

B. L. FOSTER

PH.D



1







This is to certify that the

dissertation entitled

PLANT COMPETITION IN RELATION TO PRODUCTIVITY IN OLD-FIELD PLANT COMMUNITIES

presented by

Bryan L. Foster

has been accepted towards fulfillment of the requirements for

Ph.D. degree in Botany and Plant Path.

Kutherin J. Major professor

12-18-96 Date_

MSU is an Affirmative Action/Equal Opportunity Institution

0-12771

LIBRARY Michigan State University

PLACE IN RETURN BOX to remove this checkout from your record. TO AVOID FINES return on or before date due.

- J

	DATE DUE	DATE DUE
34 0.817		
CT 140133	<u>NOV 0 5 20</u>	
MSU Is An A	firmative Action/Equal C)pportunity institution c/circ\datadue.pm3-

PLANT COMPETITION IN RELATION TO PRODUCTIVITY IN OLD-FIELD PLANT COMMUNITIES

By

Bryan L. Foster

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

W. K. Kellogg Biological Station and Department of Botany and Plant Pathology

ABSTRACT

PLANT COMPETITION IN RELATION TO PRODUCTIVITY IN OLD-FIELD PLANT COMMUNITIES

By

Bryan L. Foster

I conducted three manipulative field experiments: 1) to examine the effects of living plant neighbors and accumulated plant litter on the recruitment and growth of target plants across gradients of plant productivity and community biomass, and 2) to examine the impact of nutrient enrichment, increased productivity and litter accumulation on species richness in southwest Michigan old-fields.

Plant removal experiments conducted at eleven old-field sites showed that the surrounding plant community suppressed the recruitment and growth of three native grass species (*Andropogon gerardi, Schizachyrium scoparium, Sorghastrum nutans*) across a wide range of productivity. The net suppressive effect of the surrounding plant community on two of the three target species increased in magnitude with community biomass as predicted by biomass-dependent theories of plant competition. Non-linear dependence of net community effects on community biomass indicated that biomassdependent theories of competition may be most applicable to narrow ranges of low productivity. The degree to which the effects of plant litter contributed to the net effect of the plant community on target plant performance depended on the life history stage examined. Inhibitory litter effects on seedling recruitment increased with community biomass and contributed to the net effect of the community on recruitment at sites of intermediate community biomass, but litter had little impact on established transplants at any of the sites.

In a two-year experiment carried out in a grass-dominated old-field, nitrogen enrichment increased living plant and litter biomass and reduced species richness by inhibiting the colonization of forb species. Community responses to litter removal and litter addition treatments that were carried out in conjunction with nitrogen enrichment showed that declines in species richness and forb density were due to effects associated with increases in both living plant and litter biomass.

The results highlight the potential importance of effects associated with both living plant biomass and accumulated plant litter in influencing plant recruitment, species diversity, and the distribution of native grasses across old-field productivity gradients. The general significance of these findings are discussed with respect to existing theories of plant community organization.

ACKNOWLEDGMENTS

First, I wish to acknowledge and thank my advisor, Kay Gross, for her generous support and advise throughout my entire graduate career. Without her encouragement, patience, and insight, this work would not have been possible. I am grateful to the other members of my committee, Mike Klug, Gary Mittelbach, and Phil Robertson for all of their help along the way and for their critical review of my work. I thank Steve Tonsor, a former committee member, for valuable advise early on in the development of this work. I would also like to acknowledge Scott Wilson and Heather Reynolds for providing insightful comments and suggestions on portions of this dissertation.

I greatly value the interactions I've had with the graduate students and faculty of KBS and thank them all for there influence and support over the years. I especially thank fellow graduate students Paco Moore, Lisa Huberty, and Casey Huckins for their assistance, warm friendship, and spirited conversation.

A number of people provided invaluable technical and field assistance during the course of my research. My sincere thanks goes to Char Adams, Alice Gillespie, and John Gorentz for saving me on numerous occasions. I thank Jay Leversee and Paco Moore for assistance in the field, Allison Porter for critical help in the greenhouse, and Olivia Damon for her skills in running the Alpkem.

iv

For encouragement and support in countless ways I thank Bill and Betty Foster, and Jack and Renee O'Neill. Most of all I would like to express my deepest appreciation and love to Ann and Thomas Foster. Their unwavering encouragement, patience, love, and laughter have made this all possible.

Generous financial support for this work was provided by the KBS graduate Research Training Group (RTG) funded by NSF grant DIR-09113598, NSF LTER grant BSR 8702332, two George H. Lauff Research Awards, the Department of Botany and Plant Pathology, and the Graduate Program in Ecology and Evolutionary Biology (EEB).

TABLE OF CONTENTS

LIST OF TABLES v				
LIST OF FIGURES				
CHAPTER 1 INTRODUCTION	1			
Organization of the dissertation	5			
Study species	6			
Study sites	7			
CHAPTER 2 REMOVAL EXPERIMENT I: PARTITIONING THE				
EFFECTS OF PLANT BIOMASS AND LITTER ON ANDROPOGON				
GERARDI IN OLD-FIELD VEGETATION	12			
INTRODUCTION	13			
METHODS	15			
Study sites	15			
Experimental design and methods	17			
Resource measurements	19			
Data analysis	20			
RESULTS	24			
Community biomass and species composition	24			
Resources	24			
Seed addition	28			
Transplants	37			
DISCUSSION	41			
Magnitude of plant community effects	43			
CHAPTER 3 REMOVAL EXPERIMENT II: PARTITIONING THE				
EFFECTS OF PLANT BIOMASS AND LITTER ON THREE NATIVE GRASSES IN OLD-FIELD VEGETATION	47			
INTRODUCTION	48			
METHODS	51			

Study sites	51
Experimental design and methods	52
Light measurements	57
Data analysis	57
RESULTS	60
Community biomass and species composition	60
Light penetration	61
Seed addition	61
Transplants	74
DISCUSSION	81
Partitioning the effects of living neighbors and litter	83
Implications for native grass distributions and species	
diversity	86
, ,	
CHAPTER 4 SPECIES RICHNESS IN A SUCCESSIONAL GRASSLAND:	
EFFECTS OF NITROGEN ENRICHMENT AND PLANT LITTER	88
INTRODUCTION	89
METHODS	92
Study site	92
Experimental treatments	93
Seed addition	95
Light measurements	96
Vegetation sampling and data analysis	96
RESULTS	97
Community responses	97
Andropogon recruitment	104
DISCUSSION	107
Community responses	107
Plant responses and light availability	110
Andronogon recruitment	111
Productivity, diversity, and plant litter	112
CHAPTER 5 CONCLUSIONS	115
LIST OF REFERENCES	120

LIST OF TABLES

Table 1. Locations, identification numbers, and vegetation characteristics of the eleven study sites. Letters correspond to site locations shown on the Kellogg Biological Station map (Fig. 1). Biomass values are presented as means \pm 1 SE. Total community biomass is the sum of aboveground living plant biomass and plant litter. Methods for assessing plant biomass and species composition are presented in the methods sections of chapters 2 and 3. Nomenclature follows Fernald (1950).	9
Table 2. Community characteristics of the five study sites. Biomass values are presented as means ± 1 SE ($n = 5$ for each site). For each biomass type, values within a column with the same letter are not significantly different ($P > 0.05$; Tukey's HSD). Nomenclature follows Fernald (1950).	16
Table 3. Treatment effects and means square ratios used in the mixed- model, within-subjects ANOVA. $S = Sites$, $B(S) = Blocks$ within Sites, N = Neighbors, $L = Litter$.	22
Table 4. Results of ANOVA for site and treatment effects on mean seasonal light penetration.	25
Table 5. Results of ANOVA for site and treatments effects on mean seasonal soil nitrogen concentration. Nitrogen concentrations were measured only in the two treatments where all plant material (neighbors and litter) was either removed or left intact.	29
Table 6. Results of ANOVA for site and treatment effects on Andropogon density and total shoot biomass in the seed addition experiment.	30
Table 7. Results of ANOVA for site and treatment effects on the RGR oftransplants in the seedling transplant experiment.	38
Table 8. Vegetation characteristics of the nine study sites. Biomass values are shown as means ± 1 SE ($n = 6$ for each site). Biomass values within a column with the same letter are not significantly different ($P > 0.05$; Tukey's HSD).	53

Table 9. Results of two-way ANOVA for community effects on density and total shoot biomass (seed addition).	. 69
Table 10. Results of two-way ANOVA for community effects on the RGR of transplants.	. 77
Table 11. Mean biomass of grass species (g/m^2) in the five experimental treatments. ANOVA's were performed for species that were present in all treatments. Species are listed from greatest to least in biomass. Means within rows with different letters are significantly different ($P < 0.05$, Tukey's HSD). See methods section for treatment codes.	101
Table 12. Forb biomass (g/m^2) and density $(no./m^2)$ in the five experimental treatments. Means are presented for life history groups and for the ten most common forb species. ANOVA's were performed only on life history groups and species that were present in all treatments. Species are listed from greatest to least in density. Means within rows with different letters are significantly different ($P < 0.05$, Tukey's HSD).	102
See methods section for treatment codes.	102

LIST OF FIGURES

Figure 1. Map of the Kellogg Biological Station with letters showing the locations of the 11 study sites. See Table 1 for a description of these sites.	11
Figure 2. A) Mean seasonal light penetration (mean + 1 SE) in relation to the experimental treatments. Treatments with neighbors removed are indicated by - N, and treatments with neighbors left intact are indicated by +N. Treatments with litter removed are indicated by - L, and treatments with litter left intact are indicated by shading and by +L. Brackets above and below the bars specify within-site mean comparisons made at each level of the two treatment factors (ns = $P > 0.05$; *= $P < 0.05$). B). Mean seasonal nitrogen concentrations (mean + 1 SE) in the two treatments where all vegetation (neighbors and litter) was either removed or left intact. Sites are ranked from lowest to highest community biomass.	26
Figure 3. A) <i>Andropogon</i> density and B) total shoot biomass (mean + 1 SE) in relation to the experimental treatments (seed addition experiment).	31
Figure 4. Relationships between the community effects on Andropogon density (dependent variables) and community biomass (independent variable) in the seed addition experiment. A) Mean community effects plotted against mean community biomass ($n = 5$). B) Community effects calculated for all blocks plotted against block community biomass ($n = 25$). Dashed line represents the no effect line. Note log scale for community biomass.	34
Figure 5. Relationships between the community effects on Andropogon total shoot biomass (independent variables) and community biomass (dependent variable) in the seed addition experiment. A) Mean community effects plotted against mean community biomass ($n = 5$). B) Community effects calculated for all blocks plotted against block community biomass ($n = 25$).	36
Figure 6. RGR ($g \cdot g^{-1} \cdot d^{-1}$) of <i>Andropogon</i> transplants (mean + 1 SE) in relation to the experimental treatments.	39

Figure 7. Relationships between the community effects on the RGR of transplants (dependent variables) and community biomass (independent variable) in the transplant experiment. A) Mean community effects plotted against mean community biomass ($n = 5$). B) Community effects calculated for all blocks plotted against block community biomass ($n = 30$).	40
Figure 8. Experimental block layout illustrating the arrangement of the experimental treatment plots and the transplant and seed addition subplots. T_1 and T_2 refer to the position of the two transplants in each transplant subplot.	54
Figure 9. Mean seasonal light penetration (mean + 1 SE) in relation to the experimental treatments. Treatments with neighbors removed are indicated by - N, and treatments with neighbors left intact are indicated by +N. Treatments with litter removed are indicated by - L, and treatments with litter left intact are indicated by shading and by +L. Letters above the bars specify the significance of neighbor (N) and litter (L) effects within the sites (ns = $P > 0.05$; * = $P < 0.05$). At sites with a significant neighbor x litter interaction, brackets above and below the bars specify treatment mean comparisons made at each level of the two treatment factors (ns = $P > 0.05$; * = $P < 0.05$).	62
Figure 10. Andropogon density (A) and total shoot biomass (B; mean + 1 SE) in relation to the experimental treatments (seed addition).	63
Figure 11. Schizachyrium density (A) and total shoot biomass (B; mean + 1 SE) in relation to the experimental treatments (seed addition).	66
Figure 12. Relationships between the community effects on Andropogon density (A) and total shoot biomass (B; dependent variables) and community biomass (independent variable). Dashed line represents the no effect line.	70
Figure 13. Relationships between community effects on <i>Schizachyrium</i> density (A) and total shoot biomass (B; dependent variables) and community biomass (independent variable).	72
Figure 14. RGR ($g \cdot g^{-1} \cdot d^{-1}$) of transplants (mean + 1 SE) in relation to the experimental treatments. NT = not tested statistically.	75
Figure 15. Relationships between the community effects on Andropogon transplant RGR (g·g ⁻¹ ·d ⁻¹) and community biomass (independent variable). ns $P > 0.05$, ** $P < 0.001$.	78

•

Figure 16. Relationships between the community effects on <i>Schizachyrium</i> transplant RGR (g·g ⁻¹ ·d ⁻¹) and community biomass (independent variable). ns $P > 0.05$, ** $P < 0.001$, *** $P < 0.0001$.	79
Figure 17. Relationships between the community effects on <i>Sorghastrum</i> transplant RGR (g·g ⁻¹ ·d ⁻¹) and community biomass (independent variable). ns $P > 0.05$.	80
Figure 18. Diagrammatic representation of the experimental block and treatment plot layout. Block numbers are indicated by roman numerals. The litter addition (LA) plots that were added after the initiation of the experiment are indicated by heavy lines	4.
Figure 19. Treatment effects on living biomass (A), litter biomass (B), grass biomass (C), forb biomass (D), forb density (E), and species richness (F). Means (+ 1 SE) with different letters are significantly different ($P < 0.05$). See methods section for treatment codes. ANOVA $F_{4,20}$ values: ns $P > 0.05$, *** $P < 0.001$, **** $P < 0.0001$.	98
Figure 20. Treatment effects on light penetration. Means (+ 1 SE) with different letters are significantly different ($P < 0.05$). ANOVA F _{4,20} value: **** $P < 0.0001$	99
Figure 21. Treatment effects on <i>Andropogon</i> density (A), and biomass per plant (B). Means (+ 1 SE) with different letters are significantly different ($P < 0.05$). ANOVA F _{4,20} values: **** $P < 0.0001$	05
Figure 22. Treatment effects on <i>Andropogon</i> germination (A), and survivorship (B). Means (+ 1 SE) with different letters are significantly different ($P < 0.05$). ANOVA F _{4,20} values: *** $P < 0.001$, **** $P < 0.0001$ 10	06

CHAPTER 1

INTRODUCTION

.

INTRODUCTION

A major goal of plant ecologists is to develop models of community organization that predict community composition and diversity at any location in the landscape. Attaining this goal is not only of interest to ecologists, but is also of value to those that seek to manage or restore the diversity of ecological communities. As a result, much work in plant ecology has centered on describing and explaining ecological processes across environmental gradients, including gradients in plant productivity, soil fertility, disturbance, and physical stress (Newman 1973, Grime 1979, Tilman 1988, Bertness and Callaway 1991, Wilson and Tilman 1991, Campbell and Grime 1992).

There has been considerable interest and debate focused on the unimodal relationship that is often observed between plant species diversity and plant productivity. This "hump-shaped" relationship, which has been documented in a number of ecosystems (Dix and Smiens 1967, Al-Mufti et al. 1977, Puerto et al. 1990), exhibits an increase in species diversity up to some intermediate level of plant productivity, followed by a decline in diversity with further increases in productivity. Although there is some debate as to the generality of the unimodal diversity curve (Abrams 1995), several mechanisms have been proposed to explain it (Tilman 1988, Tilman and Pacala 1993, Huston and DeAngelis 1994). A great deal of attention has centered on the mechanisms responsible for reduced diversity at high levels of productivity (declining portion of the unimodal diversity curve), not only due to theoretical interest, but also because of the potential negative consequences that long-term eutrophication has for the conservation of plant diversity. Grime (1973, 1979) and others (Huston 1979, Thompson and Grime 1988, Keddy 1990) have argued that diversity often declines with increases in productivity because the overall magnitude of competition occurring among plants increases, thus leading to dominance by a few superior competitors in the most productive habitats. Tilman (1988) and Tilman and Pacala (1993) proposed that species coexistence depends upon the spatial heterogeneity of resources and suggest that low resource heterogeneity in highly productive habitats may limit the number of species that can coexist there, thus promoting low diversity. Goldberg and Miller (1990) argued that strong competition for light limits the number of species in productive habitats by increasing the mortality of seedlings and species of small stature.

These theories of plant community organization all have in common the idea that increased competitive exclusion leads to reduced diversity in highly productive habitats. However, there continues to be disagreement in the literature regarding just how competition varies across gradients in plant productivity. Productivity-dependent theories of competition advocated by Grime (1973, 1979) and others (Huston 1979, Southwood 1988, Keddy 1990) suggest that the overall magnitude of competition occurring among plants is lowest in unproductive habitats, but increases with productivity as plant biomass and plant demand for both above- and below-ground resources increase. Others have argued that competition should be very strong in habitats of low productivity due to strong competition for soil resources, and that competition will change more in quality (shift from below- to aboveground) than in quantity as productivity increases (Newman 1973, Tilman 1988, Taylor et al. 1990). This has led to a productivity-independent view of competition which predicts that the over-all magnitude of competition should be unrelated to productivity. This latter prediction is often associated with the resource ratio hypothesis of competition (Tilman 1982, 1988).

However, it should be noted that the resource ratio hypothesis makes no explicit prediction regarding the over-all magnitude of competition and relates only to how the outcome of competition between species changes as resource supply rates change. The prediction that the over-all magnitude of competition between plants is unrelated to productivity is a verbal extension of this hypothesis.

A number of recent experimental studies have been conducted to examine how the over-all magnitude of plant competition varies across gradients of plant productivity or soil resource availability. These studies have provided mixed results with some studies supporting the productivitydependent view of competition and showing increasing competition with productivity (Gurevitch 1986, Wilson and Keddy 1986, Bonser and Reader 1995, Kadmon 1995), while some results are consistent with the productivityindependent view and report no relationship (Fowler 1990, Wilson and Shay 1990, Wilson and Tilman 1991, 1993). Inconsistency in these previous results has been attributed to different measures of competition (absolute versus relative measures; Grace 1993, Kadmon 1995), differences in the range of productivity examined (Goldberg and Barton 1992, Bonser and Reader 1995, Kadmon 1995), whether or not the gradient is natural or experimentally created (Goldberg and Barton 1992, Kadmon 1995), and differences in target species (Wilson and Tilman 1995). At the present time there are too few studies encompassing these different conditions to adequately assess which of the opposing views is most applicable to natural plant communities.

While most of the focus in these studies has been on resource competition occurring among living plants and its role in influencing plant species diversity, these studies do not address other potential mechanisms of plant-plant interaction that may affect individual plant performance and

plant species diversity across productivity gradients. One mechanism which I focus on in this dissertation involves the role of accumulated plant litter in herbaceous old-field communities. A number of studies have shown that plant litter can either promote or inhibit plant performance in natural communities (Fowler 1986, Wilms et al. 1986, Facelli and Pickett 1991a). As a whole these studies indicate that the magnitude (intensity or strength) of litter effects and their direction (interference versus facilitation) may vary significantly among sites that differ in plant productivity and litter accumulation.

In this dissertation I describe the results of three manipulative field experiments designed to examine how the effects of accumulated plant litter can combine or interact with the exploitative effects of living plant neighbors to limit species diversity and affect the performance of individual target species across gradients of productivity, community biomass and soil fertility in old-field vegetation.

Organization of the Dissertation

In addition to this Introductory chapter (Chapter 1), there are three empirical chapters and a Concluding chapter. Chapter 2 describes the results of an experimental field study that I conducted to examine variation in the effects of living plant neighbors and litter on the recruitment and growth of a native perennial grass across five herbaceous old-field communities that differ in community biomass and soil fertility. Chapter 3 presents the results of a second field experiment that I conducted the following year which extends the objectives of the first experiment to incorporate more field sites, a greater range of plant productivity, and additional target species. In chapter 4 I

present the results of a two-year field experiment where I manipulated plant litter levels and added nitrogen fertilizer to field plots to examine the shortterm effects of increased fertility, increased living plant biomass, and increased litter biomass on species richness in a grass-dominated old-field. In the concluding chapter (Chapter 5) I briefly summarize the findings of the three field experiments and discuss there general significance with respect to existing theories of plant community organization and ecological applications.

Study species

A major part of this dissertation examines the effects of living plant neighbors and accumulated plant litter on the recruitment and growth of three target grass species that were experimentally introduced into a number of old-field sites as both seeds and transplants. These species include: Andropogon gerardi Vitman (Big bluestem), Schizachyrium scoparium Nash (Little bluestem), and Sorghastrum nutans (L.) Nash (Indian grass). These species are all perennial C₄ bunchgrasses native to southwest Michigan and are the dominant species of the tallgrass prairies of North America (Bazzaz and Parrish 1982). I chose these species for study because one of the goals of the research was to examine potential biotic constraints to the re-colonization of current successional communities in southwest Michigan by historically dominant native species (Gotshall 1972). These species are similar with respect to photosynthetic pathway, life history, growth form, growth rate, and ability to compete for soil resources (Parrish and Bazzaz 1982, Tilman and Wedin 1991), but are distributed somewhat differently across environmental gradients. In intact prairies, Andropogon and Sorghastrum are distributed

similarly across broad gradients of plant productivity, soil moisture, and soil fertility (Weaver 1954, Smeins and Olson 1970), while *Schizachyrium* is typically more restricted in distribution to the more xeric, infertile sites (Weaver 1954, Bazzaz and Parrish 1982). The more limited distribution of *Schizachyrium* appears to be related to it adaptation to xeric conditions (Weaver 1954, Knapp 1985). *Schizachyrium* has lighter seeds (Rabinowitz 1978, Foster, unpublished data) than *Andropogon* and *Sorghastrum* and is considered to be a poor competitor for light (L. Wallace, personal communication), both factors which may restrict this species from establishing and persisting in the most productive sites.

In the current successional landscape of southwest Michigan, all three of these species are largely restricted to low to mid- productivity old-field sites. These species are generally absent from the most productive sites that are typically dominated by introduced perennial grasses. Site pre-emption by the early-colonizing introduced grasses and dispersal limitation likely interact to limit the current distribution of these native grasses. Because fire is currently rare in this landscape, litter accumulation may be an important factor limiting the re-colonization of productive sites by these native prairie species which evolved in the presence of periodic fire and which are not likely to be adapted for establishment in dense litter (Tilman 1993).

Study sites

The three field experiments presented in this dissertation were all conducted in herbaceous old-fields communities at the W. K. Kellogg Biological Station (KBS) located in southwest Michigan (Kalamazoo County; 42° 24' N, 85° 24' W). A total of eleven sites were used in these studies (Table

1, Fig. 1). All of these sites had been abandoned from row crop agriculture for at least 15 years and were dominated by perennial grasses at the time of study. The sites varied substantially in species composition (see Burbank et al. 1992), above-ground living plant biomass, and litter biomass (Table 1). Soils underlying the sites are classified as sandy loam, but differ in the amount of top-soil lost to agricultural-related erosion.

Five of the eleven study sites were used in the first competition experiment (Chapter II; sites A-E; Table 1, Fig. 1). Three of the sites used in the first competition experiment (B, C and E) plus six additional ones (F-K; 9 sites total) were used in the second competition experiment (Chapter III). The nitrogen addition experiment described in chapter IV was conducted at site C. Table 1. Locations, identification numbers, and vegetation characteristics of the eleven study sites. Letters correspond to site locations shown on the Kellogg Biological Station map (Fig. 1). Biomass values are presented as means \pm 1 SE. Total community biomass is the sum of aboveground living plant biomass and plant litter. Methods for assessing plant biomass and species composition are presented in the methods sections of chapters 2 and 3. Nomenclature follows Fernald (1950).

	Site ID #	Site ID #			
Site	1994 Exp.	1995 Exp.	Total community	Four most abundant	Relative
Location	Chapter 1	Chapter III	biomass (g/m ²)	species	biomass (%)
A	1	-	207.9 ± 31.9	Centaurea maculosa	24.0
				Poa compressa	22.5
				Achillea millefolium	11.4
				Aster pilosis	8.7
				Rubus alleghaniensis	6.3
В	2	4	454.6 ± 33.4	Agropyron repens	85.2
				Achillea millefolium	7.3
				Bromus inermis	6.4
С	3	5	527.5 ± 39.4	Bromus inermis	58.1
				Poa pratensis	10.3
				Achillea millefolium	10.1
				Agropyron repens	5.1
D	4	-	658.5 ± 73.7	Bromus inermis	88.3
				Poa pratensis	7.5
Е	5	7	1205.5 ± 48.4	Agropyron repens	71.0
				Arrhenatherum elatius	28.3
F	-	1	79.1 ± 16.1	Andropogon virginicus	50.0
				Rubus alleghaniensis	13.9
				Danthonia spicata	9.9
				Solidago nemoralis	5.7
G	-	2	129.1 ± 43.2	Rubus alleghaniensis	27.8
				Danthonia spicata	17.2
				Centaurea maculosa	14.7
				Andropogon virginicus	11.0
Н	-	3	221.4 ± 14.8	Andropogon virginicus	49.8
				Danthonia spicata	9.8
				Rubus alleghaniensis	6.0
				Desmodium rotundifolium	4.8
Ι	-	6	626.9 ± 115.7	Bromus inermis	78.0
				Agropyron repens	10.3
				Poa pratensis	3.8
				Daucus carota	3.2

J	-	8	1470.9 ± 102.4	Bromus inermis Poa pratensis Solidago canadensis Agropyron repens	44.2 19.1 17.4 15.4
К	-	9	1973.3 ± 223.8	Bromus inermis Poa pratensis Agropyron repens Barbarea vulgaris	90.6 4.9 2.5 0.1

Table 1. (Cont'd)



Figure 1. Map of the Kellogg Biological Station with letters showing the locations of the 11 study sites. See Table 1 for a description of these sites.

CHAPTER 2

REMOVAL EXPERIMENT I: PARTITIONING THE EFFECTS OF PLANT BIOMASS AND LITTER ON ANDROPOGON GERARDI IN OLD-FIELD VEGETATION

INTRODUCTION

Experimental field studies designed to examine variation in plant interactions among habitats or along environmental gradients often use plant removal experiments to compare the performance of target plants growing in the presence and absence of the surrounding plant community (Wilson and Keddy 1986, Wilson and Tilman 1991, 1993, Bertness and Hacker 1994, Kadmon 1995). When negative effects of the surrounding community on target plants are observed in these experiments, the effect is most often attributed to competition with plant neighbors for limiting resources (Wilson and Shay 1990, Wilson and Tilman 1991, 1993, Bonser and Reader 1995). However, in many types of vegetation, especially grassland and old-field communities, the performance of plants can also be affected by accumulated dead plant biomass or plant litter (Hulbert 1969, Goldberg and Werner 1983, Fowler 1986, Hamrick and Lee 1987, Facelli and Pickett 1991a, Facelli 1994). As a result, measures of competition obtained from removal experiments, and variation in these measures observed across different habitats, may reflect the effects of both living plant neighbors and litter. In this study I investigated how these two different types of effects may combine to determine the net effect of the surrounding plant community on target plants in old-field vegetation. In addition, I examined how the magnitude of these effects vary across old-field sites that differ in community biomass and soil nitrogen availability.

A number of field studies in herbaceous vegetation have shown that plant litter can significantly affect the performance of individual plants, and as a result influence the structure of plant communities. Large quantities of litter can inhibit the establishment, growth, and survival of plants, and thus contribute to low species diversity in highly productive communities (Haslam 1971, Goldberg and

Werner 1983, Bergelson 1990, Carson and Peterson 1990, Tilman 1993). Other studies suggest that litter may often facilitate the establishment and growth of plants and enhance species diversity in unproductive environments by improving moisture conditions (Fowler 1986, Willms et al. 1986). As a whole, these studies suggest that the role of plant litter may vary across environments and that changes in species composition and diversity along gradients of community biomass and plant productivity may reflect variation in the balance between the effects of plant neighbors and litter.

In this study, I examined the effects of living plant neighbors and litter on a single target species, the C₄ grass Andropogon gerardi Vitman (Big bluestem), in herbaceous old-fields in southwest Michigan. Andropogon gerardi (hereafter referred to by genus) is a dominant species in the tall-grass prairies of the United States where it is distributed widely across gradients of soil resource availability and plant productivity (Bazzaz and Parrish 1982). Andropogon was a dominant species in many prairie and oak savanna communities of southwest Michigan at the time of settlement by Europeans (Gotshall 1972). However, in the current successional landscape of southwest Michigan, Andropogon is largely restricted to low fertility sites, and is infrequent in the more fertile sites that are commonly dominated by non-native C_3 grasses such as Agropyron repens L. Beauv. and Bromus inermis Leysser. The apparent poor ability of native C_4 grasses, such as Andropogon, to colonize and occupy fertile sites after abandonment from agriculture, is likely related to a combination of: 1) delayed seed input, due to the isolation of source populations in the landscape, and inherently low allocation to seed production (Tilman and Wedin 1991a); and 2) site pre-emption and inhibition by fast-growing C₃ grasses which are effective at rapidly colonizing and dominating fertile sites shortly after abandonment (Tilman 1987, Tilman and Wedin 1991b, Foster 1992). Because fire is largely absent from this landscape,

effects associated with litter accumulation in the most productive sites may be important in restricting the distribution of native C₄ grasses to lower productivity sites. In this study, I addressed the following questions regarding the effects of the surrounding plant community on *Andropogon* at a five old-field sites:

1) How do living plant neighbors and litter affect the recruitment and growth of *Andropogon* in old fields?

2) How do the separate effects of neighbors and litter contribute to the net effect of the surrounding plant community on *Andropogon*?

3) Do these effects vary in magnitude among the different study sites, and if so, are they correlated with above-ground community biomass.

METHODS

Study sites

This study was conducted in five herb-dominated old-field sites at the W. K. Kellogg Biological Station (KBS) of Michigan State University in southwest Michigan (Kalamazoo County; 42° 24' N, 85° 24' W). All five sites had been abandoned from row crop agriculture for at least 15 years and were largely dominated by non-native perennial grasses. (Table 2; Burbank et al. 1992). Naturally occurring individuals of *Andropogon* were found growing at sites 1 and 3. Soils underlying the sites are classified as sandy loam, but differ in the amount of top-soil lost to agricultural-related erosion. Assignment of site numbers (1-5) Table 2. Community characteristics of the five study sites. Biomass values are presented as means ± 1 SE (n = 5 for each site). For each biomass type, values within a column with the same letter are not significantly different (P > 0.05; Tukey's HSD). Nomenclature follows Fernald (1950).

Site	Neighbor biomass (g/m ²)	Litter biomass (g/m ²)	Total community biomass (g/m ²)	Dominant Species (> 5% Rel. biomass)	Relative biomass (%)
1	184.2 ± 24.8^{a}	23.7 ± 8.0^{a}	207.9 ± 31.9a	Centaurea maculosa	24.0
				Poa compressa	22.5
				Achillea millefolium	11.4
				Aster pilosis	8.7
				Rubus alleghaniensis	6.3
2	222.9 ± 15.6 ^a	231.7 ± 21.6 ^b	454.6 ± 33.4b	Agropyron repens	85.2
				Achillea millefolium	7.3
				Bromus inermis	6.4
3	310.8 ± 11.9b	216.7 ± 31.1b	527.5 ± 39.4bc	Bromus inermis	58.1
				Poa pratensis	10.3
				Achillea millefolium	10.1
				Agropyron repens	5.1
4	337.4 ± 20.2b	321.0 ± 81.0 ^b	658.5 ± 73.7 ^c	Bromus inermis	88.3
				Poa pratensis	7.5
5	598.4 ± 31.0 ^c	607.1 ± 34.2 ^c	1205.5 ± 48.4d	Agropyron repens	71.0
				Arrhenatherum elatius	28.3

was based on a ranking of total community biomass (1 = lowest and 5 = highest biomass). In this study, I define total community biomass (or community biomass) as the sum of above-ground living plant biomass and litter biomass.

Experimental design and methods

In 1994 both seeds and seedling transplants of *Andropogon* were planted into a 2 x 2 factorial arrangement of treatments established at each site in a randomized block design. The treatments included two levels of living plant neighbors (intact and removed) and two levels of plant litter (intact and removed). At all sites except site 2, two parallel rows of five 2 x 2 m experimental blocks were established in early May. One of the rows was used for seed additions and the other row was used for transplants. At site 2, the same block layout was used with the exception that ten blocks were established for the transplant experiment instead of five. In each field, the rows of blocks were separated by buffer zones of 3 to 6 m, and blocks within rows were separated by buffer zones ranging from 2 to 4 m.

The four experimental treatments were applied to 70 x 70 cm plots located at the four corners of each block. Neighbors were removed by applying a Glyphosate herbicide solution (Roundup), and clipping the dead material after one week. Litter was removed by hand from the litter removal treatments so that the soil was left undisturbed. To minimize root encroachment into the two neighbor removal treatments, plot perimeters were trenched with a flat blade shovel to a depth of 20 cm three times during the growing season. Neighbor removal plots were periodically hand-weeded during the growing season to eliminate re-growth. Seed additions - Seeds of Andropogon were collected from a local population in the fall of 1993 and stored outside over winter in a plastic container to expose the seeds to winter temperature fluctuations. Seeds were sown by hand into the treatment plots at a rate of 1500/plot (3030/m²) in mid-May 1994. Because the goal of this experiment was to examine recruitment from seed in the absence of dispersal limitation, a seeding rate was chosen that mimicked the seed rain within natural stands of Andropogon (about 3000 seeds/m², unpublished data). Density of Andropogon plants in each plot was determined in June, July and late August by counting individuals within two randomly placed 10 x 20 cm quadrats. Final density determined in late August is reported here and is used throughout as a measure of Andropogon recruitment. In late August, all shoot biomass of Andropogon was harvested from each plot. In addition, above-ground biomass of plant neighbors and litter was harvested from the intact plots (neighbors and litter intact). All plant material was oven-dried at 60° C to constant mass and then weighed.

Seedling transplants - Seedlings for the transplant experiment were obtained by germinating seeds in the greenhouse in late April 1994. Approximately 6-8 days after germination, 1000 seedlings were transferred into individual seedling plug containers (2.54 cm diameter x 10.16 cm deep) containing a 3:1:1 mixture of peat moss, commercial potting soil, and old-field soil. After 14-17 days of additional growth, 480 seedlings were randomly selected for the experiment from a group of approximately 800 healthy seedlings. The initial shoot biomass of each seedling was estimated from a regression of seedling biomass on longest leaf length (L) obtained from a subsample of the remaining healthy seedlings (Initial transplant biomass = 0.004L - 0.011, R^2 = 0.65, P < 0.0001, n = 100).

In late May, four seedlings were transplanted into each 70 x 70 cm field plot by inserting seedling plugs into pre-formed holes made with a narrow bladed trowel. Within each plot, transplants were separated by approximately 20 cm. All individual transplants were watered (0.2 L/day) for eight consecutive days following planting to encourage initial establishment. Only 16 of the 480 transplants died and there were no plots where less than three transplants survived until the end of the experiment. The shoots of all surviving transplants were harvested in early September. Above-ground biomass of neighbors and litter was harvested from the intact plots. Neighbors were sorted by species to document the species composition of each site. All plant tissue was dried and weighed as described previously.

Resource measurements

To determine how light penetration to the soil surface varied among the sites and was affected by the experimental treatments, photosynthetically active radiation (PAR) was measured above the vegetation and at the ground surface of each plot in the transplant experiment with a PAR ceptometer probe (Decagon Devices Inc.). PAR measurements were taken three times over the course of the experiment at approximately monthly intervals (early June - late August). In plots where litter was left intact, light measurements were made by inserting the ceptometer beneath the litter layer. In the neighbor removal plots, measurements were made at plot edges between the hours of 11 am and 2 pm when the sun was directly overhead to minimize the effects of transplants on light readings. Light penetration was expressed as the percentage PAR reaching the ground surface. Mean seasonal light penetration was calculated for each plot by averaging over the three sampling dates.

Soil nitrogen concentration (N) was also measured at three times over the course of the experiment in two treatments in the seedling transplant experiment: neighbors and litter removed; neighbors and litter left intact. At each sampling date, two soil cores (2.5 cm in diameter x 15 cm deep) were taken from each plot. All cores were taken at least 10 cm away from the base of transplant shoots and care was taken to minimize disturbance to the plots. The two cores from each plot were composited for analysis. Subsamples (10g) were extracted for 24 hours in a 2 mol/L KCL solution, filtered, and then analyzed colorimetrically with an Alpkem auotoanalyzer for ammonium and nitrate. Soil nitrogen concentrations are expressed as the sum of extractable ammonium and nitrate concentrations (μ g N/g dry soil). Mean seasonal nitrogen concentrations were calculated for each plot by averaging over the three sampling dates.

Data analysis

Community biomass - To examine whether sites differed in neighbor biomass, litter biomass and total community biomass (sum of neighbor and litter biomass), I used one-way analysis of variance (ANOVA) and Tukey HSD tests. These analyses were performed on biomass data from the intact treatment (neighbor and litter biomass left intact).

Resources and target plant performance - Percent light penetration, total soil nitrogen, Andropogon seedling density and total shoot biomass (seed addition experiment), and transplant growth (transplant experiment) were analyzed using a mixed-model, within-subjects ANOVA (Zar 1996) with one among-subjects grouping factor (site). In this model the experimental blocks are considered to be the subjects of the analysis with the experimental treatments applied to each. Variation due to blocks within sites is considered random, while site and

treatment effects are considered fixed. Error terms used to test the significance of main effects and interactions all contain the random component of variance due to blocks within sites (see Table 3). After testing the significance of the interaction terms, unplanned comparisons were used to make the appropriate comparisons of treatment means (Sokal and Rohlf 1981). Analyses of transplant growth were performed on plot mean values (mean of all surviving transplants). Relative growth rate (RGR, Chiariello et al. 1989) was calculated for each transplant as:

$$RGR = [ln(B_2) - ln(B_1)]/(t_2 - t_1)$$

where B_2 is the transplant biomass at harvest, B_1 is the estimated transplant biomass at planting, and $t_2 - t_1$ is the number of days growth between harvest (t_2) and planting (t_1). Light penetration data were arcsine-square root transformed to reduce heteroscedasticity. *Andropogon* total shoot biomass and density data were log transformed and square-root transformed respectively to improve normality and reduce heteroscedasticity (Sokal and Rohlf 1981). Untransformed data are presented in the figures.

Magnitude of community effects - The magnitude of the effect of the surrounding plant community on Andropogon performance (density, total shoot biomass, and RGR of transplants) was examined using a relative community effect index (diffuse competition, Wilson and Keddy 1986; competition intensity, Wilson and Tilman 1993). This index estimates the degree to which Andropogon was inhibited or facilitated by the surrounding plant community by comparing plant performance in plots cleared of all plant material (neighbors and litter) to that in plots where all plant material was left intact. Positive values indicate inhibition, negative values indicate facilitation, and values of zero indicate no net effect of the surrounding community. To assess the importance of litter in
Table 3. Treatment effects and means square ratios used in the mixed-model, within-subjects ANOVA. S = Sites, B(S) = Blocks within Sites, N = Neighbors, L = Litter.

Source of variation	Effect MS/Error MS
Among Blocks	
S	S/B(S)
Within Blocks	
Ν	$N/N \times B(S)$
N x S	$N \times S/N \times B(S)$
L	$L/L \times B(S)$
L x S	$L \times S/L \times B(S)$
N x L	$N \times L/N \times L \times B(S)$
NxLxS	$N \times L \times S/N \times L \times B(S)$

contributing to the net effect of the community on *Andropogon* performance, a separate index was calculated for plots that were left intact and for plots where only litter was removed. These indices were calculated for each experimental block as:

Net Effect =
$$(P_C - P_{NL})/P_C$$

Neighbor Effect = $(P_C - P_N)/P_C$

where P_C is plant performance in plots cleared of neighbors and litter, P_{NL} is performance in plots with neighbors and litter left intact, and P_N is performance in plots with only neighbors left intact (litter removed). An additional index was calculated to measure the effect of litter alone and was calculated as:

Litter Effect = $(P_C - P_L)/P_C$

where P_L is plant performance in plots with only litter left intact (neighbors removed).

I used one-way ANOVA and Tukey HSD tests to examine site differences for each community effect index (net, neighbor and litter effects). I then examined correlations between each index and community biomass using linear regression in two ways. First, I analyzed the site means of each community effect index and of community biomass (n = 5). Second, to examine relationships across the entire range of community biomass, thus including both within and among site variation, I analyzed the community effect indices and community biomass measured in each individual block (n = 25, seed addition experiment; n = 30, transplant experiment). Preliminary data inspection indicated that the community effect indices tended to vary non-linearly with community biomass. As a result, community biomass was log transformed prior to linear regression analysis. I carried out similar analyses using total soil nitrogen measured in the intact plots as the independent variable in place of community biomass. The results of these analyses were very similar, so for brevity I report only the analyses using community biomass as the independent variable. SYSTAT statistical software (version 5.2.1; Wilkinson 1992) was used for all analyses.

RESULTS

Community biomass and species composition

Neighbor biomass, litter biomass, and total community biomass varied significantly among the five sites (neighbor biomass, $F_{4, 25} = 55.59$, P < 0.0001; litter biomass, $F_{4, 25} = 26.28$, P < 0.0001; total community biomass, $F_{4, 25} = 57.91$, P < 0.0001; Table 2). There was a six-fold increase in mean community biomass from site 1 to site 5. Mean litter biomass increased 25-fold across these sites and was positively correlated with community biomass ($R^2 = 0.96$, P < 0.05, n = 5). Most sites were dominated by perennial grasses. A perennial forb (*Centaurea maculosa* Lam.) and perennial grass (*Poa compressa* L.) were co-dominant at site 1.

Resources

Light penetration to the soil surface varied significantly among the sites, with neighbors, litter, and with interactions between litter and sites, and between neighbors and litter (Table 4, Fig. 2A). Neighbors reduced light penetration to the soil surface at all sites in plots where litter was removed, but in plots where litter

Source of variation	df	MS	F
Among Blocks			
Site	4	0.4946	52.61**
Block	20	0.0094	
Within Blocks			
Neighbors	1	1.7493	164.77**
Neighbors x Site	4	0.0029	0.28 ^{ns}
Neighbors x Block	20	0.0106	
Litter	1	3.3350	297.40**
Litter x Site	4	0.1817	16.20**
Litter x Block	20	0.0112	
Neighbors x Litter	1	0.4847	49.17**
Neighbors x Litter x Site	4	0.0420	4.26*
Neighbors x Litter x Block	20	0.0099	

Table 4. Results of ANOVA for site and treatment effects on mean seasonal light penetration .

Figure 2. A) Mean seasonal light penetration (mean + 1 SE) in relation to the experimental treatments. Treatments with neighbors removed are indicated by - N, and treatments with neighbors left intact are indicated by +N. Treatments with litter removed are indicated by - L, and treatments with litter left intact are indicated by shading and by +L. Brackets above and below the bars specify within-site mean comparisons made at each level of the two treatment factors (ns = P > 0.05; * = P < 0.05). B). Mean seasonal nitrogen concentrations (mean + 1 SE) in the two treatments where all vegetation (neighbors and litter) was either removed or left intact. Sites are ranked from lowest to highest community biomass.





was present, neighbors reduced light penetration to the soil surface only at site 1. At site 1, litter levels were so low that litter had no effect on light penetration. However, in the other four sites, light penetration in plots containing litter only was similar to that in plots containing both neighbors and litter. This suggests that light levels at the soil surface in the intact vegetation of these sites was determined more by litter than by neighbors. Mean seasonal light penetration measured in the intact plots declined logrithmically with community biomass (light penetration = -0.193 (log community biomass) + 1.315, $R^2 = 0.52$, P < 0.0001, n = 25) and mean seasonal nitrogen concentration (light penetration = -0.282 (log N) + 0.423, $R^2 = 0.51$, P < 0.0001, n = 25).

The removal of all plant material (neighbors and litter) increased mean seasonal nitrogen concentrations significantly across all sites (Table 5, Fig. 2B), ranging from 56% at site 5 to 218% at site 1. Mean seasonal nitrogen concentration measured in the intact plots was positively correlated with community biomass ($R^2 = 0.83$, P < 0.0001, n = 25).

Seed addition

Seedling recruitment - The number of Andropogon seedlings that established in the plots did not differ significantly among the five sites, but did vary in response to neighbors and litter, and with the interaction between litter and sites (Table 6). Across all sites, the removal of neighbors led to a significant increase in Andropogon density (Fig. 3A). The significant interaction between sites and litter indicates that the degree to which litter affected Andropogon density varied among sites. At sites 1 and 2, litter removal had no significant effect on Andropogon density. However, at the three sites with the greatest community Table 5. Results of ANOVA for site and treatments effects on mean seasonal soil nitrogen concentration. Nitrogen concentrations were measured only in the two treatments where all plant material (neighbors and litter) was either removed or left intact.

Source of variation	df	MS	F		
Among Blocks					
Site	4	17.360	7.78***		
Block	20	2.229			
Within Blocks					
Vegetation	1	123.884	73.17***		
Vegetation x Site	4	0.280	0.16 ^{ns}		
Block	20	1.693			
^{ns} $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.					

		Density		Total shoot biomass	
Source of variation	df	MS	F	MS	F
Among Blocks					
Site	4	41.438	0.95 ^{ns}	12.542	15.86***
Block	20	43.425	0.791		
Within Blocks					
Neighbors	1	3659.415	112.52***	101.729	171.84***
Neighbors x Site	4	18.252	0.56 ^{ns}	9.182	15.51***
Neighbors x Block	20	32.523		0.592	
Litter	1	1325.331	43.57***	27.010	48.40***
Litter x Site	4	322.504	10.60***	8.156	14.62***
Litter x Block	20	30.416		0.558	
Neighbors x Litter	1	96.930	3.79 ^{ns}	5.732	9.67**
Neighbors x Litter x Site	4	24.481	0.96 ^{ns}	2.649	4.47**
Neighbors x Litter x Block	20	25.556		0.593	

Table 6. Results of ANOVA for site and treatment effects on *Andropogon* density and total shoot biomass in the seed addition experiment.

^{ns} P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

Figure 3. A) *Andropogon* density and B) total shoot biomass (mean + 1 SE) in relation to the experimental treatments (seed addition experiment).





biomass (sites 3-5), the removal of litter significantly increased Andropogon density.

The magnitude of the net and litter effects on *Andropogon* density differed significantly among the 5 sites, whereas the magnitude of the neighbor effect did not (net, F4, 20 = 4.97, P < 0.01; neighbor, F4, 20 = 0.88, P = 0.49; litter, F4, 20 = 3.63, P < 0.05; Fig. 4A). The mean net effect on density ranged from 57% at the site supporting the lowest community biomass (site 1) to 97% at the site with the greatest community biomass (site 5), and was positively correlated with mean community biomass (Fig. 4A). The mean neighbor effect ranged from 49% at site 4 to 72% at site 2 and was not significantly correlated with mean community biomass. The mean litter effect on *Andropogon* density ranged from -30% at site 1 to 80% at site 5, and was positively correlated with mean community biomass.

There was considerable within-site variation in the magnitude of the community effects, especially at the site with the lowest community biomass (site 1; Fig. 4B). Regressions performed on data that included this variation (all blocks, n = 25) were consistent with those performed on site means; the community effects on seedling recruitment were correlated with community biomass only when litter was present (net and litter effects, Fig 4B).

Total shoot biomass - The total shoot biomass of *Andropogon* in the seed addition experiment differed significantly among the sites, and in response to neighbors and litter, and with interactions among all of these factors (Table 6). The removal of neighbors increased *Andropogon* shoot biomass at all sites, both in plots where litter was removed and in plots where litter was left intact (Fig. 3B). At sites 1 and 2, the removal of litter did not significantly affect *Andropogon* shoot biomass, either in plots where neighbors were removed or in plots where neighbors were left intact. At site 3, litter removal significantly increased



Figure 4. Relationships between the community effects on *Andropogon* density (dependent variables) and community biomass (independent variable) in the seed addition experiment. A) Mean community effects plotted against mean community biomass (n = 5). B) Community effects calculated for all blocks plotted against block community biomass (n = 25). Dashed line represents the no effect line. Note log scale for community biomass.

Andropogon shoot biomass only in plots where neighbors were left intact. In contrast, litter removal significantly increased *Andropogon* shoot biomass at sites 4 and 5, both in plots where neighbors were removed and left intact.

The magnitude of all community effects on *Andropogon* shoot biomass (net, neighbor, and litter effects) differed significantly among the sites (net, $F_{4, 20}$ = 12.35, *P* < 0.0001; neighbor, $F_{4, 20}$ = 11.83, *P* < 0.0001; litter, $F_{4, 20}$ = 4.49, *P* < 0.01; Fig 5A). The mean net effect ranged from a low of 69% at site 1 to a high of 99% at site 5, and was positively correlated with community biomass (Fig 5A). The mean neighbor effect ranged from 65% at site 1 to 93% at site 5, and exhibited a tendency to increase with community biomass, but the relationship was not significant. The mean litter effect on shoot biomass ranged from -41% at site 1 to 71% at site 5 and was positively correlated with community biomass.

Regressions performed on data that included within-site variation were largely consistent with those performed on site means, except that this analysis revealed a significant positive correlation between the neighbor effect and community biomass (Fig. 5B). This confirms the non-significant positive trend observed among site means. The observation that the neighbor effect appeared to increase with community biomass in the case of *Andropogon* shoot biomass, but was unrelated to community biomass in the case of *Andropogon* density, suggests that there may have been an increase in the effects of neighbors on the growth of individual seedlings. However, because I did not measure the growth of individual seedlings, and because *Andropogon* shoot biomass is confounded by both recruitment and growth, I focus on the transplant experiment to better assess the effects of the surrounding community on individual plant growth.





Figure 5. Relationships between the community effects on *Andropogon* total shoot biomass (independent variables) and community biomass (dependent variable) in the seed addition experiment. A) Mean community effects plotted against mean community biomass (n = 5). B) Community effects calculated for all blocks plotted against block community biomass (n = 25).

Transplants

In the seedling transplant experiment, the RGR of *Andropogon* transplants differed among the sites, and varied in response to neighbors and litter, and with interactions between sites and neighbors, and between neighbors and litter (Table 7). The RGR of transplants responded positively to the removal of neighbors at all sites, both in the absence and presence of litter (Fig. 6). At sites 2, 4, and 5 the removal of litter significantly increased RGR in plots where neighbors were removed, but had no effect on RGR at any of the sites where neighbors were left intact, reflecting a significant interaction between neighbors and litter.

The magnitude of the net effect on the RGR of transplants differed significantly among the 5 sites, whereas the magnitude of the neighbor and litter effects did not (net, $F_{4, 25} = 4.28$, P < 0.01; neighbor, $F_{4, 25} = 1.88$, P = 0.15; litter, $F_{4, 25} = 1.52$, P = 0.22, Fig. 7A). The mean net and neighbor effects were similar in all fields and ranged from a low of 36% (net effect) at site 5 to a high of 51% (net effect) at site 3. Neither of these effects were significantly correlated with community biomass (Fig. 7A). The mean litter effect on transplant RGR was small relative to the net and neighbor effects, ranging from 2% at site 1 to 16% at site 5. However, the mean litter effect was positively correlated with community biomass.

There was considerable variation in the community effects on RGR within the sites (Fig. 7B). Regressions performed on data that included this variation were consistent with regressions performed on site means; the magnitude of the net and neighbor effects were unrelated to community biomass, but the magnitude of the litter effect was positively correlated with community biomass.

Source	16		-	
of variation	df	MS	<u> </u>	
Among Blocks				
Site	4	0.00019	12.03***	
Block	25	0.00002		
Within Blocks				
Neighbors	1	0.01699	1689.18***	
Neighbors x Site	4	0.00005	5.25**	
Neighbors x Block	25	0.00001		
Litter	1	0.00028	19.38***	
Litter x Site	4	0.00002	1.68	
Litter x Block	25	0.00001		
Neighbors x Litter	1	0.00026	19.25***	
Neighbors x Litter x Site	4	0.00002	1.74 ^{ns}	
Neighbors x Litter x Block	25	0.00001		
P > 0.05; P < 0.05; P < 0.05; P < 0.01; P < 0.01.				

Table 7. Results of ANOVA for site and treatment effects on the RGR of transplants in the seedling transplant experiment.



Figure 6. RGR ($g \cdot g^{-1} \cdot d^{-1}$) of Andropogon transplants (mean + 1 SE) in relation to the experimental treatments.



Figure 7. Relationships between the community effects on the RGR of transplants (dependent variables) and community biomass (independent variable) in the transplant experiment. A) Mean community effects plotted against mean community biomass (n = 5). B) Community effects calculated for all blocks plotted against block community biomass (n = 30).

DISCUSSION

In this study, living plant neighbors negatively affected all aspects of *Andropogon* performance at all five old-field sites. This suggests that resource exploitation by living plants reduced *Andropogon* seedling recruitment and growth at all of the sites and across the entire range of community biomass and soil nitrogen availability examined. Plant litter inhibited recruitment at the sites with the greatest neighbor and litter biomass, but was of little consequence to the growth of established plants at any of the sites in the presence of both living neighbors and litter. Across sites, the net effect of the surrounding community on recruitment was positively correlated with community biomass, largely due to increasing interference by litter. However, the net effect of the community on the growth of established plants was unrelated to community biomass. These results suggest that both living plants and litter can limit the recruitment success of *Andropogon* in old-fields, and that the negative impact of litter on recruitment is likely to be most pronounced at productive sites that support a continuous layer of dense litter.

Although numerous removal experiments have shown that the surrounding plant community can affect target plant performance, this study is the first to measure the separate and combined effects of living neighbors and litter on target plants across a range of environments. Although the effects of living neighbors were generally greater in magnitude than the effects of litter, litter significantly reduced the recruitment of *Andropogon* at sites with the greatest community biomass. This observation is consistent with the findings of a number of studies investigating the effects of plant litter on individual species (Werner 1975, Goldberg and Werner 1983, Fowler 1986, Hamrick and Lee 1987, Carson and Peterson 1990). Fowler (1986) and Hamrick and Lee (1987) found that, although small amounts of litter tended to enhance seedling establishment of selected herbaceous species, large amounts of litter strongly inhibited seedling establishment. Werner (1975) found that germination of the herbaceous biennial, *Dipsacus sylvestris*, was strongly inhibited by grass litter in old-fields, and that the degree of this inhibition increased with litter cover. Goldberg and Werner (1983) showed that the removal of litter in the most productive areas of a 30 year oldfield greatly enhanced the seedling emergence of two *Solidago* species.

There are a number of mechanisms by which a dense litter layer can inhibit the recruitment of plants from seed. Litter can act as a physical barrier, preventing the movement of seeds to the soil surface or by impeding the emergence of newly germinated seedlings (Sydes and Grime 1981, Facelli and Pickett 1991a). A large amount of litter can greatly reduce light penetration to the soil surface, limiting germination and seedling growth (Facelli and Pickett 1991b). Other indirect effects associated with the dark moist conditions under the litter mat, such as increased susceptibility of seedlings to fungal attack and invertebrate herbivores, have been documented (Facelli, 1994).

In this study, the mechanisms by which litter inhibited seedling recruitment are not known. The fates of individual seedlings were not followed throughout the growing season, so I cannot distinguish whether the negative effects of the surrounding plant community on *Andropogon* recruitment were due to reduced germination, increased mortality, or a combination of these factors. However, field observations made over the growing season suggested that litter inhibited both germination and seedling survival at the site with the greatest litter biomass (site 5) due to mechanical impedance. Many of the seeds added to plots containing litter at site 5, remained lodged in the litter layer throughout much of the growing season. A large number of these lodged seeds germinated in the litter, but subsequently died within a few days, likely due to the inability

of roots to reach the soil. Extreme reduction of light by litter may have been an important factor limiting the emergence and growth of *Andropogon* seedlings in the sites with the greatest litter biomass. Light levels at the soil surface in the intact plots of sites 3-5 were extremely low, generally less than 5% of full sun (Fig. 1). Light levels in plots where only litter was present were similar, indicating that litter reduced light levels at the soil surface to a greater degree than the living plants.

For established plants in the transplant experiment, the removal of plant litter from plots where neighbors were left intact did not lead to any significant changes in growth. This suggests that the reduced growth of established plants in these communities was due almost entirely to the exploitative effects of living neighbors rather than inhibition by litter. However, in three of the five sites (sites 2, 4 and 5) litter significantly reduced transplant growth in plots where living neighbors had been removed, accounting for the significant neighbor by litter interaction. This indicates that the observed effects of living neighbors and litter were non-additive, suggesting that litter has the potential to reduce the growth of established plants, but that these effects are inconsequential in the intact communities due to the much stronger exploitative effects of living neighbors. The causes of reduced transplant growth in this study in plots where only litter was present is unknown.

Magnitude of plant community effects

The relative community effect indices used in this study allowed me to compare the magnitude of community effects across the different study sites. The results show that the net community effect on both the recruitment of *Andropogon* and the growth of established *Andropogon* transplants differed significantly

among the sites, but that effects on recruitment were more spatially variable. Although a number of site factors may have contributed to strong site differences in the net effect on recruitment, the strong positive dependence of the net community effect index on community biomass, as well on soil nitrogen concentration (results not presented here), suggests that this variation reflects the impact of plant biomass, soil fertility or productivity on the magnitude of plant interactions as predicted by Grime (1979) and others (Southwood 1988, Keddy 1990). Interestingly, the effect of the surrounding community on recruitment was not correlated with community biomass when litter had been removed (neighbor effect). This, and the observed positive correlation between the effect of litter alone (litter effect) and community biomass, suggests that the increase in the net effect on *Andropogon* recruitment was more the result of an increase in the interference effects of plant litter rather than an increase in the effects of living plants.

Unlike what I found for *Andropogon* recruitment, both the net and neighbor effects on established transplant growth were unrelated to community biomass. This result is inconsistent with theories of community organization which predict an increase in competition with productivity (Grime 1979, Southwood 1988, Keddy 1990). As was the case with *Andropogon* recruitment, the effect of litter alone on transplant growth, although small relative to the effect of living neighbors, increased significantly with community biomass. Again, this appears to reflect the potential effects of litter that were not realized in the intact communities due to the much greater effects of living neighbors.

My interpretations of the community effect indices assume that I properly standardized interspecific interactions among target plants and neighbors so as to make them comparable among the different sites. In this experiment, intraspecific interactions among target plants were possible because each

experimental plot contained more than one individual target plant. Miller (1996) pointed out that because intraspecific and interspecific competition may both vary along gradients, indices of competition that standardize interspecific competition by plant performance in plots where intraspecific interactions are occurring may result in an insensitive measure of competition. In this study intraspecific competition was likely important in the neighbor removal plots of the seed addition experiment where *Andropogon* densities were quite high. If intraspecific competition did vary among the sites in these plots, it likely increased with community biomass and soil nitrogen availability because total shoot biomass increased significantly with these factors. This would probably have led to underestimates of recruitment in the removal plots at the most productive sites due to a greater likely-hood of self-thinning. If this was the case then I may have underestimated the magnitude of community effects in the seed addition experiment at the sites with the greatest community biomass and soil nitrogen availability. Despite the possibility of an insensitive measure, I found that the net and litter effects on recruitment increased strongly with community biomass, suggesting that if anything, I underestimated the magnitude of litter interference effects on recruitment at the sites with the greatest community biomass.

The result that plant litter contributed strongly to the over-all inhibitory effect of the community on the recruitment of *Andropogon* at sites with the greatest plant biomass is consistent with a number of studies showing that the accumulation of large amounts of litter can limit plant diversity in productive systems by interfering with species colonization (e. g. Carson and Peterson 1990, Tilman 1993). I suggest that theories designed to explain variation in plant interactions and species diversity along gradients in community biomass and

associated gradients in productivity and soil fertility should take into account the potential impact of litter on recruitment, as well as other non-exploitative interactions that potentially occur among plants.

In addition, although this study was conducted at only five sites and over just one growing season, the results suggest that it may be during the recruitment phase of the life history, when seeds and seedlings are especially susceptible to the effects of litter, that Andropogon is most sensitive to variation in community biomass. If this is correct, an important implication is that the inclusion of regeneration processes in plant competition studies may often lead to different conclusions regarding how plant interactions vary along environmental gradients compared to those based upon the responses of established plants alone. This is of particular significance because regeneration processes have often been found to be more important in determining the distribution of species in space and time than the performance of established plants (Grubb 1977, Gross and Werner 1982). These results also suggest that the distribution of native C_4 prairie grasses such as Andropogon along old-field biomass gradients in southwest Michigan may be more strongly constrained by limits to recruitment than by competition experienced during the established phase of the life history.

CHAPTER 3

REMOVAL EXPERIMENT II: PARTITIONING THE EFFECTS OF PLANT BIOMASS AND LITTER ON THREE NATIVE GRASSES IN OLD-FIELD VEGETATION

INTRODUCTION

An important goal of plant ecologists is to develop models of population and community regulation that suitably predict the dynamics and outcomes of species interactions at any location. As a result, over the past decade there has been a great deal of interest in describing and explaining variation in the magnitude of plant competition, especially with respect to variation in community biomass or standing crop associated with gradients in soil resource availability and plant productivity (Wilson and Keddy 1986, Wilson and Tilman 1991, 1993, Bonser and Reader 1995, Kadmon 1995, Twolan-Strutt and Keddy 1996). There is continuing disagreement among plant ecologists regarding the expected relationship between the magnitude of plant competition and community biomass. Biomass-dependent theories of plant competition (Grime 1979, Keddy 1990) predict that the magnitude of competition will increase with community biomass. This prediction is based on the assumption that neighboring plants are most likely to come into contact with each other and compete at sites supporting high plant biomass and that plant demand for both above- and below-ground resources increases with plant productivity and community biomass. Others have argued that the magnitude of competition should be just as strong in low productivity habitats as in high productivity habitats, and that competition tends to change more in quality (from below- to above-ground) than in quantity as productivity or community biomass increases (Newman 1973, Tilman 1988, Taylor et al. 1990). This has led to an alternative biomass-independent view of competition which predicts that the magnitude of competition should be unrelated to productivity or community biomass.

Experimental studies designed to test these contrasting views have yielded mixed results with some studies finding an increase in competition with community biomass as predicted by the biomass-dependent theories (Wilson and Keddy 1986, Bonser and Reader 1995, Kadmon 1995), and others finding no relationship at all (Fowler 1990, Wilson and Shay 1990, Wilson and Tilman 1991, 1993). To determine the general usefulness of community biomass as a predictor of competition across different habitats and communities, it is clear that more studies need to be conducted that encompass a greater number of focal species and greater range of community biomass and productivity.

To practically measure the magnitude of competition in the field, many studies have used neighbor removal experiments where the performance of target plants growing in field plots with the surrounding plant community removed is compared to performance in plots with the community left intact. In almost all of these experiments where target plant performance was found to be reduced in the intact plots, the effect was assumed to be due to resource exploitation by living plant neighbors. Although this assumption may hold for some types of vegetation, in many grassland and old-field communities, additional effects associated with accumulated plant litter may also affect the establishment and growth of individual plants (Goldberg and Werner 1983, Fowler 1986, Hamrick and Lee 1987, Facelli 1994). As a result, indices of competition obtained from neighbor removal experiments in grasslands and old-field communities may often reflect the combined effects of living plants and litter on target plants.

In this study I investigated variation in the effects of both living plant neighbors and litter on three native grass species in southwest Michigan oldfields that differ in plant community biomass. I use the term community

biomass to refer to the sum of above-ground living plant biomass and litter and use this measure as an index of plant productivity. The three target species: Andropogon gerardi (Big bluestem), Schizachyrium scoparium (Little bluestem), and Sorghastrum nutans (Indian grass), are all C₄ perennial bunch-grasses. These species represent the dominant grasses of the tall-grass prairies (Bazzaz and Parrish 1982) and all were important components of the pre-settlement prairie and savanna communities of southwest Michigan (Gotshall 1972). Despite similarity among these species in photosynthetic pathway, growth form, relative growth rate, and ability to compete for soil nutrients (Parrish and Bazzaz 1982, Tilman and Wedin 1991), Schizachyrium differs somewhat from the other two species in distribution across environmental gradients. In intact prairies, Andropogon and Sorghastrum are distributed similarly across broad gradients of plant productivity, soil moisture, and soil fertility (Weaver 1954, Smeins and Olson 1970), while Schizachyrium is typically more restricted in distribution to the more xeric, infertile sites (Weaver 1954, Bazzaz and Parrish 1982). The prevalence of Schizachyrium in unproductive, xeric sites in prairies has been attributed to its tolerance of moisture stress, exemplified by the high water use efficiency (Weaver 1954, Knapp 1985). Physiological trade-offs associated with adaptation to low moisture conditions may limit the competitive ability of Schizachyrium in the more mesic and productive sites. Schizachyrium also has smaller seeds than Andropogon and Sorghastrum (Rabinowitz 1978, Foster, unpublished data) which may limit its ability to colonize productive sites that support large amounts of ground cover.

In the current successional landscape of southwest Michigan, all three of these native species are largely restricted to low fertility sites and are generally absent from more productive old-fields on fertile sites that are

typically dominated by introduced C₃ grasses. Competition with earlycolonizing, fast-growing introduced grasses combined with limited seed dispersal may be important in inhibiting the re-colonization of fertile sites by native grasses after site abandonment from agriculture (Tilman and Wedin 1991, Foster and Gross, in press, Tilman 1993). Also, because fire is no longer an important factor in this landscape, litter accumulation may inhibit the recolonization of productive sites by native prairie species that evolved in the presence of periodic fire and which are not likely adapted for establishment in dense litter (Tilman 1993).

In this study I conducted a neighbor removal experiment in which seeds and transplants of the three native grasses were added to a factorial arrangement of removal treatments within each of nine old-field sites. The primary goals of this experiment were: 1) to determine the degree to which site to site variation the effects of the surrounding plant community on target plant recruitment and growth could be explained by plant community biomass; and 2) to partition the effects of living plant neighbors and plant litter in order determine how each contribute to the net effect of the surrounding plant community on target plant performance.

METHODS

Study sites

This study was conducted in nine old-field sites at the W. K. Kellogg Biological Station (KBS) of Michigan State University in southwest Michigan (Kalamazoo County; 42° 24' N, 85° 24' W). Sites were selected to encompass the entire range of community biomass common to old-fields in southwest

Michigan. All nine sites had been abandoned from row crop agriculture for at least 16 years and are currently dominated by introduced perennial grasses (Table 8; see Burbank et al. 1992). Isolated individuals of *Andropogon* were found at sites 1 and 5. *Schizachyrium* and *Sorghastrum* were not found at any of the study sites although populations of these species were located within several kilometers of each site. Soils underlying the sites are classified as sandy loam, but differ in the amount of top-soil lost to agricultural-related erosion. Assignment of site numbers (1-9) was based on ranking of mean plant community biomass (1 = lowest, 9 = highest biomass).

Experimental design and methods

In 1995 both seeds and seedling transplants of three native C₄ perennial grasses were planted into a 2 x 2 factorial arrangement of treatments established at each site in a randomized block design. The experimental treatments included two levels of living plant neighbors (intact and removed) and two levels of plant litter (intact and removed). At all sites, six 3 x 3.5 m experimental blocks were established in early May 1995 (Fig. 8). Within all sites (except sites 1 and 3), adjacent blocks were separated by buffers zones of approximately 2 m. At sites 1 and 3, blocks were separated by greater distances ranging from 5 - 15 m to avoid shading from several isolated shrubs. Each block contained four parallel 0.5×3 m experimental treatment plots separated by 0.5 m buffer areas. Each plot within each block contained 6 subplots, three for seed additions and three for transplants (one seed addition and one transplant subplot per target species). The three seed addition subplots (30 x 30 cm) were adjacent to each other at one end of the block and

		Litter	Total		
	Neighbor	biomass	community	Four most abundant	Relative
Site	biomass (g/m^2)	(g/m^2)	biomass (g/m ²)	species l	biomass (%)
1	68.8 ± 15.2a	10.4 ± 1.5a	79.1 ± 16.1a	Andropogon virginicus	50.0
				Rubus alleghaniensis	13.9
				Danthonia spicata	9.9
				Solidago nemoralis	5.7
2	109.6 ± 43.7a	19.6 ± 5.9a	129.1 ± 43.2ab	Rubus alleghaniensis	27.8
				Danthonia spicata	17.2
				Centaurea maculosa	14.7
				Andropogon virginicus	11.0
3	182.3 ± 15.1b	39.1 ± 2.3b	221.4 ± 14.8bc	Andropogon virginicus	49.8
				Danthonia spicata	9.8
				Rubus alleghaniensis	6.0
				Desmodium rotundifolium	<i>m</i> 4.8
4	2596 + 27.5bc	91. 9 ± 23.7b	351.6 ± 50.3cd	Agroputon tepens	85.2
-				Achillea millefolium	7.3
				Bromus inermis	6.4
				Melilotus alba	0.1
5	348.1 ± 17.9cd	235.2 ± 50.7c	583.3 ± 54.9de	Bromus inermis	58.1
				Poa pratensis	10.3
				Achillea millefolium	10.1
				Agropyron repens	5.1
6	398.8 ± 56.2cd	220.4 ± 57.5cd	626.9 ± 115.7de	Bromus inermis	78.0
				Agropyron repens	10.3
				Poa pratensis	3.8
				Daucus carota	3.2
7	745.2 ± 105.3de	397.6 ± 42.4cde	1142.8 ± 142.8ef	Agropyron repens	71.0
				Arrhenatherum elatius	28.3
				Silene alba	0.1
				Polygonum scandens	0.1
8	915.2 ± 55.1e	555.7 ± 54.3de	1470.9 ± 102.4f	Bromus inermis	44.2
				Poa pratensis	19.1
				Solidago canadensis	17.4
				Agropyron repens	15.4
9	1235.9 ± 174.4e	737.3 ± 68.5e	1973.3 ± 223.8f	Bromus inermis	90.6
				Poa pratensis	4.9
				Agropyron repens	2.5
				Barbarea vulgaris	0.1

Table 8. Vegetation characteristics of the nine study sites. Biomass values are shown as means ± 1 SE (n = 6 for each site). Biomass values within a column with the same letter are not significantly different (P > 0.05; Tukey's HSD).



Experimental Block Layout

Figure 8. Experimental block layout illustrating the arrangement of the experimental treatment plots and the transplant and seed addition subplots. T_1 and T_2 refer to the position of the two transplants in each transplant subplot.

were separated by buffer zones of 20 cm. The three transplant subplots (50 x 50 cm) were also adjacent to each other, but had no buffer zones between them. Species were randomly assigned to both the seed addition and transplant subplots within each experimental plot.

In early May, the experimental treatments were applied to the four 0.5 x 3.5 m plots located within each block. Neighbors were removed either by clipping or mowing and by applying Glyphosate herbicide solution (Roundup) to the re-growth a week later. Litter was removed by hand from the litter removal treatments so that the soil was left undisturbed. To minimize root encroachment into the two neighbor removal treatments, plot perimeters were trenched with a flat blade shovel to a depth of 20 cm twice during the growing season. The borders between subplots were also trenched to prevent below-ground interaction between the different target species. Neighbor removal plots were periodically hand-weeded during the growing season to eliminate vegetation re-growth.

Seed additions - Seeds of the three target species were collected from local populations in the fall of 1994 and stored in an unheated garage over winter in a metal container to expose the seeds to winter temperature fluctuations. Seeds were sown by hand into all of the 30 x 30 cm subplots at a rate of 300/subplot (3030/m²) in late May 1995. The seedlings were censused and target shoot biomass was harvested in late September 1995. Seedling density at the time of harvest is used in this study as a measure of target plant recruitment. All plant material was oven-dried at 60° C to constant mass and then weighed.

Seedling transplants - Seedlings of each of the three target species were obtained by germinating seeds in flats in a heated greenhouse in mid-May 1995. Approximately 7-9 days after germination, 700 - 900 seedlings of each

species were transferred into individual seedling cone-containers (2.54 cm diameter x 10.16 cm deep) containing a 3:1:1 mixture of peat moss, commercial potting soil, and old-field soil. After 22-25 days additional growth, 432 seedlings of each species were selected for the experiment. Initial shoot biomass (B) of these seedlings was estimated from regressions of seedling biomass on longest leaf length (L) obtained from subsamples of the remaining healthy seedlings (*Andropogon*: B = 0.005L - 0.017, $R^2 = 0.71$, P < 0.001, n = 30; *Schizachyrium*: B = 0.008L - 0.034, $R^2 = 0.76$, P < 0.001, n = 30; *Sorghastrum*: B = 0.002L + 0.016, $R^2 = 0.44$, P < 0.001, n = 30).

In early June, two seedlings of each species were transplanted into their respective transplant subplots by inserting seedling plugs into pre-formed holes made with a 2.54 cm diameter soil corer. Within each subplot, the two transplants were separated by approximately 20 cm. All individual transplants were watered (0.2 L/day) for twelve consecutive days following transplanting to encourage initial establishment. At sites 5, 8 and 9 most of the transplants in the neighbor removal treatments were heavily browsed by deer within two days after planting. The browsed transplants were replaced with new ones and a 1.5 m tall fence made from poultry netting was placed around the perimeter of the neighbor removal treatment plots at all sites to prevent further deer browsing. Fencing was not placed around the treatment plots where neighbors were left intact because the target plants growing in these plots were not browsed. The presence of fences had no significant affect on light levels at the soil surface in any of the sites. By the end of the experiment, only 16 Andropogon seedlings and 27 Schizachyrium transplants had died. However, 66 Sorghastrum transplants died, most of which were located at sites 1 and 2. In late September the shoots of all surviving transplants were harvested, dried and weighed.

Community biomass - Above-ground biomass of neighboring plants and litter was estimated for all sites in the seed addition subplots where both neighbors and litter had been left intact. For six of these sites, plant neighbors were sorted by species to document species composition (Table 8). Species composition for the other three sites (4, 5 and 7) had been assessed in a previous study (Foster and Gross, in press) and data from that study are given in table 8. Plant material from all sites was dried and weighed as described previously.

Light measurements

Photosynthetically active radiation (PAR) was measured in mid-June above the vegetation and at the soil surface in the transplant section of each plot with a PAR ceptometer probe (Decagon Devices Inc.) to determine how light penetration to the soil surface varied among the sites and was affected by the experimental treatments. In plots where litter was left intact, light measurements were made by inserting the ceptometer beneath the litter layer. In the neighbor removal plots, measurements were made at plot edges at mid-day when the sun was directly overhead to minimize the impact of transplants on light readings. Light penetration is expressed as the percentage PAR reaching the ground surface.

Data analysis

Community biomass - Site differences in neighbor biomass, litter biomass and community biomass (sum of neighbor and litter biomass) were examined using one-way analysis of variance (ANOVA). This analysis was
performed on biomass data from the intact treatment (neighbor and litter biomass left intact).

Light penetration and target plant performance - Percent light penetration, seedling density and total shoot biomass (seed addition experiment), and transplant growth (transplant experiment) were analyzed using two-way analysis of variance separately for each site. In cases where the interaction between neighbors and litter was significant, contrasts among neighbor levels were compared at each level of litter and contrasts among litter levels were compared at each level of neighbors using unplanned comparisons (Sokal and Rohlf 1981). Due to a lack of germination in a large proportion of the plots at all sites in the seed addition experiment, data on *Sorghastrum* density and total shoot biomass data are not reported here. In addition, *Sorghastrum* transplant RGR data from sites 1 and 2 were eliminated from all statistical analyses due to high plant mortality at these sites. Analyses of transplant growth were performed on plot mean values. Relative growth rate of each transplant (RGR, Chiariello et al. 1989) was calculated as:

 $RGR = [\ln(B_2) - \ln(B_1)]/(t_2 - t_1)$

where B_2 is the transplant biomass at harvest, B_1 is the estimated transplant biomass at planting, and $t_2 - t_1$ is the number of days growth between harvest (t_2) and planting (t_1). Light penetration data were arcsine-square root transformed to reduce heteroscedasticity. *Andropogon* total shoot biomass and density data were log transformed and square-root transformed respectively to improve normality and reduce heteroscedasticity (Sokal and Rohlf 1981). Untransformed data are presented in the figures.

Magnitude of community effects - The magnitude of the effects of the surrounding plant community on target plant performance (density, total shoot biomass, and RGR of transplants) was examined using a relative community effect index (diffuse competition, Wilson and Keddy 1986; competition intensity, Wilson and Tilman 1993). This index estimates the degree to which target plants were inhibited or facilitated by the surrounding community by comparing plant performance in plots cleared of all plant material (neighbors and litter) to that in plots where all plant material was left intact. Positive values indicate inhibition, negative values indicate facilitation, and values of zero indicate no net effect of the surrounding community. To assess the importance of litter in contributing to the total net effect of the community on target performance, a separate index was calculated for plots that were left intact and those where only litter was removed. These indices were calculated for each experimental block as:

Net Effect = $(P_C - P_{NL})/P_C$

Neighbor Effect = $(P_C - P_N)/P_C$

where P_C is plant performance in plots cleared of all plant material (living neighbors and litter), P_{NL} is performance in plots with neighbors and litter left intact, and P_N is performance in plots with only neighbors left intact (litter removed). An additional index was calculated to measure the effect of litter alone and was calculated as:

where P_{Lit} is plant performance in plots with only litter left intact (neighbors removed).

Two-way ANOVA and Tukey HSD tests were used to examine site and species differences in each community effect index (total, neighbor and litter effects). Effects on the RGR of *Sorghastrum* at sites 1 and 2 could not be examined because of missing data. As a result I performed two separate two-way ANOVA's on transplant RGR: 1) an analysis that included data from all nine sites and two species (*Sorghastrum* omitted); 2) an analysis with data from sites 1 and 2 omitted and all three species included.

I examined the degree of inter-dependence between the community effects and community biomass using linear regression on site means (n = 9). For *Sorghastrum* RGR, regressions were performed on data for sites 3-9 only. In cases where a community effect index showed evidence of non-linear dependence on community biomass, I log-transformed community biomass prior to the analyses. These data are shown in the figures un-transformed with logarithmic best-fit curves presented to illustrate non-linearity. SYSTAT statistical software (version 5.2.1; Wilkinson 1992) was used for all analyses.

RESULTS

Community biomass and species composition

Total community biomass and its two components, neighbor and litter biomass differed significantly among the nine sites (Table 8). Total community biomass increased 25-fold From site 1 to site 9. Neighbor and litter biomass increased 18- and 71-fold, respectively, from site 1 to site 9 and were positively correlated to each other ($R^2 = 0.87$, P < 0.0001, n = 9). The nine study sites were primarily dominated by perennial grasses, though the differed somewhat in species composition (Burbank et al. 1992; Table 8).

Light penetration

The extent to which living plant neighbors and litter affected light reaching the soil surface varied substantially among the nine study sites (Fig. 9. At the three sites with the lowest community biomass (sites 1-3), the removal of neighbors significantly increased light penetration, but removal of litter had no effect. In contrast, at sites 4-9 light penetration varied significantly with neighbors, with litter, and with the interaction between the two. At these sites, neighbor removal increased light penetration in the plots where litter was removed, but had no effect where litter was left intact. At sites 4-7, litter removal increased light penetration in both the presence and absence of neighbors, while at sites 8 and 9, litter removal increased light penetration only in plots where neighbors were removed. Mean light penetration measured in the intact plots declined logrithmically with mean community biomass (light penetration = -0.231(log community biomass) + 1.62, $R^2 = 0.86$, P < 0.0001, n = 9).

Seed addition

Significance of treatment effects - In the seed addition experiment, the number of Andropogon seedlings recruited into the plots was increased significantly by the removal of living plant neighbors at all nine study sites (Fig. 10A). At the two sites with the greatest community biomass (sites 8 and 9) where there were significant interactions between neighbors and litter, the



Figure 9. Mean seasonal light penetration (mean + 1 SE) in relation to the experimental treatments. Treatments with neighbors removed are indicated by - N, and treatments with neighbors left intact are indicated by +N. Treatments with litter removed are indicated by - L, and treatments with litter left intact are indicated by shading and by +L. Letters above the bars specify the significance of neighbor (N) and litter (L) effects within the sites (ns = P > 0.05; * = P < 0.05). At sites with a significant neighbor x litter interaction, brackets above and below the bars specify treatment mean comparisons made at each level of the two treatment factors (ns = P > 0.05; * = P < 0.05).

Figure 10. Andropogon density (A) and total shoot biomass (B; mean + 1 SE) in relation to the experimental treatments (seed addition).



Figure 10.

removal of neighbors significantly increased *Andropogon* density, both in the absence and presence of litter. At sites 1-4, the removal of litter had no effect on *Andropogon* density. At sites 5-7, litter removal significantly increased *Andropogon* density. At sites 8 and 9 where litter biomass was greatest, litter removal increased *Andropogon* density significantly only in plots where neighbors were removed, accounting for the neighbor by litter interaction.

The removal of neighbors increased *Andropogon* shoot biomass significantly at all but the site with the lowest community biomass (site 1; Fig. 10B). At sites 5-9 where there were significant interactions between neighbors and litter, the removal of neighbors significantly increased *Andropogon* shoot biomass both in the absence and presence of litter. At sites 1-4, litter removal had no effect on *Andropogon* shoot biomass. At sites 5-7, litter removal significantly increased *Andropogon* shoot biomass, both in the absence and presence of neighbors. At sites 8 and 9, litter removal increased *Andropogon* shoot biomass significantly only in plots where neighbors were removed, accounting for the neighbor by litter interaction.

The treatment responses of *Schizachyrium* in the seed addition experiment were similar to the responses of *Andropogon* (Fig. 11). The number of *Schizachyrium* seedlings that recruited into the plots was increased significantly by the removal of living plant neighbors at all sites except site 1 (Fig. 11A). At sites 8 and 9, where there were significant interactions between neighbors and litter, the removal of neighbors significantly reduced *Schizachyrium* density, both in the absence and presence of litter. At sites 1-4, the removal of litter had no effect on *Schizachyrium* density. At sites 5-7, litter removal significantly increased *Schizachyrium* recruitment. At sites 8 and 9, litter removal increased *Schizachyrium* density Figure 11. *Schizachyrium* density (A) and total shoot biomass (B; mean + 1 SE) in relation to the experimental treatments (seed addition).



Figure 11.

significantly only in plots where neighbors were removed, accounting for the neighbor by litter interaction.

The removal of neighbors increased *Schizachyrium* shoot biomass significantly at all sites except sites 1 and 2 (Fig. 11B). At sites 6-9 where there were significant interactions between neighbors and litter, the removal of neighbors significantly increased *Schizachyrium* shoot biomass in both the absence and presence of neighbors. At sites 1-4, litter removal had no effect on *Schizachyrium* shoot biomass. At site 5, litter removal significantly increased *Schizachyrium* shoot biomass. At site 6, litter removal significantly increased *Schizachyrium* shoot biomass only in plots where neighbors were present. At site 7, litter removal increased *Schizachyrium* shoot biomass in both the absence and presence of neighbors, while at sites 8 and 9, litter removal significantly increased *Schizachyrium* shoot biomass only in plots where neighbors were removed.

Magnitude of community effects - In the seed addition experiment, the net, neighbor and litter effects on both seedling density and shoot biomass differed significantly among the sites, but there were no differences among species (*Andropogon* and *Schizachyrium*) and no interaction between sites and species (Table 9, Fig 12 and 13). For both species, the net, neighbor, and litter effects on density and shoot biomass were all positively correlated with total community biomass (Fig. 12 and 13). The net and litter effects on the density of both species increased logrithmically with community biomass, while relationships between neighbor effects on density and community biomass of both species, all three measures of community effect (net, neighbor, and litter effects) increased logrithmically with community biomass.

		Density	Total Shoot biomass
Effect/Source	df	(F value)	(F value)
Net			
Site	8	9.2***	10.2***
Species	1	1.5ns	0.1 ^{ns}
Site x Species	8	0.4ns	0.1ns
Neighbor			
Site	8	5.6***	1.1***
Species	1	0.1 ^{ns}	0.1 ^{ns}
Site x Species	8	0.4 ^{ns}	0.1ns
Litter			
Site	8	4.3***	4.2***
Species	1	0.1 ^{ns}	0.1ns
Site x Species	8	0.3ns	0.3ns

Table 9. Results of two-way ANOVA for community effects on density and total shoot biomass (seed addition).

ns P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.

Figure 12. Relationships between the community effects on Andropogon density (A) and total shoot biomass (B; dependent variables) and community biomass (independent variable). Dashed line represents the no effect line.



Figure 12.

Figure 13. Relationships between community effects on *Schizachyrium* density (A) and total shoot biomass (B; dependent variables) and community biomass (independent variable).



Figure 13.

Transplants

Significance of treatment effects - The removal of neighbors significantly increased the RGR of Andropogon and Schizachyrium transplants all nine study sites (Fig. 14A and B). The removal of neighbors increased the RGR of Sorghastrum at sites where its responses could be tested statistically (sites 3-9; Fig. 14C). Litter removal increased the RGR of Andropogon and Sorghastrum transplants only at site 7 in plots where neighbors were removed, and had no effect on the RGR of Schizachyrium at any of the sites.

Magnitude of community effects - The net effect of the plant community on the RGR of transplants varied significantly with sites, but not with species (Table 10). However, there was a significant site by species interaction reflecting a greater net effect on *Schizachyrium* than on the other species at site 6, but a weaker net effect on *Schizachyrium* than on the other species at sites 7 and 8 (Figs. 15, 16, and 17). The neighbor effect on transplant RGR varied significantly among sites, but litter effects did not vary significantly among sites or species (Table 10). For both *Andropogon* and *Schizachyrium*, the net and neighbor effects on RGR increased logrithmically with total community biomass (Fig. 15 and 16). Litter effects on *Andropogon* and *Schizachyrium* were not correlated with community biomass. None of the three community effects on *Sorghastrum* transplants were correlated with community biomass (Fig. 17).



Figure 14. RGR ($g \cdot g^{-1} \cdot d^{-1}$) of transplants (mean + 1 SE) in relation to the experimental treatments. NT = not tested statistically.



Figure 14.

Effect/Source	Sites 1-9, Sorghastrum omitted (df, F value)		Sites 3-9, Sorghastrum included (df, F value)	
Net				
Site	8	20.0***	6	6.5***
Species	1	0.1ns	2	0.4 ^{ns}
Site x Species	8	2.9**	12	3.1***
Neighbor				
Site	8	13.4***	6	4.1***
Species	1	4.0ns	2	3.0ns
Site x Species	8	1.4 ^{ns}	12	1.7ns
Litter				
Site	8	0.1 ^{ns}	6	1.4ns
Species	1	0.9ns	2	0.1ns
Site x Species	8	0.6 ^{ns}	12	0.6ns

Table 10. Results of two-way ANOVA for community effects on the RGR of transplants.

ns P > 0.05; * P < 0.05; ** P < 0.01; *** P < 0.001.



Figure 15. Relationships between the community effects on Andropogon transplant RGR ($g \cdot g^{-1} \cdot d^{-1}$) and community biomass (independent variable). ns P > 0.05, ** P < 0.001.



Figure 16. Relationships between the community effects on *Schizachyrium* transplant RGR ($g \cdot g^{-1} \cdot d^{-1}$) and community biomass (independent variable). ns P > 0.05, ** P < 0.001, *** P < 0.0001.



Figure 17. Relationships between the community effects on *Sorghastrum* transplant RGR (g·g⁻¹·d⁻¹) and community biomass (independent variable). ns P > 0.05.

DISCUSSION

In this experiment I found that the surrounding plant community suppressed target plant performance at all nine study sites. For two of the three target species (Andropogon and Schizachyrium,) the net suppressive effect of the surrounding community on both seedling recruitment and transplant growth increased significantly with community biomass. These relationships were strongly non-linear, indicating that the net effects of the community increased most rapidly with community biomass at the low end of the gradient and then leveled off. Similar non-linear dependence of competition on plant biomass has been observed in wetland communities (Shipley et al. 1991), old-fields (Bonser and Reader 1995), and desert grasslands (Kadmon 1995). Taken as a whole, these results are most consistent with biomass-dependent view of plant competition that predict that the magnitude of competition occurring among plants increases with community biomass, plant productivity or soil fertility (Grime 1979, Keddy 1990). However, the strong non-linearity of these relationships suggests that the degree to which competition depends on community biomass or productivity may depend upon the range of community biomass or productivity examined.

Several authors have argued that the inconsistent results obtained from studies examining variation in competition may be related to differences in the range of community biomass or productivity over which competition was measured (Goldberg and Barton 1992, Bonser and Reader 1995, Kadmon 1995). Goldberg and Barton (1992) pointed out that results from experiments conducted across natural productivity gradients most often support the prediction that competition increases with productivity, while experiments conducted across experimental gradients are usually more consistent with the predictions of the biomass-independent view. Goldberg and Barton (1992) argue that these different results may be due to a more restricted range of productivity in studies using experimental gradients. In a previous field experiment that I conducted in 1994 over a more limited range of community biomass in these old-fields (208 - 1205 g/m2; Foster and Gross, in press), I found that the net community effect on *Andropogon* recruitment increased with community biomass as found in the current study. However, unlike in the current study, the net effect of the plant community on the growth of *Andropogon* transplants varied little, and was unrelated to community biomass.

To examine whether the different results obtained for transplants in the two experiments could be attributed to differences in the range of biomass over which effects were measured, I re-analyzed data from the current study, but excluded data from sites that fell below the minimum level of community biomass used in the previous study (sites 1 and 2 omitted). The results of this re-analysis were largely consistent with the results from the previous experiment: the net effects on the recruitment of both *Andropogon* and *Schizachyrium* increased with community biomass as observed for *Andropogon* in the previous study (*Andropogon*: $R^2 = 0.78$, P < 0.01; and *Schizachyrium*: $R^2 = 0.73$, P < 0.05). However, the net effects on transplant growth for all three target species were not correlated with community biomass over the more limited range of biomass, although the net effect on *Andropogon* transplants did exhibit a tendency to increase across this range that was marginally significant (*Andropogon*: $R^2 = 0.48$, P = 0.07; and *Schizachyrium*: $R^2 = 0.32$, P = 0.20; *Sorghastrum*: $R^2 = 0.30$, P = 0.20).

This result suggests that target plants recruiting from seed were sensitive to changes in community biomass across the entire range of biomass

examined, although these effects were most pronounced from low to medium biomass sites than from medium to high biomass sites. In contrast, the growth of established transplants appeared to have been sensitive to changes in community biomass only at the low end of the biomass gradient. This indicates that the range of biomass and productivity examined can be of critical importance in competition studies, greatly influencing conclusions regarding how competition is affected by productivity. In fact, the conclusion in this study that the net effect of the plant community on *Sorghastrum* transplant growth was unrelated to community biomass may reflect the more restricted range of community biomass over which data was available for this species.

Although results for the entire range of biomass are most consistent with the biomass-dependent view of competition (Grime 1979, Keddy 1990), in the case of competition between established plants, it may be more useful to view both biomass-dependent and biomass-independent views as being applicable across different ranges of biomass or productivity. Because net effects on transplants increased significantly only across a very limited range of low community biomass, the biomass-independent view may be the most relevant for all but the most extremely unproductive old-field communities.

Partitioning the effects of living neighbors and litter

In this study, living plant neighbors reduced most aspects of target plant performance at each of the sites, indicating that resource exploitation by living plants suppressed recruitment and growth across a wide range of plant community biomass. Plant litter inhibited the recruitment of *Andropogon* and *Schizachyrium* from seed at sites of medium to high community

biomass, but had little impact on the growth of established transplants at any of the sites. Interestingly, the removal of litter at sites 8 and 9 which supported the greatest neighbor and litter biomass, led to increases in recruitment only when neighbors had also been removed, while litter removal at sites of intermediate neighbor and litter biomass increased recruitment both in the presence and absence of neighbors. This suggests that litter was less of a constraint to seedling recruitment in the intact vegetation at sites with the greatest community biomass than it was at sites of intermediate community biomass. The negative impact of litter at sites 8 and 9 within plots where living neighbors had been removed suggests that litter had a strong potential for limiting seedling recruitment at these sites that was not realized in the intact plots due to the much stronger impact of living plant neighbors. These strong suppressive effects of living neighbors were likely related to effects on light availability. Unlike at sites of intermediate community biomass, living plant biomass was so great at sites 8 and 9 that neighbors reduced light at the soil surface to very low levels and to the same degree as did litter and neighbors combined.

These results indicate that litter contributed to the net effect of the surrounding plant community on recruitment at sites of intermediate community biomass, but contributed little to the net effect of the plant community on transplant growth at any of the sites. For seedling recruitment, the separate effects of living neighbors and litter increased with community biomass, indicating that both effects contributed to variation in net effects on recruitment among the study sites. The observed increases in litter effects with increased community biomass illustrates that plant litter was capable of inhibiting seedling recruitment by itself at sites of intermediate to high community biomass. However, significant disparity between net and

neighbor effects occurred only at sites of intermediate productivity, thus indicating that the potential inhibitory impact of litter on recruitment was not detectable in the intact vegetation at sites with the greatest community biomass due to the strong effects of living plant neighbors on light availability. For transplants, litter had a relatively small effect on RGR at all sites compared to the net and neighbor effects. This, and the fact that there was very little disparity between the net and neighbor effects for any species, suggests that litter did not contribute significantly to the net effects of the community on transplant growth nor variability in the net effects observed among sites.

The strong suppressive effect of plant litter on recruitment observed in this study at sites of medium to high community biomass are consistent with a number of studies showing negative impacts of litter on germination, seedling emergence, growth and survival (Werner 1975, Goldberg and Werner 1983, Hamrick and Lee 1987, Bergelson 1990, Facelli and Pickett 1991a). Such negative effects of litter are usually observed at relatively high levels of litter accumulation where litter can reduce light levels at the soil surface, alter microclimate, and act as a mechanical barrier to seeds and seedlings (Facelli and Pickett 1991a). Smaller amounts of litter has been found to enhance plant performance in some environments by ameliorating environmental stresses (Fowler 1986, Wilms et al. 1986). Facilitory effects of plant litter are most common in arid environments where plants are often exposed to extreme moisture stress. In the study, I found no strong evidence of facilitation by litter, probably because of the relatively benign climate and high rainfall in this region.

Implications for native grass distributions and species diversity

In this study, the established plant community suppressed the recruitment of Andropogon and Schizachyrium at most of the study sites. However, seedlings were able to successfully establish some seedlings at all sites in the presence of vegetation, suggesting that the absence of these species from these study sites may reflect dispersal limitation, in addition to any constraints on recruitment imposed by the established plant community. Seedling recruitment of Andropogon and Schizachyrium in the presence of vegetation tended to be highest, and the suppressive effects of the plant community were lowest at the most unproductive sites. This suggests that dispersal limitation may be the most important constraint to establishment in unproductive sites, while dispersal limitation and interference effects of vegetation may both be important in reducing recruitment at the more productive sites. At the three most productive sites in this study (sites 7-9), both seedling recruitment and total shoot biomass were very low in the presence of vegetation, indicating that the effects of the established plant community may be sufficient to prevent colonization by these species in highly productive communities that support large amounts of living biomass and litter even when there is no limit to dispersal. Andropogon and Schizachyrium differed little from each other in their ability to establish seedlings at any of the study sites. In contrast, Sorghastrum was largely unable to establish seedlings at any site. The inability of Sorghastrum to establish from seed was primarily due to poor germination brought about by low seed viability and likely does not reflect a genetic difference in this species ability to establish seedlings. However, the high mortality of Sorghastrum transplants

at the two most unproductive sites (sites 1 and 2) may reflect species differences.

Several studies suggest that strong interference effects of established vegetation on seedling recruitment can contribute to reduced species diversity in highly productive old-field and grassland communities by reducing rates of species colonization (Carson and Peterson 1990, Tilman 1993). Most previous mechanisms proposed to explain reduced diversity with increased productivity assume that intense resource competition among living plants (primarily for light) reduces diversity in productive habitats by increasing the rate of species loss (Goldberg and Miller 1990, Tilman and Pacala 1993, Huston and DeAngelis 1994). However, the number of species in a habitat is determined by the balance between extinction and colonization (MacArthur and Wilson 1969). The results showing that seedling recruitment of two native grass species was inhibited by the established plant community are consistent with the view that constraints to colonization may contribute to low species diversity in productive old-field communities (Tilman 1993). The results also show that the mechanism responsible for reduced colonization in productive habitats may include the suppressive effects of accumulated plant litter on seedling recruitment in addition to resource competition by living plants.

CHAPTER 4

SPECIES RICHNESS IN A SUCCESSIONAL GRASSLAND: EFFECTS OF NITROGEN ENRICHMENT AND PLANT LITTER

INTRODUCTION

The addition of limiting nutrients to herbaceous plant communities frequently leads to increases in plant production and declines in plant species diversity (Bakelaar and Odum 1978, Tilman 1987, Carson and Barrett 1988, Pysek and Leps 1991, Tilman 1993). There has been a great deal of interest in the mechanisms responsible for reduced diversity at high levels of plant productivity and in response to nutrient addition, not only due to theoretical interest, but also because of practical concerns regarding the consequences that long-term eutrophication has for the conservation and restoration of native plant communities (Berendse and Elberse 1990, Marrs et al. 1996). A number of prominent theories have focused on resource competition and its potential role in determining the effects of productivity and soil fertility on species diversity in plant communities (Grime 1973, 1979, Newman 1973, Goldberg and Miller 1990, Tilman and Pacala 1993, Huston and DeAngelis 1994). Most of these theories suggest that intense competition for light among living plants causes the rate of competitive exclusion to increase at high levels of productivity, leading to a reduction in species richness (Abrams 1995). Although resource exploitation by living plants is undoubtedly important in limiting the diversity of many plant communities, these theories do not consider the potential impact of non-living plant biomass or accumulated plant litter in contributing to reduced diversity at high levels of productivity. For example, a number of studies suggest that the accumulation of a dense litter layer is an important factor limiting the diversity of highly productive grasslands and old fields through its inhibitory impact on seedling establishment and thus species colonization (Goldberg and Werner 1983, Carson and Peterson 1990, Tilman 1993).

Plant litter plays an important role in many plant communities by directly or indirectly affecting individuals and populations (Sydes and Grime 1981, Knapp and Seastedt 1986, Carson and Peterson 1990, Facelli and Pickett 1991a, Facelli 1994). There are studies illustrating positive (facilitation) and negative (inhibition) effects of plant litter on the performance of plants. In general, facilitation by litter is most common in extremely unproductive or arid environments where even small amounts of litter can ameliorate stressful environmental conditions (e. g. low moisture levels; Fowler 1986, Willms et al. 1986, Hamrick and Lee 1987). Inhibition by litter is most commonly observed in highly productive, but undisturbed environments where litter accumulation can be quite high (Haslam 1971, Werner 1975, Goldberg and Werner 1983, Carson and Peterson 1990, Facelli and Pickett 1991a, Tilman 1993, Foster and Gross, in press). Together, these studies suggest that litter may be an important factor influencing species diversity along productivity and fertility gradients via changes in the direction (facilitation versus inhibition) and magnitude of litter effects.

In this study I investigated the effects of nitrogen enrichment and litter accumulation on species richness in a southwest Michigan successional grassland. Prior to European settlement, the herbaceous component of the upland prairie and savanna communities of southwest Michigan were largely occupied by native C₄ grasses and a diverse array of prairie forbs, and it is generally recognized that these species and communities were maintained by frequent fire (Gotshall 1972). In tallgrass prairies, fire serves to remove plant litter, thus altering species composition and diversity (Hulbert 1969, Knapp and Seastedt 1986, Tilman 1993). Litter accumulation has been frequently cited as an important factor contributing to reduced yield and reduced diversity under conditions of fire suppression in tallgrass prairie (Hulbert 1969, Knapp and Seastedt 1986). In the current successional landscape of southwest Michigan, upland herbaceous old-fields are typically dominated by introduced C₃ grasses such as *Bromus inermis* and *Agropyron repens* which are capable of invading and dominating fields shortly after abandonment from agriculture (Tilman and Wedin 1991a, Foster 1992). Because fire is currently absent from this landscape, litter accumulation may be an important factor limiting species colonization success and species richness in the most productive fields, especially those that have become eutrophied due to past agricultural activity (fertilization, manure application etc.). Litter accumulation may be particularly important in inhibiting the colonization of productive old-fields by native grassland species that evolved in the presence of fire and which generally lack adaptations for establishment in dense litter (Tilman 1993).

The primary goals of this study were to examine the short-term effects of nitrogen enrichment on community biomass, species abundance, and species richness within a moderately productive successional grassland in southwest Michigan, and to examine the extent to which these effects could be attributed to changes in litter biomass independently of changes in standing crop or living biomass. To critically examine the role of litter in contributing to changes in community structure associated with nutrient enrichment and increased productivity, it is necessary to manipulate litter levels in conjunction with fertilization. In this study, I report the results of a two year field experiment in which the experimental addition of nitrogen fertilizer was accompanied by the experimental removal and addition of plant litter.

Another objective of this study was to examine the impact of nitrogen enrichment and litter accumulation on the re-colonization potential of a

single native species. This was done by adding seed of a native C_4 perennial grass, Andropogon gerardi, (Big bluestem) to the experimental plots. Andropogon was absent from the site at the time of the study, both as established plants and as seed, thus allowing assessment of seedling recruitment from a known seed pool. Although this once-dominant prairie species is common in the current landscape, it is primarily restricted to low and medium fertility sites and is largely absent from the most fertile old-fields. The seed additions allowed me to assess whether the absence of Andropogon from the study site, and from the more productive old-fields in the region, may be due more to dispersal limitation or to inhibition by living vegetation and litter.

METHODS

Study site

This study was conducted in southwest Michigan at the W. K. Kellogg Biological Station (KBS, Kalamazoo County; 42° 24' N, 85° 24' W). The experimental site was located within a mid-successional old-field (20-30 years post-abandonment) that was dominated by the introduced C₃ grasses: *Bromus inermis, Agropyron repens,* and *Phleum pratense.* These species accounted for over 80% of the total community biomass. The most common forb species included *Achillea millefolium* (native), *Daucus carota* (introduced), *Hypericum perforatum* (introduced), and *Potentilla recta* (introduced). Soils underlying the field site are a well-drained, Oshtemo sandy loam formed from glacial till and are of moderate fertility for the region (Foster and Gross, in press).
Experimental treatments

In mid April 1994, six 2.5 x 2.5 m experimental blocks were established at the study site (Fig. 18). The blocks were arranged in two parallel columns of three blocks each that were separated by a 2m buffer strip. Blocks within each column were separated by buffer zones of 1m. Within each block, four 1 x 1 m treatment plots were established and placed so that there was a 0.5m buffer between each plot (one plot at each corner of the block). Four experimental treatments were randomly assigned to the four treatment plots within each block. The treatments included; a control (C), litter removal (LR), nitrogen addition (NA), and nitrogen addition + litter removal (LRNA). I later added a litter addition treatment (LA) to examine the effects of increased litter biomass independent of nitrogen enrichment. The goal was to add a quantity of litter similar to the additional amount expected to accumulate in the NA plots. To accommodate this extra treatment, one additional 1 x 1 m plot for the LA treatment was added to each block in June 1994. These plots were systematically positioned 0.5 m away from one side of each of the original blocks as shown in figure 1. As a result, there was not a complete randomization of all treatments within the blocks.

Litter was removed from the LR plots in April and November 1994 by clipping around the perimeter of the plots and then gently lifting the litter mat by hand. This assured that there was no disturbance to the soil surface. Litter was removed in November to remove the current years production that had died and fallen into the plots. In March 1995, a small amount of litter blown into these plots over the winter was removed by hand. Nitrogen was applied to the NA and LRNA plots as commercial ammonium nitrate

Figure 18. Diagrammatic representation of the experimental block and treatment plot layout. Block numbers are indicated by roman numerals. The litter addition (LA) plots that were added after the initiation of the experiment are indicated by heavy lines.

fertilizer at a rate of 48 g N \cdot m⁻² \cdot yr⁻¹. The pelletized fertilizer was applied twice annually (24 g N per application), in late April and mid June of 1994 and 1995.

During the first growing season (1994), the litter addition plots were left untreated until late November when additional litter was added. Litter was added in November because a significant increase in litter biomass, due to nitrogen enrichment, did not occur until the end of the first growing season. Litter collected nearby was weighed, and then spread evenly across the litter addition plots. The amount of litter to be added was determined by collecting litter from a 0.1 x 1m strip in the C and NA treatment plots. The litter was weighed and the mean difference in litter biomass was calculated. After weighing, this litter was returned to the C and NA plots. The litter added to the LA treatment plots was held in place by loosely stretching two strands of bailing wire across each plot and anchoring the ends of the wire in the soil.

Seed addition

To examine the effects of nitrogen enrichment and litter on the recruitment of *Andropogon gerardi*, locally collected seeds of *Andropogon* were added to each experimental plot in May 1995. Within each plot, seeds were added to a marked 30 x 30 cm quadrat at a rate of 3030 seeds/m² (300 seeds per quadrat). Seeds were evenly broadcast by hand from approximately 30 cm above the soil. Germination and survivorship of *Andropogon* seedlings was monitored by censusing the experimental plots on a bi-weekly basis throughout the growing season. On each of six census dates, newly germinated seedlings were marked with toothpicks of a color specific to a

given census. Individual plants marked in previous censuses were accounted for as dead or alive.

Light measurements

To determine how the experimental treatments influenced the quantity of light reaching the soil surface, photosynthetically active radiation (PAR) was measured in each of the plots in early August 1995. PAR measurements were taken approximately 50 cm above the vegetation and at the soil surface in each plot using a PAR ceptometer probe (Decagon Devices Inc.). In plots where litter was left intact, measurements were made by inserting the ceptometer probe beneath the litter layer. Light penetration was expressed as the percentage of the PAR above the vegetation that reached the soil surface.

Vegetation sampling and data analysis

All above-ground living plant biomass and litter was harvested in late August 1995 from three 30 x 30 cm quadrats located in each plot. In addition, all above-ground biomass of *Andropogon* was harvested from the separately marked, 30 x 30 cm quadrat located in each plot. All living biomass was sorted by species, and the number of individual forbs were counted. Numbers of individuals of the dominant clonal grass species were not counted due to my inability to distinguish genetic individuals. All plant material was dried at 60° C to constant mass and weighed.

Treatment effects on plant biomass (living biomass and litter), forb density, species richness, and *Andropogon* density, biomass per plant,

germination and survivorship were examined using a randomized block design ANOVA (recognizing that the treatments were not completely randomized within blocks) and Tukey HSD tests. Because no significant block effects were found in this study, only treatment F values are reported in the results. Biomass data were log (x+1) transformed, density and richness data were square-root transformed, and *Andropogon* survivorship data were arcsine transformed before analysis to meet the assumptions of ANOVA. Untransformed means are presented in the figures and tables. Statistical analyses were performed using SYSTAT Version 5.2.1 (Wilkinson 1992). Plant species nomenclature follows Fernald (1950).

RESULTS

Community responses

Plant Biomass - Nitrogen enrichment resulted in a significant increase in community productivity as reflected by an increase in living biomass in both the presence and absence of litter (Fig. 19A), and an increase in litter biomass (Fig. 19B). However, litter removal had no effect on living biomass, either in the unfertilized or fertilized treatments. As intended, litter removal significantly reduced litter biomass in both the unfertilized and fertilized treatments. Litter addition had the intended effect of increasing litter biomass to levels similar to that found in the fertilized treatment where litter was left intact (NA treatment). Litter addition had no effect on living biomass (Fig. 19A).

The experimental manipulations altered the amount of light reaching the soil surface (Fig. 20). Nitrogen enrichment significantly reduced light



Figure 19. Treatment effects on living biomass (A), litter biomass (B), grass **biomass** (C), forb biomass (D), forb density (E), and species richness (F). Means (+ 1 SE) with different letters are significantly different (P < 0.05). See methods **section** for treatment codes. ANOVA F_{4,20} values: ns P > 0.05, ******* P < 0.001.



Figure 20. Treatment effects on light penetration. Means (+ 1 SE) with different letters are significantly different (P < 0.05). ANOVA F_{4,20} value: **** P < 0.0001.

levels in both the presence and absence of litter. Litter removal increased light levels significantly in the unfertilized treatments, but had no effect on light in the fertilized treatments. Litter addition significantly reduced light to levels observed in the fertilized treatments.

The strong positive response of living biomass to nitrogen enrichment primarily reflects the response of grasses (Fig. 19C). Grass biomass increased significantly with nitrogen enrichment due to increases in the biomass of the dominant grass species, *Bromus inermis* (Table 11). None of the other grass species were significantly affected by nitrogen enrichment. Grass biomass was unaffected by litter removal and litter addition. In contrast, the biomass of the subordinate forb community, which was much lower than that of grasses overall, did not differ significantly among the treatments (Fig. 19D). For life history groups and individual species of forbs that could be examined statistically, there were no significant treatment effects on biomass, despite considerable differences in the magnitude of the means among the treatments (Table 12).

Forb density - Unlike forb biomass, forb density responded strongly to the experimental treatments (Fig. 19E), reflecting the impact of nitrogen enrichment and litter on forb seedling establishment. Nitrogen enrichment reduced forb density significantly in both the presence and absence of litter. Litter removal led to an increase in mean forb density. However, this effect was statistically significant only in the fertilized treatments where litter removal increased forb density up to levels found in the controls. Litter addition significantly reduced forb density to the same level as found in the fertilized plots that contained litter (NA), indicating that the reduction in forb density caused by nitrogen enrichment in these plots was largely due to increased litter biomass.

Table 11. Mean biomass of grass species (g/m^2) in the five experimental treatments. ANOVA's were performed for species that were present in all treatments. Species are listed from greatest to least in biomass. Means within rows with different letters are significantly different (P < 0.05, Tukey's HSD). See methods section for treatment codes.

		<u> </u>	Biomass			-
	С	LR	LA	NA	LRNA	F 4, 20
Bromus inermis	200.3a	215.2a	272.4a	703.3b	571.1b	25.7****
Agropyron repens	64.4	43.6	32.6	69.2	95.4	2.2ns
Phleum pratense	40.3	28.7	22.9	53.4	43.9	0.6ns
Poa pratensis	16.7	18.3	9.2	13.2	33.5	2.8ns
Panicum sp.	3.1	5.2	2.2	2.6	7.9	0.1ns
Poa compressa	2.3	1.2		0.7	0.2	-

ns *P* > 0.05, **** *P* < 0.0001

0
~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~
C
0
- C
-
5
$\sim$
in the second second
•
$\sim$
J.
<b>G</b>

left history groups and for the ten most common forb species. ANOVA's were performed only on life history groups  $(g/m^2)$  and for the ten most common forb species. ANOVA's were performed only on life history groups and species that were present in all treatments. Species are listed from greatest to least in density. Means within rows with different letters are significantly different (P < 0.05, Tukey's HSD). See methods section for treatment codes.

			Biomass						Density			
	υ	LR	LA	NA	LRNA	F4, 20	υ	LR	LA	NA	LRNA	F4, 20
Annual forbs	0.06	3.94			1.42	ł	3.4	49.9			19.1	ı
<b>Biennial forbs</b>	26.50	12.31	10.75	2.60	2.26	1.5ns	53.9ab	88.7a	16.3b	9.5b	43.8ab	4.8**
Perennial forbs	49.40a	45.20ab	16.60b	27.50ab	16.01ab	2.1ns	84.8a	114.0a	14.1b	13.0b	46.6ab	10.6***
Daucus carota	25.90	9.70	10.75	2.60	2.22	0.8ns	44.9ab	85.9a	16.3b	8.9b	41.6ab	3.8*
Achillea millefolium	31.70	33.33	16.48	17.50	15.34	0.9ns	24.7	22.5	10.7	6.2	25.8	1.8ns
Hypericum perforatum	3.50	1.69		0.01	0.17	ı	42.7	25.3		9.0	6.2	ı
Potentilla recta	0.70	0.70	0.01		0:30	·	10.1	14.6	0.6		8.4	·
Oxalis stricta		0.05			0.03	ı		16.3			8.9	ı
Trifolium repens		06.0				1		25.3				ı
Rumex acetosella	1.03	0.03			0.20	·	3.4	10.7			5.6	ı
Medicago lupulina	0.06	2.27			0.02	·	3.4	11.2			2.3	ı
Mullugo verticillata		0.11				ı		10.1				ı
Chenopodium album		0.04			0.25	,		2.8			5.6	ı
ns $P > 0.05$ . * $P < 0.05$ . **	P < 0.01.	*** $P < 0.0$	01.									

The densities of annual, biennial, and perennial forbs all reflect the impact of the experimental treatments (Table 12). There were no annual forbs in the two treatments with elevated levels of litter (LA and NA treatments), suggesting that the accumulation of litter caused by nitrogen enrichment may have inhibited the establishment of annuals from the seed bank. The mean density of biennial forbs (represented primarily by *Daucus carota*), was reduced by nitrogen enrichment in the presence and absence of litter, but these effects were not statistically significant. Mean biennial forb density was increased by litter removal, and decreased by litter addition. However, neither of these effects were statistically significant either. Biennial forb density was significantly lower in the two treatments with elevated levels of litter (LA and NA) compared to the litter removal treatment that was not fertilized (LR). Nitrogen enrichment significantly reduced the density of perennial forbs, while litter addition significantly reduced it.

Species Richness - Species richness varied in response to the experimental treatments in a similar manner as did forb density (Fig. 19F). Nitrogen enrichment reduced mean species richness, although this effect was significant only when litter was left intact. Litter removal increased mean species richness, but just as for forb density, this effect was significant only in the fertilized treatments where litter removal increased species richness up to levels found in the controls. Litter addition significantly reduced species richness relative to the control and to the same degree as observed in the fertilized treatment where litter was left intact (NA treatment) suggesting that the reduction in species richness in these plots caused by nitrogen enrichment was largely due to inhibition by litter.

# Andropogon recruitment

Final density and biomass per plant - Nitrogen enrichment reduced the final density and biomass per plant of Andropogon to very low levels, both in the presence and absence of litter (Fig. 21). In the unfertilized treatments, litter removal significantly increased Andropogon density and biomass per plant. However, in the fertilized treatments, the removal of litter had no effect on either measure. Litter addition reduced Andropogon density and biomass per plant to the same low level as found in the fertilized plots.

Germination and survivorship - I examined Andropogon germination and survivorship (Fig. 22) to assess the relative importance of each in determining Andropogon recruitment (final density). Nitrogen enrichment significantly reduced germination and seedling survivorship in both the presence and absence of litter. Litter removal significantly increased germination in both the unfertilized and fertilized treatments, but had no affect on survivorship. Litter addition significantly reduced germination to levels found in the fertilized plots where litter was left intact. Litter addition reduced mean survivorship, but this effect was not statistically significant.



**Figure 21.** Treatment effects on *Andropogon* density (A), and biomass per **Plant** (B). Means (+ 1 SE) with different letters are significantly different (P < 0.05). ANOVA F_{4,20} values: **** P < 0.0001.



Figure 22. Treatment effects on Andropogon germination (A), and survivorship (B). Means (+ 1 SE) with different letters are significantly different (P < 0.05). ANOVA F_{4,20} values: *** P < 0.001, **** P < 0.0001.

# DISCUSSION

#### Community responses

In this study, nitrogen enrichment over two growing seasons led to an increase in community productivity and a reduction in both forb density and species richness. A major objective of this study was to assess the impact of accumulated plant litter in contributing to community changes associated with nitrogen enrichment, independent of fertilization and increased living biomass. The results suggest that the inhibitory effects associated with increased litter biomass on the establishment of subordinate forb seedlings contributed strongly to the observed decline in species richness. Two lines of evidence support this conclusion. First, the removal of litter increased forb density and species richness in the fertilized plots up to levels found in the controls. Second, the addition of litter reduced forb density and species richness that the increase in litter biomass associated with nitrogen enrichment led to a reduction in forb density and species richness independently of the increase in living biomass.

Species responses to nitrogen enrichment - The strong increase in community productivity associated with nitrogen enrichment was due entirely to the large biomass response of the dominant grass species, *Bromus inermis*. Interestingly, none of the other grass or forb species that could be examined statistically exhibited a significant biomass response (either positive or negative) to nitrogen enrichment. In contrast, the density of forbs was reduced by nitrogen enrichment in both the presence and absence of litter, an indication that the establishment of forb seedlings was inhibited by increased living biomass. The apparent inability of most species to take advantage of increased nitrogen availability was likely due to resource pre-emption by Bromus. Because Bromus was the most dominant species at the site in terms of biomass (> 80% relative biomass) and coverage (evenly distributed across all of the experimental plots), it is likely that it was in a better position than other species to utilize added nitrogen. This effect was likely enhanced by the fact that fertilizer was first applied early in the growing season when C3 grasses such as Bromus are typically most active in terms of growth (Waller and Lewis 1979, Hetrick et al. 1990). A rapid response of Bromus to nitrogen enrichment was visibly evident within two weeks of the first fertilizer application. In the fertilized treatments, *Bromus* culms where considerably taller and the leaves were noticeably greener than in the control, indicating more rapid growth and higher leaf nitrogen concentrations respectively. It is likely that the initial pre-emption of added nitrogen by Bromus, and the resulting increase in biomass and plant height, led to the preemption of light as well. This, in turn, could have suppressed the subordinate forb species and further inhibited their ability to utilize the subsequent applications of nitrogen for growth.

Species responses to litter manipulations - Surprisingly, there were no significant biomass responses to the litter manipulations by any of the individual species, or by species grouped as grasses, forbs, or by life history categories. In contrast, the litter manipulations strongly affected the density of forbs by affecting the establishment of seedlings. Species richness responded to the litter manipulations in a similar manner as forb density, indicating that the decline in species richness in response to nutrient enrichment and increased productivity in plots where litter was left intact was largely due to the negative impact of plant litter on forb seedling recruitment.

Although there is no direct evidence, there are a several potential direct and indirect mechanisms that may have contributed to the negative effects of litter on forb density and species richness in this study. Litter can act as a mechanical barrier to seeds and seedlings, thus directly preventing the germination and emergence of some species due to physical impedance (Fenner 1985, Sydes and Grime 1981, Hamrick and Lee 1987, Persson et al. 1987, Facelli and Pickett 1991a). Increases in litter biomass in this experiment caused by fertilization and litter addition may have increased the effectiveness of this barrier, possibly preventing many of the recently dispersed seeds from reaching the soil surface, and allowing few seedlings to penetrate upwards towards the light.

Plant litter can indirectly effect plant performance in a number of ways by altering light levels and other factors that influence microclimate such as temperature, moisture and humidity (Bazzaz 1979, Goldberg and Werner 1983, Gross 1984, Carson and Peterson 1990, Facelli and Pickett 1991a). The negative effects of litter on forb seedling recruitment observed in this study may partially reflect the elimination of germination cues caused by the dampening effects of increased litter biomass on environmental fluctuations (Facelli and Pickett 1991a). In addition, it is likely that the moist and darkened conditions under the litter in the fertilized treatment could have promoted the increased activity of fungal pathogens and invertebrate herbivores, resulting in enhanced seed and seedling mortality (Goldberg and Werner 1983, Facelli 1994). Although herbivory was not measured in this study, the occurrence of herbivorous mollusks (slugs) were greatest in the litter addition plots and the nitrogen addition plots where litter was left intact (unpublished data).

# Plant responses and light availability

In this study, the effects of living and litter biomass on light availability likely played an important role in reducing forb density and species richness. Light levels at the soil surface were reduced to equally low levels in the litter addition and fertilized plots, including the fertilized plots where litter had been removed. This indicates that both living and litter biomass were equally effective in attenuating light. Significant reductions in light levels and forb densities in response to nitrogen enrichment in plots where litter was removed strongly suggest that light attenuation by living biomass contributed to the observed reductions in forb density and species richness. Further reduction in forb density and species richness evident in the litter addition plots and in the fertilized plots that contained litter, suggests that in addition to effects caused by light attenuation by living plants, additional effects associated with litter accumulation further reduced forb density and species richness.

It is reasonable to assume that the observed reductions in forb density and species richness that can be attributed to increases in living plant biomass were caused primarily through the effects of shading. However, a question arises regarding the degree to which the negative impacts of litter addition were caused by effects of shading versus other litter effects unrelated to light availability (mechanical impedance, microclimatic effects etc.). These separate effects of litter can potentially be isolated by comparing responses in the litter addition plots to responses in the fertilized plots where litter was removed (LRNA). The observed significant difference in forb density and species richness between these two treatments can be attributed to the inhibitory effects of litter unrelated to light availability if it assumed that the separate

effect of living biomass on forb seedlings can be used as a reliable surrogate measure of the isolated effect of litter biomass on forb seedlings which occurred purely as a result of shading. This assumption is reasonable given that living and litter biomass reduced light availability to equally low levels in this study. With this assumption in mind, it can be inferred that the observed reductions in forb density and richness attributable to litter addition cannot be entirely explained by shading alone. As a result, it is likely that multiple mechanisms involving light attenuation by both living plants and litter, and various other direct and indirect effects of litter unrelated to light availability all combined to reduced forb seedling recruitment and species richness in this study.

# Andropogon recruitment

The purpose of adding *Andropogon* seeds to the experimental plots was to more closely examine the effects of nitrogen enrichment and litter on recruitment from seed. The results give some insight into the potential role of established vegetation in affecting the colonization success of this native species in southwest Michigan old-fields that differ in soil fertility and plant productivity. Unlike what was observed for forb density, the removal of litter in the unfertilized treatments led to a large significant increase in *Andropogon* density, indicating that litter represents a significant constraint to recruitment in this field. However, despite inhibition by litter, *Andropogon* was able to successfully establish a reasonable number of seedlings in the control plots, suggesting that the absence of this species from this study site, and other fields of similar composition and productivity, may be due primarily to limits on dispersal. In contrast, nitrogen enrichment and litter addition reduced both *Andropogon* recruitment and growth (density and biomass per plant) to near zero in this study. This results suggests that the absence of *Andropogon* from the more highly productive fields in southwest Michigan that support high standing crops may be due to inhibition of seedling recruitment by the established vegetation in addition to any limits on dispersal. In this study, the strong negative effect of litter addition and nitrogen addition on *Andropogon*, and the lack of the positive response to litter removal in the fertilized plots that was observed in the case of forbs, indicates that the negative effect of nitrogen enrichment on *Andropogon* recruitment in plots where litter was left intact can be suitably explained by the separate effects of either litter or living biomass. The results also indicate that litter reduced *Andropogon* recruitment primarily through inhibition of germination and that living plants inhibited recruitment by reducing both germination and survivorship.

The management implications of the results from these seed additions are that in successional grasslands and old-fields of moderate productivity, litter removal accomplished through burning or mechanical methods may be very effective in facilitating the recruitment of native grasses from seed. However, in highly productive communities, litter removal may be much less effective in this regard due to intense competitive inhibition imposed by productive shoot growth.

# Productivity, diversity, and plant litter

Most theories designed to explain the interdependence of species diversity and habitat productivity invoke the role of resource competition and make the tacit assumption that the relevant plant interactions involved

are exploitative in nature. In other words, competitive exclusion occurs through the direct consumptive effects of living roots and shoots on resources. However, this study and others provide strong evidence that declines in species richness with increased fertility and productivity in oldfield and grassland communities may be closely tied to inhibitory effects associated with accumulated plant litter. As in this study, Carson and Peterson (1990) found that experimental additions of plant litter reduced plant density and species richness in a *Solidago* dominated old-field. From this they argued that low diversity in highly productive old-fields and reductions in diversity occurring in response to nutrient enrichment may often be due to a combination of both inhibition by litter and resource competition associated with living plants. Tilman (1993) found that declines in species richness associated with long-term nitrogen enrichment in experimental grasslands were more strongly tied to variation in litter biomass than to variation in living biomass. These results were largely attributed to the negative impacts of a dense litter layer on the establishment of seedlings and the colonization of new species in the most productive sites.

An assumption implicit in the resource-competition-based diversity theories is that increased productivity reduces species richness because it causes an increase in the rate of species loss (Tilman 1993). However, the number of species within a habitat at a given time can be determined by a balance between extinction and colonization (MacArthur and Wilson 1969). Tilman (1993) found that extinction and colonization rates were equally important in determining the species richness of grasslands, and argued that earlier theories should be modified to account for the effects of productivity on colonization. The results of this study are consistent with the conclusions of Tilman (1993) that increased productivity can reduce species richness in grassland by reducing rates of species colonization. Although I did not directly measure species gains and loss over time in this study, it was clear that the decline in species richness associated with nitrogen enrichment was primarily due to the inhibition of forb seedling establishment. The strong negative impact of nitrogen enrichment on the germination, survival, and recruitment of *Andropogon* highlights the role of increased productivity in limiting the colonization potential of a single species.

To my knowledge this is the first study utilizing litter manipulations in conjunction with fertilization to explicitly examine the independent effects of living plants and accumulated plant litter in contributing to community changes associated with nutrient enrichment and increased productivity. The results are in concordance with the frequently observed decline in species richness in response to increased plant productivity, but suggests that the mechanism responsible for this decline may often involve the inhibitory effects of litter on species colonization in addition to the exploitative effects of living plants. I suggest that theories designed to explain the interdependence of species richness and productivity in herbaceous vegetation should take into account the potential impacts of plant litter on community organization.

# CHAPTER 5

# CONCLUSIONS

Results from the removal experiments discussed in Chapters 2 and 3 showed that the surrounding plant community suppressed the recruitment and growth of the three target species across a wide range of community biomass. When considering the entire range of community biomass examined (Chapter 3) the magnitude of the effects of the surrounding plant community (net effects) on both recruitment and growth of Andropogon and Schizachyrium increased with community biomass as predicted by the biomass-dependent theories of plant community organization (Grime 1979, Keddy 1990). However, these relationships were nonlinear, indicating that the degree of inter-dependence between net community effects on target plants and community biomass was stronger from low to medium biomass than it was from medium to high biomass. In fact, net community effects on established Andropogon and Schizachyrium transplants increased with community biomass only over a very narrow range of low biomass, indicating that the biomass-independent view of plant competition may be more applicable, in the case of established plants, for most old-field plant communities in southwest Michigan. Unlike net effects on established transplants, the net effects on seedling recruitment of Andropogon and Schizachyrium were sensitive to changes in community biomass across the entire range examined, although more sensitive from low to medium biomass than from medium to high biomass. The non-linear relationships observed in this study between net effects and community biomass across a broad range of biomass may explain why some studies measuring competition over more restricted ranges of productivity often find no relationship between competition and productivity. In fact, the conclusion in

this study that the net effect of the plant community on *Sorghastrum* transplant growth was unrelated to community biomass may reflect the more restricted range of community biomass over which effects were measured for this species.

I suggest that it is important to include the entire range of productivity or plant biomass of a region when examining variation in competition to test prior predictions regarding the relationship between competition and productivity. My results suggest that it may be especially important to include the most infertile, and unproductive habitats in competition studies because it is across such sites where individual plants may be most sensitive to changes in competitor biomass.

The degree to which the effects of accumulated plant litter contributed to the net effect of the community on target plants in this study depended on the life history stage examined. Inhibitory effects of litter increased with community biomass and contributed to the net effect of the community on target plant recruitment at sites of intermediate community biomass. However, litter had little impact on established transplants and contributed little to net effects.

These removal experiments revealed a high degree of site to site variability in plant community effects on the recruitment and growth of native grasses and highlight the potential importance of accumulated plant litter in suppressing seedling recruitment in productive old-field communities. The results suggest that the absence of native  $C_4$  grasses in many southwest Michigan old-fields and their apparent restriction to unproductive sites is related to a combination of dispersal limitation and the inhibitory impact of both living plant neighbors and litter on colonization success in the most productive sites that support high standing crop and litter biomass. Such constraints to species colonization imposed by the established vegetation may be important in contributing to low diversity in highly productive communities as suggested by other studies (Carson and Peterson 1990, Tilman 1993).

The nitrogen enrichment / litter manipulation experiment (Chapter 4) demonstrated the short term effects of nitrogen enrichment, increased productivity and litter accumulation on species colonization and species richness within a single old-field site. Nitrogen enrichment led to a large increase in the biomass of both living plants and plant litter primarily by enhancing the productivity of the dominant grass species (*Bromus inermis*). This increase in productivity resulted in a significant decline in forb seedling recruitment, *Andropogon* recruitment from added seed, and species richness. Results of the litter manipulations suggested that these declines were due to suppressive effects associated with both increased living biomass and plant litter. These results are in accordance with declines in species diversity observed in other studies, but indicate that the mechanism responsible for reduced diversity may involve both the inhibitory effects of plant litter and resource competition occurring among living plants.

Tilman (1993) argued that if there is empirical evidence that productivity influences the rate at which species colonize communities, then diversity theories will have to be modified to account for this. Tilman (1993) demonstrated that declines in species richness with increased productivity in Minnesota grasslands were due to changes in both colonization and extinction rates. Furthermore, reduced colonization rates appeared to be strongly related to increased litter biomass.

The results of the three experiments discussed in this dissertation demonstrate the potential effects of productivity on native grass and forb

colonization, and on the species diversity of old-field plant communities. I suggest that current theories of community organization, as applied to grassland and old-field vegetation, should be modified to account for the effects of productivity and community biomass on species colonization, and the role that accumulated plant litter potentially plays in this process.

The results of these experiments have implications for management goals which seeks to enhance or restore native plant diversity in disturbed successional landscapes. Results from the seed addition experiments suggest that low-impact approaches to species re-establishment may be feasible in southwest Michigan old-fields that are of low to intermediate productivity. In relatively infertile and low productivity old-fields, the establishment of native grasses might be accomplished solely by mediating dispersal limitation through the addition of seed. In old-fields of intermediate productivity, the removal of accumulated plant litter (either through periodic prescribed burns or mechanical methods) may be effective in combination with seed additions to enhance the establishment success of native grasses and to promote higher species diversity. LIST OF REFERENCES

.

# LIST OF REFERENCES

- Abrams, P. A. 1995. Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? Ecology 76:2019-2027.
- Al-Mufti, M. M., C. L. Sydes, S. B. Furness, J. P. Grime, and S. R. Band. 1977. A quantitative assessment of shoot phenology and dominance in herbaceous vegetation. Journal of Ecology 65:759-91.
- Bakelaar, R. G and E. P. Odum. 1978. Community and population level responses to fertilization in an old-field ecosystem. Ecology 59:660-665.
- Bazazz, F. A. 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10:351-371.
- Bazzaz, F. A., and J. A. D. Parrish. 1982. Organization of grassland communities. Pages 233-254 in J. R. Estes, editor. Grasses and grassland communities. Oklahoma State University Press, Stillwater, Oklahoma, USA.
- Berendse, F. and W. T. Elberse. 1990. Competition and nutrient availability in heathland and grassland ecosystems. Pages 93-116 in J. B. Grace and D. Tilman, editors. Perspectives on Plant competition. Academic Press, San Diego, California, USA.
- Bergelson, J. 1990. Life after death: site pre-emption by the remains of *Poa annua*. Ecology 71:2157-2165.
- Bertness, M. D., and R. Callaway. 1991. Positive interactions in communities. Trends in Ecology and Evolution 9:191-193.
- Bertness, M. D., and S. D. Hacker. 1994. Physical stress and positive associations among marsh plants. American Naturalist 144:363-372.
- Bonser, S. P., and R. J. Reader. 1995. Plant competition and herbivory in relation to vegetation biomass. Ecology 76:2176-2183.
- Burbank, D., K. S. Pregitzer, and K. L. Gross. 1992. Vegetation of the W. K. Kellogg Biological Station. Michigan State University Agricultural Experiment Station Research Report Number 501.

- Campbell, B. D., and J. P. Grime. 1992. An experimental test of plant strategy theory. Ecology 73:15-29.
- Carson, W. P., and G. W. Barrett. 1988. Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. Ecology 69:984-994.
- Carson, W. P., and C. J. Peterson. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85:8-13.
- Chiariello, N. R., H. A. Mooney, K. Williams. 1989. Growth, carbon allocation and cost of plant tissues. Pages 327-365 in R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. Plant Physiological Ecology. Chapman and Hall, New York, USA.
- Dix, R., and F. Smeins. 1967. The prairie, meadow and marsh vegetation of Nelson county, North Dakota. Canadian Journal of Botany. 45:21-58.
- Facelli, J. M. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. Ecology 75:1727-1735.
- Facelli, J. M., and S. T. A. Pickett. 1991a. Plant litter: its dynamics and effects on plant community structure. The Botanical Review 57:1-31.
- Facelli, J. M., and S. T. A. Pickett. 1991b. Plant litter: light interception and effects on an old-field plant community. Ecology 72:1024-1031.
- Fenner, M. 1985. Seed Ecology. Chapman and Hall, New York, New York, USA.
- Fernald, M. L. 1950. Gray's manual of Botany. Dioscorides Press, Portland, Oregon, USA.
- Foster, B. L. 1992. The role of land use history in structuring an old field plant community. Thesis. Michigan State University, East Lansing, Michigan, USA.
- Foster, B. L. and K. L. Gross. (in press). Partitioning The effects of plant biomass and litter on Andropogon *gerardi* in old-field vegetation. Ecology.
- Fowler, N. L. 1986. Microsite requirements for germination and establishment of three grass species. American Midland Naturalist 115:131-145.

-----. 1990. The effects of competition and environmental heterogeneity on three coexisting grasses. Journal of Ecology 78:389-402.

- Goldberg, D. E., and P. A. Werner. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). Oecologia 60:149-155.
- Goldberg, D. E., and T. E. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology 71:213- 225.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist 139:771-801.
- Gotshall, T. B. 1972. The vegetation of Kalamazoo County at the time of settlement. Pages 1-21 in R. Brewer, editor. The ecology of Kalamazoo County. Western Michigan University Press, Kalamazoo, Michigan, USA.
- Grace, J. B. 1993. The effects of habitat productivity on competition intensity. Trends in Ecology and Evolution. 8:229-230.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344- 347.

-----. 1979. Plant strategies and vegetation processes. J. Wiley & Sons, Chichester, England.

- Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. Journal of Ecology 72:369-387.
- Gross, K. L., and P. A. Werner. 1982. Colonizing abilities of "biennial' plant species in relation to ground cover: implications for their distributions in a successional sere. Ecology 63:921-931.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107-145.
- Gurevitch, J. 1986. Competition and the local distribution of the grass *Stipa* neomexicana. Ecology 67:46-57.
- Hamrick, J. L., and J. M. Lee. 1987. Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). American Journal of Botany 74:451-457.

- Haslam, S. M. 1971. Community regulation in *Phragmites communis* Trim. I. monodominant stands. Journal of Ecology 59:65-73.
- Hetrick, B. A. D., G. W. T. Wilson, and T. C. Todd. 1990. Differential responses of  $C_3$  and  $C_4$  grasses to mycorrhizal symbiosis, phosphorus fertilization, and soil microorganisms. Canadian Journal of Botany 68:461-467.
- Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie. Ecology 50:874-877.
- Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist. 113:81-101.
- Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. American Naturalist 144:954-977.
- Kadmon, R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. Journal of Ecology 83:253-262.
- Keddy. P. A. 1989. Competition. Chapman and Hall, London, England.

———. 1990. Competitive hierarchies and centrifugal organization in plant communities. Pages 266-290 in J. B. Grace and D. Tilman, editors. Perspectives on Plant Competition. Academic Press, San Diego, California, USA.

- Knapp, A. K. 1985. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. Oecologia 65:35-43.
- Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. Bioscience 36:662-668.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Marrs, R. H., J. B. Grace, and L. Gough. 1996. On the relationship between plant species diversity and biomass: a comment on a paper by Gough, Grace and Taylor.
- Miller, T. E. 1996. On quantifying the intensity of competition across gradients. Ecology 77:978-981.

- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. Nature 244:310.
- Parrish, J. A. D., and F. A. Bazzaz. 1982. Competitive interactions in plant communities of different successional ages. Ecology 63:314-320.
- Persson, S., N. Malmer, and B. Wallen. 1987. Leaf litter fall and soil acidity during half a century of secondary succession in temperate deciduous forests. Vegetatio 73:31-45.
- Puerto, A., M. Rico, M. D. Matias, and J. A. Garcia. 1990. Variation is structure and diversity in Mediterranean grasslands related to trophic status and grazing intensity. Journal of Vegetation Science. 1:445-452.
- Pysek, P., and J. Leps. 1991. Response of a weed community to nitrogen fertilization: a multivariate analysis. Journal of Vegetation Science 2:237-244.
- Rabinowitz, D. 1978. Abundance and diaspore weight in rare and common prairie grasses. Oecologia 37:213-219.
- Shipley, B., P. A. Keddy, and L. P. Lefkovitch. 1991. Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. Canadian Journal of Botany 69:1420-1424.
- Smeins, F. E., and D. E. Olson. 1970. Species composition and production of a native northwestern tall grass prairie. American Midland Naturalist 84:398-410.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York. USA.
- Southwood, T. R. E. 1988. Tactics, strategies, and templates. Oikos 52:3-18.
- Sydes, C., and J. P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland II: an experimental investigation. Journal of Ecology 69:249-262.
- Taylor, D. R., L. W. Aarssen, and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. Oikos 58:239-250.
- Thompson, K., and J. P. Grime. 1988. Competition reconsidered: a reply to Tilman. Functional Ecology 2:114-116.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

-----. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189-214.

------. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

——. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? Ecology 74:2179-2191.

- Tilman, D., and D. Wedin. 1991a. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology 72:685-700.
- Tilman, D., and D. Wedin. 1991b. Dynamics of nitrogen competition between successional grasses. Ecology 72:1038-1049.
- Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13-25 in R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, Illinois, USA.
- Twolan-Strutt, L., and P. A. Keddy. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. Ecology 77:259-270.
- Waller, S. S., and J. K. Lewis. 1979. Occurrence of  $C_3$  and  $C_4$  photosynthetic pathways in North American grasses. Journal of Range Management 32:12-28.
- Weaver, J. E. 1954. North American prairie. University of Nebraska Press, Lincoln Nebraska, USA.

Werner, P. A. 1975. The effects of plant litter on germination in teasel, *Dipsacus sylvestris* Huds. American Midland Naturalist 94:470-476.

- Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois, USA.
- Willms W. D., S. Smoliak, and A. W. Baily. 1986. Herbage production following litter removal on Alberta native grasslands. Journal of Range Management 39:536-540.

- Wilson, S. D., and P. A. Keddy. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. American Naturalist 127:862-869.
- Wilson S. D., and J. M. Shay. 1990. Competition, fire, and nutrients in a mixed-grass prairie. Ecology 71:1959-1967.
- Wilson, S. D., and D. Tilman. 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72:1050-1065.
- Wilson, S. D., and D. Tilman. 1993. Plant competition in relation to disturbance, fertility and resource availability. Ecology 74:599-611.
- Wilson, S. D., and D. Tilman. 1995. Competitive responses of eight old-field plant species in four environments. Ecology 76:1169-1180.
- Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

