more direct relationships could focus on more homogeneous systems, such as only on communities within a single soil type. In contrast, when studying a more heterogeneous system, such as the prairie-crosstimbers continuum, proxy variables should become more dominant by explaining differences between forest and grassland vegetation. Due to the interdependence of organisms and multiple biogeochemical cycles, proxy variables will likely continue to play an important role in exploratory analysis.

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