Responses of Legumes to Herbivores and Nutrients During Succession on a Nitrogen-Poor Soil

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RESPONSES OF LEGUMES TO HERBIVORES AND NUTRIENTS DURING SUCCESSION ON A NITROGEN-POOR SOIL

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Abstract. We measured legume abundance following 13- and 5-yr experiments testing for the effects of mammalian herbivores, nutrients, and climate on plant communities in an old field and a savanna in east central Minnesota. Total legume abundance was significantly greater in plots with herbivores excluded. Within herbivore exclosures, legumes were more abundant in plots to which P, K, S, Mg, Mn, Ca, Na, and trace minerals had been added. Legumes were significantly more abundant in the savanna than in the old field. Lathyrus venosus, a rapidly growing early-maturing species, was largely responsible for these results. Two other common legumes at our study site, Amorpha canescens and Lespedeza capitata, were not significantly affected by herbivore exclosures. However, within herbivore exclosures, addition of nutrients significantly reduced Lespedeza. Late summer total legume biomass within herbivore exclosures increased strongly following exclosure establishment in 1982, declined dramatically following a severe drought in 1988, and then increased again following the drought. This trend suggested that herbivore effects we measured in 1994 resulted from long-term accumulation of legumes following the establishment of exclosures. Our results suggest that herbivores and nutrients other than nitrogen can dramatically limit the abundance of some legume species that might otherwise dominate grassland plant communities on nitrogen-poor soils. Limitation of legumes by colonization and drought may also be important. Thus, herbivores and nutrients other than nitrogen may be critical in structuring grassland plant communities and influencing succession, even on nitrogen-poor soils.

Key words: grasslands; herbivore; legume; nitrogen; soil; succession.

INTRODUCTION

Because of their ability to fix atmospheric nitrogen, leguminous plants (legumes) can be important in nutrient cycling and soil development processes on nitrogen-poor soils (Groffman et al. 1986, 1987, Van Sanbeek et al. 1986, Virginia 1986, Ledgard and Steele 1992). Thus, legumes' prevalence within plant communities can be an important factor in determining plant succession and ecosystem functioning (Chapin et al. 1986, Mooney et al. 1987, Vitousek et al. 1987, Sheehy 1989, Coates et al. 1993). In grasslands on nitrogen-poor soils, legumes might be expected to dominate because they can persist at lower available soil nitrogen levels than non-legumes (Lodge 1991, Hein and Vinall 1993, Posler et al. 1993). In many natural grasslands, however, legumes are rare (<5% of above-ground phytomass; Gadgil et al. 1986, Bartolome and McClaren 1992, Osman and Cocks 1992).

One or more of three hypotheses might explain this unexpected rarity of legumes. First, native herbivores may consume legumes preferentially because legumes often have a higher tissue nitrogen content than surrounding plant species on low N soils (Boller and Heichel 1983, Power and Zacchariassen 1993). Thus, intensity of herbivory may be much higher for legumes than for other plants, such that herbivores may reduce legumes to very low abundances (Jones and Mott 1980, Gutteridge 1985, Gadgil et al. 1986, Hein and Vinall 1993).

A second hypothesis is that legumes might be limited by nutrients other than nitrogen (Grime and Curtis 1976, Tilman 1982, Whitehead 1987, Fenner and Lee 1989). Because traits often trade off in their benefits for species facing conflicting demands (Tilman 1990), legumes might be expected to have higher requirements for nutrients other than nitrogen as a cost of maintaining their nitrogen-fixing capability, and might not compete effectively for these other nutrients (Tilman 1982). Addition of nutrients such as calcium or manganese are often necessary for optimal performance of both crop (Whitehead 1987, Fenner and Lee 1989) and wild legumes (Foote and Jackobs 1966, Tilman 1982). Therefore, a shortage of nutrients other than nitrogen may limit legume abundance.

A third hypothesis suggests that legumes may be rare in environments with high disturbance levels because they cannot quickly recolonize following disturbance. Many legumes produce large seeds, which may disperse poorly (Osman and Cocks 1992), or herbivores

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may heavily depredate reproductive parts, which may reduce seed supply (Gadgil et al. 1986, Ehrlen 1992). Areas with a recent history of soil disturbance, such as old-field grasslands, often have low legume abundance unless legumes are seeded.

Previous studies of successional grasslands and savannas at Cedar Creek Natural History Area (CCNHA) clearly show that soils are nitrogen poor (<800 mg/kg) and that plant production is limited by nitrogen (Tilman 1984, 1987). However, legumes occur in very low abundance and diversity in these grasslands (Tilman 1988). Herbivores, particularly white-tailed deer (Odocoileus virginianus), occur at high abundance and can greatly reduce the abundance of preferred plant species (Allison 1990, Inouye et al. 1994). In successional grasslands, legumes may also not have had sufficient time to recolonize after agricultural soil disturbances.

We specifically addressed the first two of these hypotheses by measuring abundance of legumes (as a group and by species) within existing long-term (13 and 5 yr) mammalian herbivore exclusion and nutrient addition experiments at CCNHA: This allowed us to test the hypothesis that (1) mammalian herbivory reduces the abundance of legumes, and (2) legume abundance is limited by the availability of one or more nutrients other than nitrogen. We also compared legume abundance and legume responses to non-N nutrient addition among three plant communities that differed in their disturbance history (savanna, undisked 60-yr-old field, and a 13-yr-old disked portion of the 60-yr-old field).

METHODS

The study was conducted at Cedar Creek Natural History Area (CCNHA), located 60 km north of Minneapolis in east central Minnesota. Detailed descriptions of the savannas and successional grasslands at CCNHA are available elsewhere (Tilman 1987, 1988, Faber-Langendoen and Tester 1993). We assessed legume abundance in three plant communities: undisked (in 1982) and disked portions of a single 60-yr post-cultivation old-field prairie grassland (Field C, Tilman 1987), and an oak savanna maintained by burning two of every three years (Field D, Tilman 1987). These communities are dominated by prairie grasses Schizachyrium scoparium, Andropogon gerardii, and/or Sorghastrum nutans, and include a diverse array of forbs and some woody species. The savanna contains scattered pine oaks (Quercus ellipsoidalis) and bur oaks (Quercus macrocarpa). The major (99% by biomass) legume species in these fields are Lathyrus venosus, Lespedeza capitata, and Amorpha canescens (hereafter referred to by genus), but these typically represent <5% of aboveground phytomass (Tilman 1987, 1988).

Experimental design

To test for herbivore and nutrient effects, we measured abundance of all legume species within parts of five existing long-term experiments established in either 1982 or 1989 as part of the Long-Term Ecological Research (LTER) program at CCNHA (summarized in Table 1). We will refer to these by the letter of the field in which they were located and by number. Experiment C-1 added nutrients on the undisked portion of the old field (Field C) inside a single herbivore enclosure. Experiment C-2 added nutrients on the disked portion of the old field inside the same enclosure as Experiment C-1. Experiment D-1 added nutrients inside an herbivore enclosure in the savanna (Field D). Experiment D-3 added nutrients inside a different herbivore enclosure in the savanna (see Tilman 1987, 1988 for additional data on Experiments C-1, C-2, D-1, and D-3). Experiment D-62 established replicate herbivore enclosures at yet another location in the savanna.

Experiments C-1, C-2, and D-1 were designed to assess the effects of nutrient addition on plant communities (Tilman 1987) in the absence of mammalian herbivores. Permanent plots for each of these experiments were surrounded by a single fence that excluded white-tailed deer (Odocoileus virginianus), and reduced densities of pocket gophers (Cynomys baxteri) and small mammals (Peromyscus leucopus and Microtus pennsylvanicus). Small mammals and pocket gophers were removed by regular trapping during each growing season.

Experiments C-1 and C-2 were conducted within the same herbivore enclosure in the old field, and had control and eight different nutrient addition treatments, with six replicate 4 x 4 m permanent plots of each. Nutrients were added twice yearly (Tilman 1987). Separately randomized sets of plots were established on either existing old field vegetation (undisked, Experiment C-1) or on an equivalent area disked (with a tractor) just prior to plot establishment (disked, Experiment C-2) within the enclosure. We sampled legume abundance in the left half (2 x 4 m) of plots of only two of the nine treatments: no nutrients (control) and all nutrients but nitrogen (non-N) in the following amounts: macronutrients (8.7 g m\(^{-2}\)yr\(^{-1}\) of P; 16.6 g m\(^{-2}\)yr\(^{-1}\) of K; 8.1 g m\(^{-2}\)yr\(^{-1}\) of S; 5.9 g m\(^{-2}\)yr\(^{-1}\) of Mg; and 16.1 g m\(^{-2}\)yr\(^{-1}\) of Ca) and trace minerals (7.1 µg m\(^{-2}\)yr\(^{-1}\) of Cu, 15.2 µg m\(^{-2}\)yr\(^{-1}\) of Zn, 8.7 µg m\(^{-2}\)yr\(^{-1}\) of Co, 140.1 µg m\(^{-2}\)yr\(^{-1}\) of Mn, 1.8 µg m\(^{-2}\)yr\(^{-1}\) of Na, and 7.9 µg m\(^{-2}\)yr\(^{-1}\) of Mo) (Tilman 1987). Experiment D-1 was conducted in the savanna inside a mammalian herbivore enclosure and was identical to Experiment C-1, except that plots were only 2 x 4 m and there were only five replicates per nutrient treatment. As with Experiment C-1, we sampled only two treatments inside the enclosure: control and addition of all nutrients but nitrogen.

We tested for herbivore effects with Experiments C-1 and D-1 by comparing control plots inside enclosures with temporary plots established outside but adjacent to each enclosure. Thus, six replicate 2 x 4 m plots were established outside the enclosure for Experiment
TABLE 1. Relevant characteristics of long-term experiments at Cedar Creek Natural History Area used in analysis of herbivore and non-N nutrient effects on legumes.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Year begun</th>
<th>Community type*</th>
<th>Herbivores excluded</th>
<th>No. replicates of herbi-</th>
<th>Nutrient treatments sampled</th>
<th>No. replicates of nutrient treatment†</th>
</tr>
</thead>
<tbody>
<tr>
<td>C-1</td>
<td>1982</td>
<td>old field, undisked</td>
<td>mammals</td>
<td>1</td>
<td>Control/non-N</td>
<td>6</td>
</tr>
<tr>
<td>C-2</td>
<td>1982</td>
<td>old field, disked</td>
<td>mammals</td>
<td>NA‡</td>
<td>Control/non-N</td>
<td>6</td>
</tr>
<tr>
<td>D-1</td>
<td>1982</td>
<td>savanna</td>
<td>mammals</td>
<td>1</td>
<td>Control/non-N</td>
<td>5</td>
</tr>
<tr>
<td>D-3</td>
<td>1982</td>
<td>savanna</td>
<td>mammals and insects</td>
<td>1</td>
<td>Control§</td>
<td>NA§</td>
</tr>
<tr>
<td>D-62</td>
<td>1989</td>
<td>savanna</td>
<td>mammals</td>
<td>1</td>
<td>Control§</td>
<td>NA§</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Plot size sampled (m²)</th>
<th>Legume species present</th>
<th>Effects tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>C-1</td>
<td>8</td>
<td>Lathyrus, Lespedeza</td>
<td>Herbivores, Nutrient Addition, Year</td>
</tr>
<tr>
<td>C-2</td>
<td>8</td>
<td>Lathyrus, Lespedeza</td>
<td>Nutrient Addition, Year</td>
</tr>
<tr>
<td>D-1</td>
<td>8</td>
<td>Lathyrus, Amorpha</td>
<td>Herbivores, Nutrient Addition, Year</td>
</tr>
<tr>
<td>D-3</td>
<td>6</td>
<td>Lathyrus, Amorpha</td>
<td>Herbivores</td>
</tr>
<tr>
<td>D-62</td>
<td>4</td>
<td>Lathyrus, Amorpha</td>
<td>Herbivores</td>
</tr>
</tbody>
</table>

* The old field is Field C, the savanna is Field D.
† Number of replicate plots per nutrient addition treatment.
‡ Plots in Experiment C-2 were not used to test for herbivore effects.
§ Plots with addition of single nutrients were not used to test for herbivore effects.
‖ Nutrient addition treatments not sampled in Experiment D-3, and there were no nutrient addition treatments in Experiment D-62.
¶ Five replicate plots associated with each herbivore treatment (control and herbivores excluded) were pooled to form a single replicate to keep size of experimental units similar in tests of herbivore effects.

C-1 in the old field, and five replicate 2 × 4 m plots were established outside the enclosure for Experiment D-1 in the savanna. Because plots for Experiment C-2 (disked) were inside the same enclosure as those for Experiment C-1 (undisked), and disking only occurred within the enclosure, we did not use plots from Experiment C-2 to test for herbivore effects.

Experiments D-3 and D-62 (both in the savanna) were used only to test for herbivore effects on legumes. Experiment D-3 was established in 1982 and added single nutrients to 1.5 × 4 m plots (including a non-nutrient control) in a randomized design, with four replicates of each treatment. However, we only sampled control plots inside the enclosure to compare with four temporary 1.5 × 4 m adjacent plots we established outside the enclosure. Experiment D-62 assessed the effects of both mammalian and insect herbivores on plants. In June of 1989, 10 2 × 2 m plots were placed randomly on existing vegetation within a 50 × 50 m area. Five of these plots had herbivores excluded by a 0.8-cm mesh wire cloth and 1.5-mm mesh window-screen fence attached to a steel frame. A window-screen "lid" was placed over the top of each plot and attached to the steel frame. We applied carbaryl methylcarbarate (Sevin) insecticide (800 µL/L solution at 0.2 L/m²) once per summer inside each plot. The cages effectively reduced insect damage and excluded small mammals and deer. During 1989–1994, pocket gopher mounds were never observed inside herbivore exclusion plots. The remaining five plots were "controls," which received a windowscreen lid (to standardize shading effects on plants) but no fence. We removed lids on all plots each fall to prevent snow damage but returned them to cages each spring. This allowed deer to browse inside herbivore enclosures during winter.

Sampling and statistics

We measured legume abundance from visual percent cover estimates obtained by covering plants of each legume species with cardboard squares of various sizes that corresponded to known fractions of sampling plots (Inouye et al. 1987, Tilman 1988). For plots in Experiments C-1 and C-2, we also counted the number of individual stems for each species in each plot. As part of a long-term study of nitrogen effects on plant production (Tilman 1987, 1988), total biomass of legumes inside herbivore enclosures in Experiments C-1, C-2, and D-1 was also measured during August each year since 1982. Within each plot, all aboveground tissue within a 10 cm × 3 m strip within each plot was clipped, sorted to species, dried at 45°C for 1 wk, and weighed.

Statistical tests were conducted using the Number Cruncher Statistical System (Jerry Hintz, Kaysville, Utah) package for microcomputers. Linear regressions were used to test whether percent cover reflected stem
density and thus absolute abundance. Because nutrients were not added to plots outside herbivore exclosures, effects of herbivores and nutrients could not be analyzed within a single ANOVA. Consequently, we performed different statistical analyses for each effect.

To determine the effects of herbivores, we compared legume abundance inside and outside exclosures in Experiments C-1, D-1, D-3, and D-62. To avoid pseudoreplication, we treated the entire fenced and accompanying unfenced or control areas in each of Experiments C-1, D-1, and D-3 as experimental units, with individual sampling plots as subsamples. Although herbivore exclosures were assigned randomly to replicate plots in Experiment D-62, we pooled data within each treatment to help standardize the size (i.e., scale) of experimental units. Thus, each experiment served as a single split-plot replicate and we tested for the significance of herbivore effects using split-plot ANOVA.

For legume species that occurred in only one experiment (e.g., Lespedeza in the old field), we compared mean abundance inside and outside the herbivore enclosure using t tests, with plots as experimental units.

We tested for nutrient effects within the herbivore exclosures of Experiments C-1, C-2, and D-1 by comparing legume abundance on control vs. non-N nutrient addition plots. We performed an unbalanced, randomized complete block one-way ANOVA with the three experiments combined. Each experiment represented a block or community type: the undisked portion of the old field (C-1), the disked portion of the old field (C-2), and the savanna (D-1). Sampling plots were the experimental units. Differences in legume abundance and response to nutrient addition among community types were analyzed as block effects within the one-way ANOVA. Because community types were unreplicated, we could not test for a nutrient × community type interaction. All a posteriori contrasts were tested with Tukey’s multiple comparison test with α = 0.05.

To analyze effects of nutrient addition and test for annual variation in total legume biomass, we performed unbalanced, randomized complete block ANOVA with community types as blocks, year and nutrient addition as treatments, and sampling plots as experimental units (Tilman 1990).

## RESULTS

Plant density (D) was strongly correlated with relative abundance (percent cover, P) for each of the three legume species (Lathyrus: D = 0.17 P + 0.75, R² = 0.95; Lespedeza: D = 0.59 P + 0.34, R² = 0.85; Amorpha: D = 0.30 P + 0.25, R² = 0.97) and thus percent cover also represented a measure of absolute abundance.

Total legume abundance was four times greater in-

### Table 2.

<table>
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<tr>
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<th>df</th>
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<td>Herbivores</td>
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<td>.04</td>
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<td></td>
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<tr>
<td>B) Nutrient effects (all plots)*</td>
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<td></td>
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<td>2</td>
<td>5.74</td>
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<td>1</td>
<td>0.53</td>
<td>.47</td>
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<tr>
<td>Error</td>
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<td>30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C) Nutrient effects (plots with legumes present only)</td>
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<td></td>
<td></td>
<td></td>
</tr>
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<td>1.21</td>
<td>2</td>
<td>25.3</td>
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<td>6.1</td>
<td>.02</td>
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<tr>
<td>Error</td>
<td>0.52</td>
<td>18</td>
<td></td>
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</table>

* See Experimental design.
nutrient addition treatments (8/17) was not significantly different ($\chi^2 = 0.12, P > 0.5$). Including empty plots potentially confounded the analysis of nutrient effects with the effects of colonization. Therefore, we reanalyzed the data by including only plots that contained legumes, and found that legumes were significantly more abundant in plots with nutrients added (Table 2C, Fig. 3A). In tests for nutrient effects on individual legume species, we again included in the analysis only plots where a species was actually present. Lathyrus abundance was significantly higher on plots with nutrients added (Fig. 3B) ($F = 4.42, df = 1.14, P = 0.04$). However, abundance of Lespedeza in the old field was significantly lower on plots with nutrients added (Fig. 3C) ($F = 6.35, df = 1.11, P = 0.03$). In the savanna, abundance of Amorpha was not significantly higher in plots with nutrients added (Fig. 3D) ($F = 0.3, df = 1.4, P = 0.71$).

Within herbivore exclusions, the abundance of all legumes combined differed significantly with block (community type) (Table 2B, C). This result reflected that legumes were three times more abundant in the savanna than in the old field (disked or undisked) (Fig. 4). This largely reflected a greater abundance of Lathyrus and Amorpha in the savanna. In addition, effects of non-N nutrient addition on total legume abundance were significant only in the savanna (Tukey’s multiple comparison test).

Within herbivore exclusions, late season biomass of legumes as a group changed significantly with year (Table 3, Fig. 5). Block (community type) effects were also significant (Table 3). These patterns reflected that legume biomass increased significantly over time following both establishment of herbivore exclusions and the decline in legume biomass in 1988 due to drought, except in the disked area of the old field (Fig. 5). How-

![Fig. 2. Effects of herbivore exclosures on mean (±1 SE) percent cover of Lathyrus venosus (dark shading) and Lespedeza capitata (hatched) in the undisked portion of the old field (Experiment C-I). Different lowercase letters indicate significant contrasts.](image)

![Fig. 3. Effects of addition of P, K, S, Mg, Mn, Ca, Na, and trace minerals, but without N addition (Fertilized) vs. controls (Unfertilized) on percent cover of (A) all legume species combined, and (B–D) individual legume species. Data are from Experiments C-1 (undisked portion of the old field), C-2 (disked portion of the old field) and D-1 (the savanna), and include only plots in which legumes actually occurred. Asterisks indicate significant contrasts after ANOVA (see Table 2C).](image)
ever, nutrient addition effects and the interaction between nutrient addition and year were not significant.

**Discussion**

Overall, both herbivores and nutrients appeared to limit the abundance of a potentially dominant legume species, *Lathyrus*. Protection from herbivory resulted in dramatically higher *Lathyrus* abundance (Fig. 1A, B). For plots inside exclosures that actually contained legumes, total legume and *Lathyrus* abundance were higher where P, K, S, Mg, Mn, Ca, Na, and trace minerals were added, but *Lespedeza* abundance was lower (Fig. 3). When protected from herbivores, total legume and *Lathyrus* abundance was higher in the savanna than in the more recently disturbed old field (Fig. 4). These responses of legumes to experimental treatments appeared to reflect long-term trends in abundance (Table 2, Fig. 5).

Because treatments were not applied in a complete two-way factorial design and we did not replicate community types (the disked and undisked portions of the old field, and the savanna), we could not properly address potential interactions among these effects. However, the difference in legume cover between inside and outside exclosures appeared to be greater in the savanna (20.1 ± 4.1%, mean ± 1 SE, \( N = 3 \)) than in the old field (8.3%, \( N = 1 \)). In addition, non-N nutrient addition significantly increased total legumes and *Lathyrus* in the savanna but not in the old field (Fig. 4). These patterns suggest that effects of herbivores and nutrients were stronger in the savanna, where legumes occurred at higher abundance and may have been more thoroughly established.

Overall, these results suggest that herbivores and lack of nutrients other than nitrogen prevent some legume species from dominatinggrassland communities on the nitrogen-poor soils at CCNHA. In the savanna, when protected from herbivores and provided with nutrients other than nitrogen, *Lathyrus* attained an average relative abundance of 83% and densities of 15 stems/m². This result supports the hypothesis that some species of legumes might be competitively dominant in the absence of herbivory (Tilman 1982, Posler et al. 1993). While addition of nitrogen has either no effect or a negative effect on legume abundance at CCNHA (Tilman 1988), our results suggest that potentially dominant legume species may be limited by nutrients other than nitrogen (Tilman 1982, Fenner and Lee 1989).

Circumstantial evidence suggests that colonization and drought may also limit legume abundance in these grasslands. The lower abundance of *Lathyrus* and its weaker response to nutrient addition in the more recently disturbed old field (Fig. 4) could be interpreted as evidence of colonization limitation. In addition, total legume biomass showed no long-term increase following protection from herbivores on the most recently disturbed community type (disked old field), but showed a dramatic increase in the savanna (Fig. 5). However, differences other than disturbance history between the savanna and the old field, e.g., microclimate or fire frequency, might explain these patterns equally well. Total legume biomass declined precipitously in association with the drought of 1988 (Fig. 5), and then increased rapidly afterward; this pattern suggests that legumes may be periodically water-limited at this site (Tilman and El-Haddi 1992).

The response of total legume abundance to experimental treatments largely reflected the response of a single species, *Lathyrus venosus*. *Lathyrus* is a cool-season species that grew more rapidly and matured earlier than the other two legume species, *Lespedeza* and *Amorpha*. Such differences in traits might explain why *Lespedeza* and *Amorpha* responded differently than *Lathyrus* to non-nitrogen nutrient addition and protection from herbivores. While *Lathyrus* was clearly capable of dominating these grassland communities in the absence of herbivory, the other two species apparently were not. Nevertheless, in the old field, *Lespedeza* abundance was significantly greater than that of *Lathyrus* in unfertilized plots in the presence of herbivores (Fig. 2). Thus, *Lespedeza* may perform better than *Lathyrus* in environments with high rates of herbivory.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
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<td>Error</td>
<td>212 713.9</td>
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**Fig. 4.** Comparison of mean (±1 SE) percent cover of all legume species combined for three plant community types: old field (Field C) disked in 1982 (Disked), old field (Field C) last cultivated in 1934 (Undisked), and oak savanna (Savanna), and two nutrient treatments: control (unfertilized) and addition of nutrients other than nitrogen (Fert/No N). Differences in lowercase letters indicate significant contrasts among community types, while an asterisk indicates a significant effect of addition of nutrients within a community type.
This result suggests that legumes may face a trade-off between competition for nutrients vs. susceptibility to herbivory (Hein and Vinall 1993, Posler et al. 1993, Power and Zachariassen 1993). Such trade-offs might be expected for plants in general (Bloom et al. 1986, Bazzaz et al. 1987, Tilman 1988, Pacala and Crawley 1992), but they may be particularly strong for legumes because of their potentially high susceptibility to herbivory.

Our results suggest that plant community structure and succession in N-poor grasslands may be strongly affected by herbivory. Succession from grassland to savanna on N-poor soils at CCNHA is very slow (requires ≳ 70 yr, Inouye et al. 1987), and appears to be ultimately controlled by the accumulation of N in soils (Tilman 1985, Zak et al. 1990). Herbivory may retard succession by severely reducing the abundance of legume species (e.g., *Lathyrus*) that would otherwise accelerate soil N accumulation (Hoglund and Brock 1978, Virginia 1986). In addition, herbivores may compound the already slow rate of recolonization by legumes following disturbance (Fig. 5) by depleting reproductive structures and reducing seed supply (Ehrlein 1992). Moreover, common legume species in grasslands (e.g., *Lespedeza*) which may be less susceptible to herbivory and more likely to persist under strong herbivore pressure, may be slower growing, and have lower tissue N and less impact on soil N accumulation and plant succession. Because of legumes’ strong impact on N-cycling in many systems (Vitousek et al. 1987, Sheehy 1989, Coates et al. 1993), herbivores may impact succession more through indirect effects on soils (Huntly 1991, Pastor et al. 1993) than through direct damage to later successional plant species (Davidson 1993, Inouye et al. 1994).

Overall, we found strong evidence that some legume species are capable of dominating savanna and successional grassland plant communities at CCNHA, but are prevented from doing so by herbivory and the lack of nutrients other than N. Circumstantial evidence (Fig. 5) suggests that slow colonization and periodic droughts may also impose limits. Because of these effects, legumes are unlikely to dominate natural, unmanipulated N-poor grasslands, in spite of their apparent competitive advantage on N-poor soils.

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