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DOES COMPETITION DRIVE COMMUNITY STRUCTURE?

An analysis of grasshopper competition

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of the requirements for a
Bachelor of Science degree in
Wildlife Management
with
University Honors

UTAH STATE UNIVERSITY
Logan, UT

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INTRODUCTION

Interspecific competition has been broadly defined as a negative-negative relationship between species that share a limiting resource. The impact of competition on ecological communities is a widely debated topic (Schoener 1982). Thus community structure is very complex and, in addition to competition, can be influenced by many factors, including climate, disease, parasites, and predation (Hairston et al. 1960; Stower & Greathead 1969; Wiens 1977). The importance of competition depends upon the importance of other processes (Welden & Slauson 1986).

Many studies have tested whether competition controls species abundances. Some studies state that competition structures communities (Janzen 1973; Benson et al. 1975; Benson 1978; Lawton & Strong 1981), while others show that competition does not (Cole 1960; Hairston et al. 1960; Wiens 1977; Cannon & Simberloff 1979; Huey 1979; Strong et al. 1984; Evans 1992). Schoener (1983) found that 90% of studies conducted to that date had detected interspecific competition, indicating its importance in ecological communities. However, Connell (1983) conducted a similar survey and concluded that competition was not important in defining community structure.

These studies suggest that competition is important for some species in some environments but not for all species in every environment. Connell (1980) predicts that competition will not occur in extreme environments, but will occur when conditions are only moderately harsh, as they are in grasslands. Benign environments, such as tropical rain forests, favor effective natural enemies such as predators and parasites whereas extremely harsh environments, such as arctic tundra, reduce populations below competitive levels (Connell 1980). Belovsky (1986) and Evans (1992) report that interspecific competition may occur when consumers are abundant relative to the availability of limiting resources.

Because of the prevalence of predators and their sensitivity to abiotic conditions, interspecific competition is thought to be rare among insects on plants (Strong et al. 1984; Evans 1992). In contrast, Belovsky (1986) suggests that interspecific competition among herbivores is common because food resources are limited. This competition may influence species' abundances and Belovsky (1986) concludes that herbivore diversity may be directly associated with food abundance. From these contrasting views, it appears that the importance of competition depends upon the degree to which resources are limiting.

Competition among insects might not be important for several reasons. Connell (1980) suggests that interspecific competition may have had a great impact in the past, causing organisms to evolve to minimize competitive effects. Interspecific competition for food resources influences community structure by causing some species to shift their diet (Engen et al. 1988; Ritchie & Tilman 1993). Belovsky (1986) suggests that competing herbivores utilize different plant parts according to availability and quality. Alternatively, Lawton and Strong (1981) report that natural enemies (including parasites and predators) and harsh climatic conditions may reduce insect densities such that resource availability increases, thus eliminating the need for competition.

Few studies have examined (1) the relationship between resource availability and species abundance, (2) the degree to which resources may be limiting and the importance of competition, and (3) whether or not these two factors determine community structure.

When food resources become limiting, the best competitors for dominant plants should account for a larger proportion of the population. Species with lower competitive abilities will decrease in abundance due to limited resource availability. In order for a species to maintain a stable population, its mortality rate must be matched by its growth rate. The resource abundance that produces growth which matches the consumer's mortality rate is

termed A^* (Figure 1a). Access to resources in greater amounts than the A^* value will produce a population increase, whereas limited resources below the A^* value will cause a decrease.

The A^* value can be used as a measure of competitive ability for a resource. Figure 1b shows an example of two species that share a resource. Species Y has a higher A^* value than species X, therefore species X is a better competitor because it requires less of this resource to survive. This model assumes that the mechanism of competitive displacement is through depression of resource availability (Tilman 1982). Once the resource level is depleted below A^*_Y , the population of species Y will decline while the population of species X

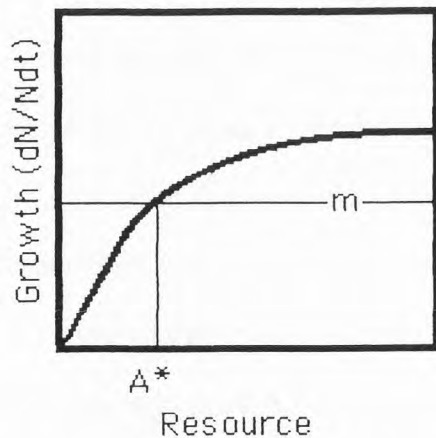


Figure 1a. Determining A^* value for a species using growth rate (dN/Ndt), mortality rate (m), and resource availability (R) (modified from Tilman 1982).

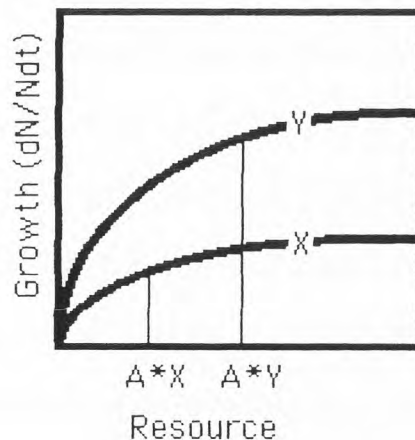


Figure 1b. A^* values for two species whose growth curves differ (modified from Tilman 1982).

continues to increase. Species X will have outcompeted species Y (adapted from Tilman 1982). This example demonstrates a more general result that species with lower A^* values will outcompete those with higher A^* values. A^* values for different species can be used to predict species abundance if the resource(s) shared by these species is known and if competition determines species abundances. If other factors (e.g. predation, weather) are more important than competition, then species abundances should not correlate with A^* values.

Objectives

This paper tests whether competition is an important factor in structuring grasshopper communities in successional grasslands. The study took place at Clear Creek Natural History Area (CCNHA), where successional patterns in plant abundance are known (Figure 2). Forbs dominate the early successional fields, *Poa pratensis* dominates mid-successional fields, while *Schizachyrium scoparium* dominates the older fields (Tilman 1988).

Nitrogen is clearly the most important resource that limits plant growth at CCNHA (Tilman 1988). During early successional stages, when light is not limiting, plant species direct most of their production into photosynthetic structures. Greater photosynthetic area allows plants to grow rapidly. As plants die and decompose, the nutrient base in the soil increases, while light penetration to the soil decreases. Eventually light becomes a limiting resource. Later successional plants use the larger amounts of nitrogen in the soil and grow extensive root systems. This allows them to eventually outcompete the early successional species (Tilman 1988).

The manner in which plant species allocate nutrients (in this case, nitrogen) to roots vs. shoots may affect the palatability of shoots to herbivores. Thus, plant species are likely to

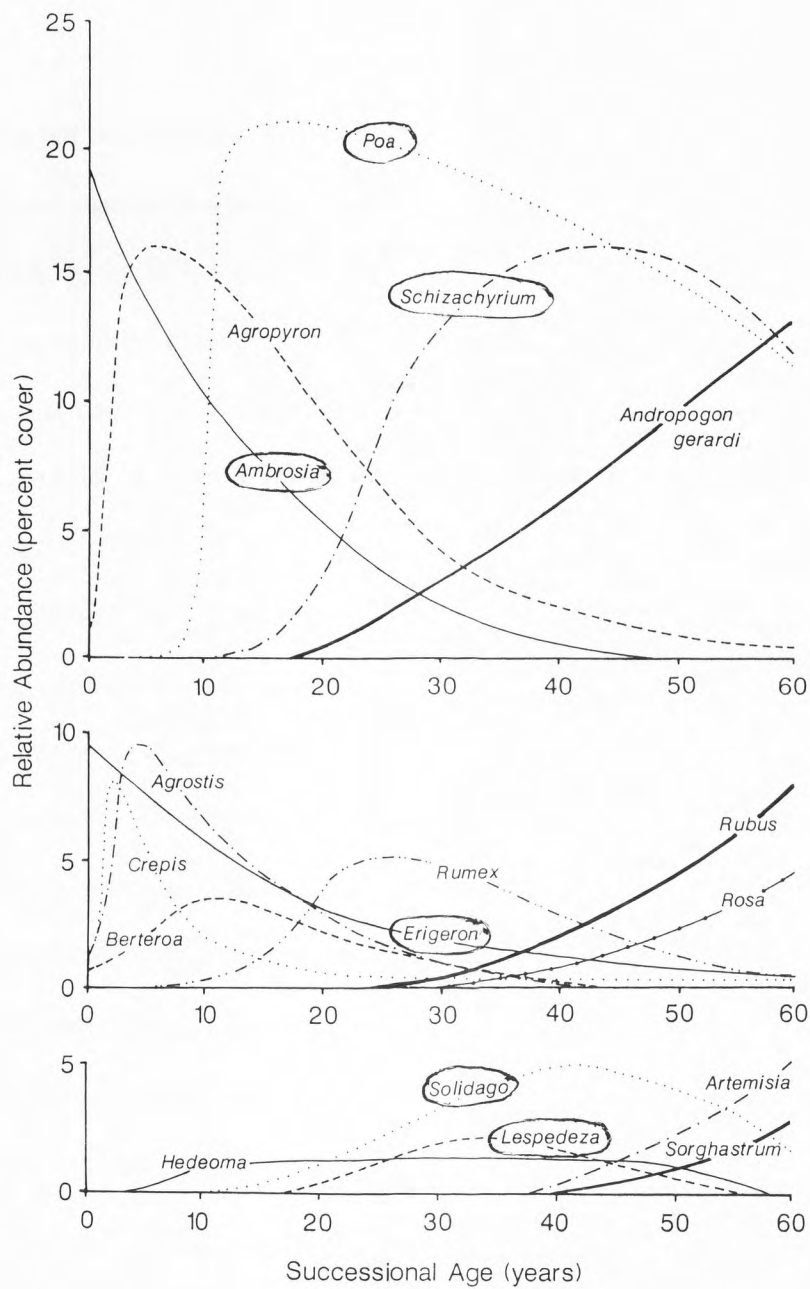


Figure 2. Dynamics of plant succession at Clear Creek Natural History Area. Species included in this study are circled (from Tilman 1988).

represent different resources to different grasshopper species. As plant species composition changes with successional age, so should grasshopper species composition. As a pioneer species is replaced by its successor, the grasshopper with the lowest A^* value for the pioneer plant species should be excluded by the grasshopper with the lowest A^* value for the later successional plant species. In addition, because later successional plant species allocate less nutrients to shoots, resources should be more limiting and competition more important at later successional stages.

I calculated A^* values for grasshoppers and plant species and analyzed these values to determine if competition was related to plant successional stage. Within each field, A^* values were compared to grasshopper abundance to decide to what degree competitive ability influenced species abundance. Across all fields, A^* values were compared with successional patterns to conclude if competition was related to field age. Specifically I proposed hypotheses to explain the abundance of grasshopper species:

- 1) Competitive ability for forbs is more important in younger fields,
- 2) Competitive ability for *Poa pratensis* is more important in middle aged fields,
- 3) Competitive ability for *Schizachyrium scoparium* is more important in older fields, and
- 4) Overall, competition is more important in later successional stages.

METHODS

Study area

Data was collected during July and August of 1989, 1990, and 1991 at Cedar Creek Natural History Area in east central Minnesota, 45 km north of Minneapolis. Grasshoppers

were sampled in 19 different fields, aged 8 years to 63 years since last disturbance. Samples were collected once a month. Plant species in the area include grasses (*Poa pratensis*, *Schizachyrium scoparium*) and various forbs (*Solidago rigida*, *S. nemoralis*, *Lespedeza capitata*, *Ambrosia coronopifolia*, *Erigeron canadensis*) (Tilman 1988).

A* values

A* values for each combination of grasshopper species and three major plant groups were calculated with the following formula:

$$A^* = (M/(P \cdot D \cdot K \cdot SR)) \cdot 60 \quad (1)$$

The forbs were grouped together due to their low individual abundances in the area. With eight grasshopper species and three vegetation species, 24 different A* values were calculated.

The equilibrium maintenance requirement (kJ/day) for each grasshopper species (M) was calculated as a function of body size. It was determined by

$$M = 4.1 \cdot (m/1000)^{0.751} \quad (2)$$

(m = average mass in grams) (Peters 1983). Proportion eaten (P) represents the percentage of the plant that a grasshopper ingested. Digestibility (D) represented the percentage of energy that the grasshopper utilized from each plant and was measured in the laboratory by M.E. Ritchie (unpublished). Gross energy content (K) of a plant species was assumed to be a constant of 20 kJ/g dry weight.

The search rate (SR) indicates how large of an area each grasshopper searches in m²/min. I used a formula empirically determined by M.E. Ritchie (unpublished)

$$((21.7 \cdot m^{0.80}) \cdot 250) / 10000 \quad (3)$$

I assumed that the grasshoppers spent 250 min/day feeding (Belovsky & Slade 1986). All SR

values were divided by 10,000 to convert units to m².

The factor 60 in equation (1) accounted for the fact that the average growth period for grasshoppers at Cedar Creek is 60 days (M. E. Ritchie, pers. comm.). Thus, A* in equation (1) is the abundance of a plant species required for the grasshopper species to persist for 60 days.

Grasshopper sampling

Total number of grasshoppers in 50 sweeps of a Muslin insect net was recorded for each of the 19 fields one day per month in July and August of each year of the study.

Melanoplus femurrubrum, *M. keeleri*, *M. bivittatus*, *Arphia conspersa*, *Spharagemon collare*, *Phoetaliotes nebrascensis*, *Ageneotettix deorum*, *Pardalophora apiculata* were the dominant grasshopper species (among a total of 13). The average count of a species was then multiplied by the mass of the grasshopper (determined in the laboratory by M. E. Ritchie) to estimate live grasshopper biomass. I used

$$\log (\text{biomass} + 1) \quad (4)$$

as an estimate of grasshopper abundance because all fields had some species with densities of 0 and abundances for different species differed by an order of magnitude. The density used in correlations with A* values was the highest density observed in any month within a year, averaged over three years.

Analysis

Statistical analysis was performed using NCSS (Number Cruncher Statistical System). To test if grasshoppers that were good competitors for one plant species were poor competitors for other plant species, correlations between A* values for all plant species were

calculated. To determine how much variability in grasshopper abundance was explained by competitive ability for each plant species, $\log(\text{biomass})$ was regressed against the A^* values for all plant groups using multiple regression. The partial r^2 value was recorded for each plant group (forbs, *Poa pratensis*, or *Schizachyrium scoparium*), as well as the total r^2 value when all plant groups were combined. Partial r^2 values reflect the ability of A^* values for a particular plant group to explain $\log(\text{biomass})$ of grasshoppers, independently of A^* values for other plant groups. The lower the partial r^2 values, the less influence competition for that food item had on community structure. Total r^2 values reflect how much variation in grasshopper biomass is explained by interspecific competition in general. This regression analysis was repeated for each field. These r^2 values were then correlated with field age to determine patterns in the importance of competitive ability. Significance ($P < 0.05$) of these correlations were tested using F-tests.

RESULTS

Calculated A^* values show that *Melanoplus bivittatus* and *Spharagemon collare* are the best competitors for forbs (Table 1). *Pardalophora apiculata*, *Phoetaliotes nebrascensis*, and *M. bivittatus* showed the lowest A^* values for *Poa pratensis*. For *Schizachyrium scoparium*, the lowest A^* values were shown by *Ageneotettix deorum*, *M. bivittatus*, *P. apiculata*, and *M. keeleri*. The correlation between the A^* values for forbs and *Schizachyrium scoparium* was negative and approached significance ($r = -0.436$, $P = 0.27$), whereas the other correlations were very insignificant ($p > .81$).

GRASSHOPPER	A*FRB	A*POA	A*SS
<i>M. femurrubrum</i>	4.052	2.163	3.467
<i>M. keeleri</i>	5.217	3.938	1.878
<i>M. bivittatus</i>	1.499	1.967	1.129
<i>A. conspersa</i>	3.475	2.539	3.213
<i>S. collare</i>	1.694	2.259	5.082
<i>P. nebrascensis</i>	4.625	1.458	2.802
<i>A. deorum</i>	18.504	2.144	0.941
<i>P. apiculata</i>	2.033	1.074	1.481

CORRELATIONS

	A*FRB	A*POA	A*SS
A*FRB	---		
A*POA	0.10251	---	
A*SS	-0.43611	0.07263	---

Table 1. A* values for individual grasshopper species and plant species (for = forbs, poa = *Poa pratensis*, ss = *Schizachyrium scoparium*).

The relationships between partial r^2 values for individual plant groups vs. field age and the r^2 for all plant groups combined verses field age are shown in figure 3. Partial r^2 values for forbs only exceeded 0.1 in 4 fields and was below 0.05 in 11 fields. Partial r^2 values for *Poa pratensis* and *Schizachyrium scoparium* exceeded 0.1 in 5 and 9 fields respectively and were below 0.05 in 6 and 8 fields respectively. The total r^2 values for all plant groups combined was above 0.1 in 16 fields and exceeded 0.5 in 2 fields. The correlations between the partial

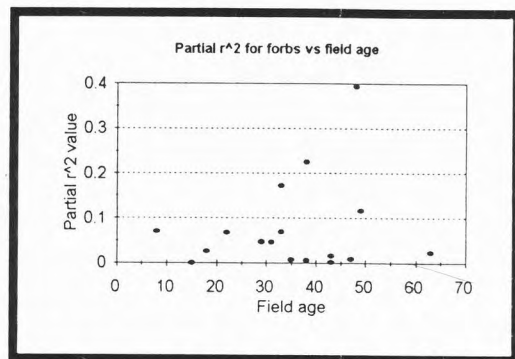
r^2 values for forbs and *Schizachyrium scoparium* vs. field age were not significant ($r = 0.269$, $P = 0.26$), but the correlation between partial r^2 values for *Poa pratensis* vs. field age ($r = 0.449$, $P = 0.05$) and the correlation between total r^2 values and field age was significant ($r = 0.430$, $P = 0.06$).

DISCUSSION

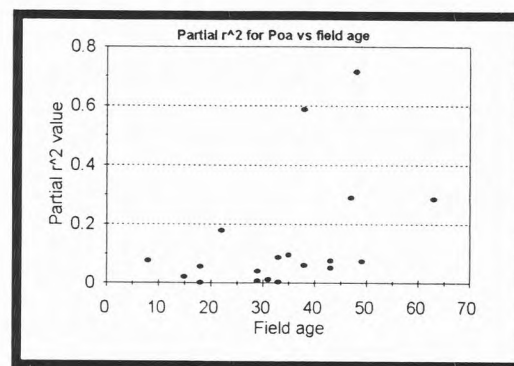
The correlations between the A^* values for plant species suggests that grasshoppers that are good competitors for forbs may be poor competitors for *Schizachyrium scoparium* and vice versa. This suggests that competitive ability for various food items may trade-off in grasshopper species. Thus, correlations between grasshopper abundance and A^* values for each plant group should change predictably with field age.

Forbs are the dominant species in young fields (Tilman 1988). Therefore, grasshopper abundance would be expected to correlate with A^* values for forbs primarily in younger fields. The partial r^2 values for forbs are very low, exceeding 0.1 in only 4 fields. Moreover, the partial r^2 values for forbs show only a weak, positive correlation with field age ($r = 0.215$) (figure 3). Thus, competition for forbs does not decrease with field age as would be predicted. This indicates that competitive ability for forbs does not explain grasshopper abundance within fields.

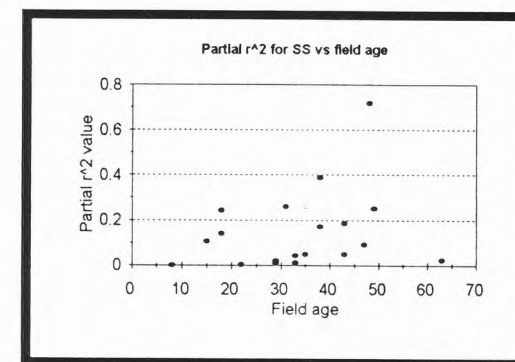
A similar relationship was observed for *Poa pratensis*. Partial r^2 values were low, suggesting that competitive ability for this resource does not explain grasshopper abundance within fields. The correlation for *P. pratensis* ($r = 0.449$) shows that as field age increases, competitive ability for *P. pratensis* explains more of the variation in grasshopper species abundance, as was predicted (figure 3).



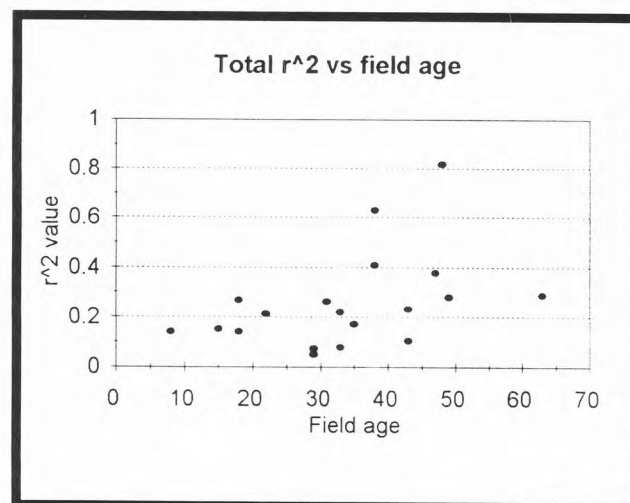
$r = 0.2146$



$r = 0.4491$



$r = 0.2691$



$r = 0.4300$

Figure 3. Scatter plots of partial r^2 values for individual food items verses field age and total r^2 value for all food items combined verses field age. Correlation values (r) are shown below each plot.

Partial r^2 values for *Schizachyrium scoparium* exceeded 0.1 in 9 fields, thus suggesting that competitive ability for this plant resource may weakly influence grasshopper abundance. The correlation between *S. scoparium* and field age ($r = 0.269$), although not significant, indicates that competition for this plant resource increases with field age, matching predicted outcomes (figure 3).

The relationship between total r^2 values for all plant groups combined and field age ($r = 0.430$, $P = 0.065$) indicates that competition becomes somewhat more important in older fields (figure 3), but not enough to influence community structure.

Interspecific competition, as inferred by correlations of grasshopper species abundances with A^* values for the dominant plant species, was generally not important in predicting species abundance for grasshoppers in these old fields. If competition was important, the A^* values for each plant group should have predicted grasshopper abundance within individual fields but there is only weak evidence for this theory.

This study supports the conclusions of Evans (1992) that grasshoppers may rarely experience interspecific competition for food resources. Other factors such as predation, weather, and colonization success could influence grasshopper abundance. Predation can have a large impact on grasshopper communities. Joern and Rudd (1982) report that robber flies (*Proctacanthus milbertii* (Diptera:Asilidae)) impact grasshopper populations, taking up to 2% of the population per day. Avian predation also can reduce grasshopper populations significantly in some locations (Joern 1986), but not others (Belovsky et al. 1990).

This analysis is limited by the successional data presented in the literature (Tilman 1988). I made basic generalizations about the abundance of plant types based upon field age. These generalizations were then used to predict which plant group A^* value would explain grasshopper abundance. However, individual fields may not follow the overall pattern

of succession, or may vary from it enough to cause different grasshopper species to be present. Such differences between fields may have confounded the predictions of grasshopper abundances from A^* values.

Counts of grasshopper species may not have been accurate. By using 50 sweeps of a net instead of capturing all species present biases the count towards the slower species. Quick grasshoppers can avoid being captured by a net. Collecting only during July and August may have biased the counts toward mid season grasshoppers. Sampling earlier in the year would have increased the counts of early season species such as *Arphia conspersa* and *Pardalophora apiculata* (Ritchie & Tilman 1992) or sampling later might have increased the counts of *Phoetaliotes nebrascensis* or *Melanoplus keeleri*. Broader sampling would present a more accurate representation of community structure.

CONCLUSIONS

Interspecific competition for plants appears to be only a weak force structuring grasshopper communities in these old fields. Competition appeared to be somewhat more important in older fields, which suggests that plant species dominant in older fields may provide less food for grasshoppers than those in younger fields. Other factors such as colonization ability and vulnerability to predation may be stronger factors controlling grasshopper species' abundances in these grasslands.

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