AN ABSTRACT OF THE THESIS OF

Jean H. Schulenberg for the Master of Science
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Title: Community Composition, Demographics, and Competitive Responses in Three Prairie Grasses
Abstract approved: James M Mayo

Succession is the serial replacement of plant species in a community over time. My thesis research focused on the influence of successional changes on community structure, life history trait expression, and competitive responses of three codominant prairie grasses, *Andropogon scoparius*, *A. gerardii*, and *Sorghastrum nutans*, growing in a 22-year old field and an undisturbed native tallgrass prairie.

Results of a comparison of community composition between the two habitat types (Chapter 1) demonstrated that species richness was highest in the old field, but that percent coverage by the three target grass species was lower in the old field. These three species predominated in the native prairie habitat but were replaced by other species of perennial grasses and perennial forbs in the old-field site. The presence of a target plant species was correlated with a decrease in species richness and species diversity in the old field but not in the native prairie.

The influence of successional stage on the expression of life history traits was investigated in Chapter 2. All three species grew at significantly different rates; native-prairie plants generally grew faster. All three species were taller in the native prairie in 1994, but had greater plant basal area in the old field in both years, suggesting that plants in the two habitats differ in their investment into particular types of vegetative growth.

All three species showed different patterns of allocation to reproduction in the two successional stages. The proportion of plants flowering and reproductive effort was higher in the native prairie for *A. gerardii* and *S. nutans*, while individuals of *A. scoparius* flowered in a significantly higher proportion and had greater reproductive effort in the old field.

Results of a common garden experiment using *S. nutans* from both habitat types showed little difference in the expression of three life history traits. This suggests that differences in these traits exhibited by plants in the field are the result of phenotypic plasticity by similar genotypes in response to the two different environments.

In Chapter 3, I examined the effects of release from competition on *S. nutans* in the field. Experimental plants in both the old-field and the native-prairie sites increased by vegetative expansion into the competitor-free zone, however, the effect was only significant in old-field plants. Plants in both sites produced fewer reproductive structures on the competitor-free side.

Results of this study suggest that resource-allocation trade-offs between vegetative and reproductive growth have enabled these species to locally adapt to their successional stage. All three species have flexible life history strategies and super-competitive abilities that lead eventually to successional dominance in the tallgrass prairie community.

Community Composition, Demographics, and Competitive Responses in Three Prairie Grasses

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by

Jean Hurley Schulenberg

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Approved for Division of Biological Sciences

Scott

Approved by Committee Member

Thomas C Eddy

Approved by Committee Member

James M Mayo

Approved by Major Advisor

Approved for the Graduate Council

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PREFACE

North American tallgrass prairie that was plowed for agriculture and subsequently abandoned undergoes a serial replacement of the plant community. Mechanisms of this replacement have been of central interest to ecologists. My study attempts to determine how prairie grasses establish midway in a succession and persist through later stages. In three separate chapters I present aspects of plant population ecology, including community structure, demographics, and competitive effects. I have repeated background information and literature citations within each manuscript.

My thesis has been prepared in a style appropriate for the journal Ecology published by the Ecological Society of America.

Running heading: Effects of successional stage on grasses

Key words: *Andropogon gerardii*; *Andropogon scoparius*; community structure; competition; life history; old field; phenotypic plasticity; population variation; *Sorghastrum nutans*; succession; tallgrass prairie.

Key phrases: common garden vs field populations; community composition in old field vs native prairie; competitive intensity in old field vs native prairie; life history traits in old field vs native prairie; phenotypic plasticity vs genetic variation.

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"Though I do not believe that a plant will spring up where no seed has been. I have great faith in a seed. Convince me that you have a seed there and I am prepared to accept wonders."

Henry D. Thoreau
Faith in a Seed
Island Press 1993

CHAPTER 1

SITE-RELATED VARIATION IN THREE PRAIRIE GRASSES

INTRODUCTION

Prairie grasses, shaped by past and continuing processes of climate, fire, and grazing, have evolved into a near-climax community (Anderson 1982; Gibson and Hulbert 1987). When native prairie is destroyed for agricultural use and fields are subsequently abandoned, secondary succession drives replacement of the plant community. Mechanisms of secondary succession are not completely understood, but have been the focus of contrasting views in ecology since Clements (1916) (see reviews in Drury and Nisbet 1973; Pickett 1976; Connell and Slatyer 1977; Pickett et al. 1987; Walker and Chapin 1988; Tilman 1988; Burrows 1990). Succession is currently viewed as sequential, but not necessarily directional, changes in species composition and abundance over time.

In initial successional stages plants occur in unstable and open environments where individuals that are good colonizers are favored over those that may be good competitors (Tilman 1990). Succession proceeds in the absence of further disturbance as changes in specific composition and abundance occur. In later stages these changes slow until a stable community persists despite mild perturbations (Horn 1974; Connell and Slatyer 1977). Plants present in a later stage community are the best competitors for a limiting resource and they represent the outcome of competitive interactions within the community (Tilman 1988; Tilman 1990). The community is less likely to experience turnover in species composition.

Specifically, species-area relationship is predicted to change over ecological time (Rosenzweig 1995). Plant-species richness and diversity increase with habitat enrichment as succession proceeds (Bazzaz 1975; Tilman 1988). Transition from colonizers to competitors includes perennial plants that fix and return nitrogen to the soil and increase mineralization over time. Higher species richness and diversity at mid-successional stages are predicted. As productivity increases, richness and diversity become asymptotic and may even decline (Rosenzweig and Abramsky 1993; Tilman et al. 1996), predicting that later stage communities may be less rich and diverse. An increased abundance of the better-competitive species is produced along the productivity gradient (Tilman and Pacala 1993), thus species cover (abundance) should be greater in later-successional stages.

I tested these specific predictions by comparing species-area relationships, species cover, species richness, and species diversity in two habitats, an old field (mid-successional stage) and a native prairie (late successional stage). I specifically tested the hypothesis that presence of highly competitive grass species influences the species composition of the surrounding area. If old-field and native-prairie sites differ in these predicted variables, is this because of the presence and abundance of certain super-competitor species? I used three codominant grasses to compare community composition on a 22-year old field and an undisturbed native prairie. I used three codominant grass species as target plants to test if species richness and species diversity on these sites, was affected by the presence of these target species. H_{A1}: Predicts age of site does make a difference in which plants were present and in what relative abundance they occurred. I tested the null hypothesis, (H_{01}:) there were no age-related differences in the physical structure of a community due to the presence of prairie grasses.

METHODS

Characteristics of the study species

I chose *Andropogon scoparius* Michx., *Andropogon gerardii* Vitman., and *Sorghastrum nutans* (L.) Nash. because they are codominants of the North American tallgrass prairie (Reichman 1987). *Panicum virgatum* L. is also considered a codominant in tallgrass prairie but this species was not a major component of either study site. The study species were well-represented on both sites. They are known colonizers of disturbed areas and are usually present to a varying degree in local old fields undergoing secondary succession. They have been used extensively to restore former grasslands in the Conservation Reserve Program (CRP) of the U.S. Department of Agriculture, Natural Resource Conservation Service.

All three species are warm-season grasses (C_4 photosynthetic pathway) with extensive root systems (Weaver 1954, 1958; Waller and Lewis 1979). *A. gerardii* is known to have roots that penetrate the soil to a depth of 3.7 m. All begin growth in early April and reproduce vegetatively by tillering from short, scaly, underground stems and sexually from a seed-bearing stalk. Seed stalks can range in height from 0.9 to 2.4 m in *A. gerardii* and *S. nutans*. *A. scoparius* is a mid-height grass with seed stalks that range in height from 0.6 to 1.5 m. The flowering period for each species is from late August to October and is followed by seed set and dehiscence. Seeds are borne on sessile spikelets (Hitchcock 1935). Seed dispersal is wind-borne and few seedlings are ever observed in the prairie (J.M. Mayo, personal communication). All three species are episodic producers of seed and may fail to set seed under some conditions.

Site characteristics

The study sites were located in mid-upland prairie in the Middle Creek drainage 8 km west of Elmdale in Chase County in east-central Kansas (NE1/4, Sec. 13, T19S, R6E). The 15.4 ha native tallgrass tract had not been burned, mowed, or grazed for at least 2 years prior to the study and remained undisturbed during the 3 year study. Vegetation on the site was dominated by the three tallgrass species and also included as minor components, *P. virgatum*, *Sporobolus asper* (Michx.) Kunth, and *Bouteloua curtipendula* (Michx.) Torr., and nitrogen-fixing legumes, e.g., *Amorpha canescens*

Pursh, *Psoralea tenuiflora* Pursh var. *floribunda* (Nutt.) Rydb., and *Schrankia nutallii* (DC.) Standl. Annual grasses and woody shrubs were not present. Topography was nearly level to sloping (1-5 %). Soils at the site were classified as Ladysmith and Irwin which are silty clay loams that are moderately well-drained and moderately fertile soils (Neill 1981). The water table was 15.2 to 18.2 m below ground. Rainfall averaged 81.3 cm (32 in) annually and provided the main source of moisture for prairie grasses.

The 8.1 ha old field was undergoing secondary succession. After many successive years of farming, crop production ceased in 1975. The three study species were distributed as isolated crowns throughout the tract but tended to be more concentrated on the west side which was closest to the native prairie site. The native prairie was the probable seed source for this old-field population. *A. scoparius* and *S. nutans* on this tract showed a clumped distribution when tested using the T-square distance sampling technique for spatial patterning as described in Ludwig and Reynolds (1986) (J.M. Mayo and A. Mayo, unpublished data). Other colonizers were perennial grasses, e.g., *S. asper, P. virgatum, Andropogon saccharoides* Swartz., *Elymus virginicus* L., *Eragrostis spectablis* (Pursh) Steud., *Bromus inermis* Leyss., *Dichanthelium oligosanthes* (Schult.) Gould, and *Schedonnardus paniculatus* (Nutt.) Trel. and weedy annual grasses, e.g., *Aristida oligantha* Michx., *Bromus japonicus* Thunb., *Bromus tectorum* L., and *Panicum capillare* L. *Desmanthus illinoensis* (Michx.) MacM. was a predominate forb but most other prairie legumes had not colonized the old field. The tract was heavily invaded by shrubs 1 to 3 m tall that formed a canopy dense enough to overshadow the tallgrass species in portions of the tract. Shrubs present were *Juniperus virginiana* L., *Ulmus americana* L., *Rosa arkansana* var. *suffulta* (Greene) Cockll., *Prunus americana* Marsh., *Gleditsia tricanthos* L., *Rhus glabra* L., *Rhus aromatica* Ait., *Rhus radicans L., Cornus drummondii* Meyer, and *Symphoricarpos orbiculatus* Moench. Bare ground formed open patches throughout and the soil on the site was classified as Ladysmith, which is a moderately well-drained soil (Neill 1981). Farming removes topsoil and greatly reduces organic material in soil (Prather 1990) and the soil on this site was eroded and nutrient poor. The water table was assumed to be similar to that of the prairie tract although terraces constructed in the 1940s prevent some run-off during rainfall and retain more of the moisture for use by plants. The two study populations were approximately 182 m apart and were separated by a continuum of prairie that was mowed annually for hay.

Species-area relationship field methods

I measured species richness in 100 one m^2 quadrats that formed contiguous subplots along a single transect across the old field and the native prairie where the three study species were present. Transects began and ended at least 20 m inside the field perimeter of each tract to avoid edge effects (Fig. 1). All species present in a quadrat were counted and were recorded as new species, which were species present for the first time, old species, which were species present but previously counted, and cumulative species, which included the total number of species per quadrats sampled. Plant nomenclature followed McGregor et al. (1986) and a list of all species found in the quadrats is given in Appendix 1.

Statistical analyses

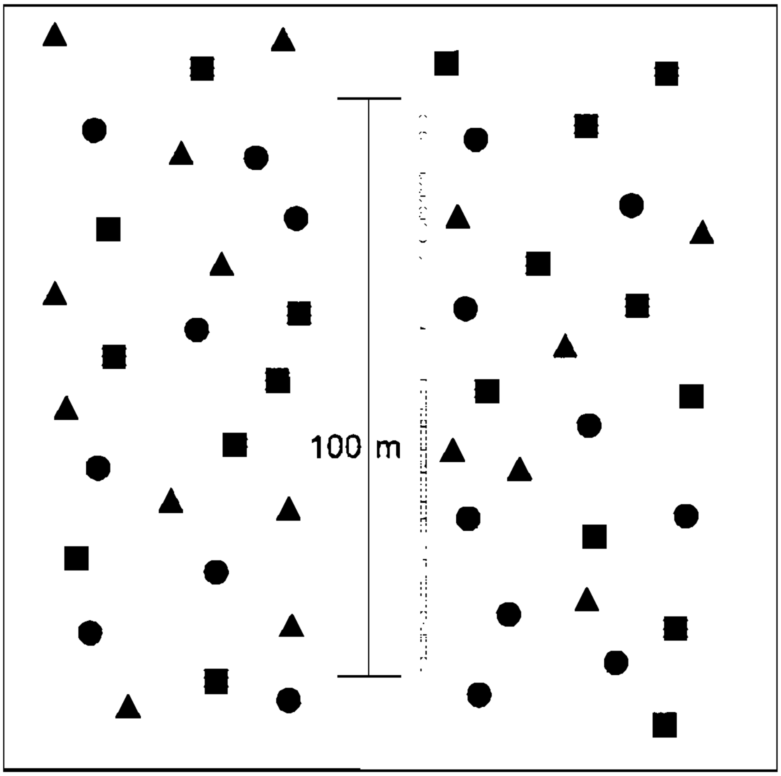
I plotted a species-area curve for each tract and then log-transformed the axes using the Arrhenius equation (Preston 1962):

$$\log S = z \log A + \log c,$$

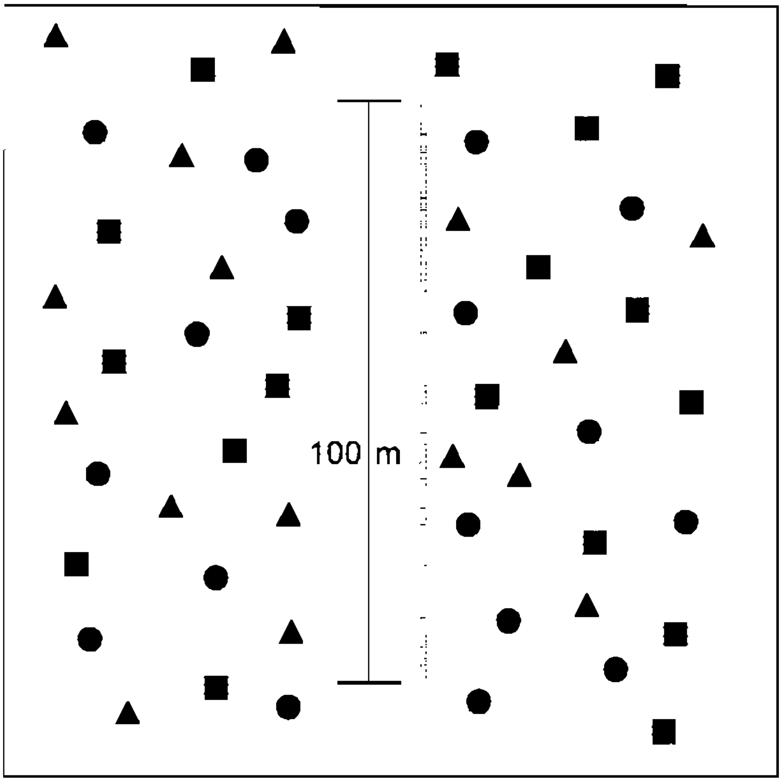
where S = species richness, z = slope, A = area, and c = a constant giving the number of species when A has a value of 1 (Rosenzweig 1995) to determine a species-area relationship for each tract. No statistical analysis was performed on the slopes (z

FIG. 1. Research design for species-area relationship based on 100 one m^2 quadrats for old field and native prairie.

Old field



Native prairie



values) of these equations because data from each tract represented only a single sample.

Community composition field methods

I measured percent cover, species richness, and species abundance to determine if community composition differed between old field and native prairie tracts. I used 30 paired, one m^2 quadrats for each tract. One quadrat for each pair was placed around a target plant and the other quadrat was placed randomly 2 m away (Fig. 2). Ten plants of each study species, *A. scoparius* (ANSC), *A. gerardii* (ANGE), and *S. nutans* (SONU) were designated as target plants in a tract. I then estimated percent basal area cover by species and recorded the number of species (richness) and the number of plants of each species (abundance) in a quadrat. The smallest cover value assigned to a species present in a quadrat was 1 %. The target plant was counted in the quadrat data.

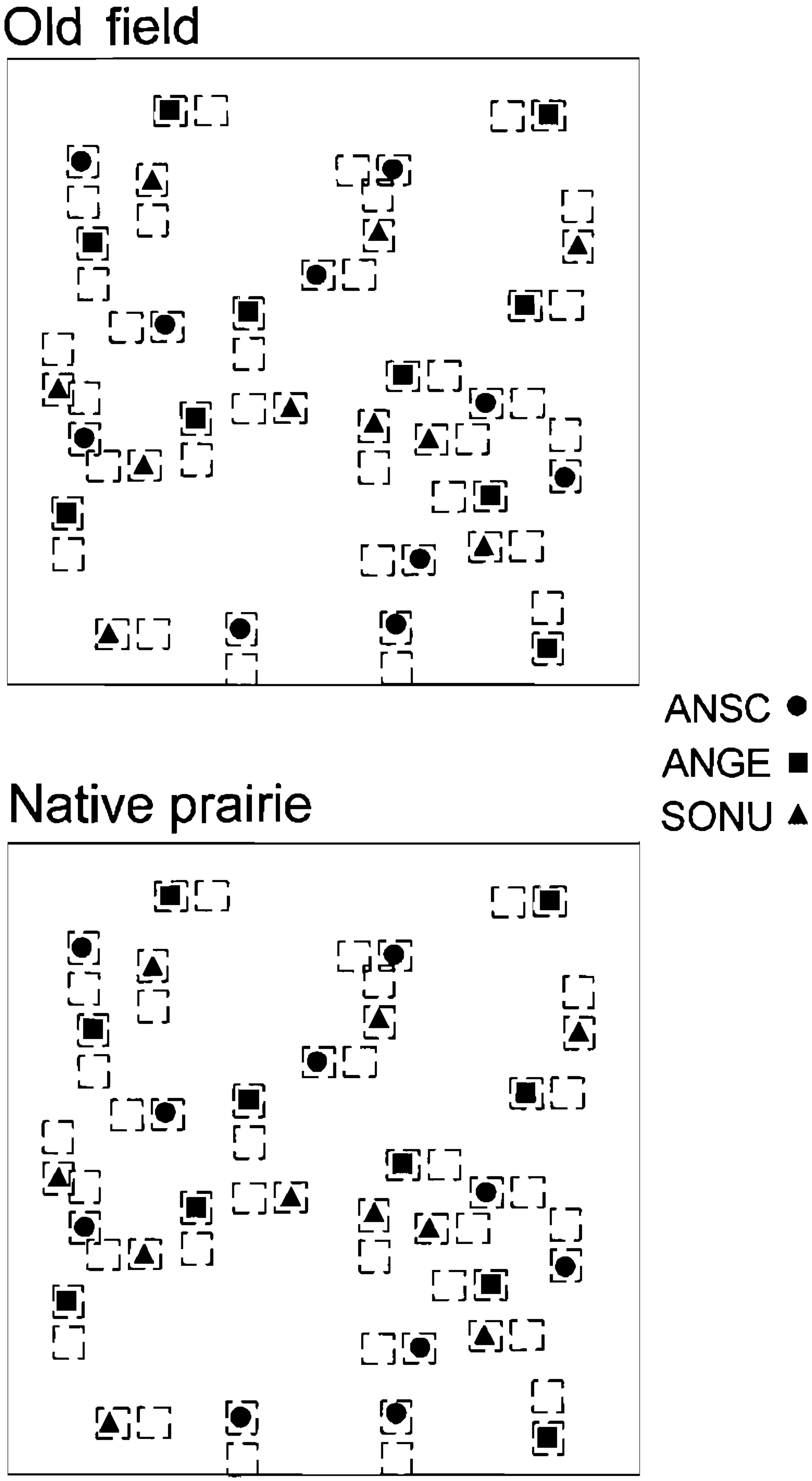
Statistical analyses

Percentage of basal area cover was plotted by species and by cover class and used to compare plant coverage on the old-field and native-prairie tracts. Effects of target plants on species richness in both tracts were analyzed in two ways. First, by a two-level analysis of variance (ANOVA) to determine the effects of tract, the number of species in the quadrats, and a tract by grass species interaction (Sokal and Rohlf 1981; SYSTAT 1992). Second, I used paired t-tests to examine the effects of the presence of each target species on total species richness in a quadrat. To obtain diversity estimates, I used Brillouin's Index as a measure of species richness, as well as, species eveness:

$$H = 1/N \log N!/N_1!\, N_2! \ldots\ldots. N_S!,$$

$$J = H/H_{MAX},$$

FIG. 2. Research design for community composition based on paired, one m^2 quadrats for old field and native prairie


Old field
Native prairie
ANSC ●
ANGE ■
SONU ▲

where N = the number of individuals in the sample and N_2 = the number of the *i*th species for $i = 1, \ldots, S$ (Zar 1984). I used Brillouin's Index because the target plant data were obtained non-randomly. H is an approximation of H' (the Shannon-Wiener measure of diversity), however, the values are always smaller and H is considered an appropriate measure for small finite plot samples (Pielou 1977; Krebs 1989). I used a two-level ANOVA of species diversity to test for the effects of tract, grass species, and a tract by grass species interaction followed by a paired t-test on species diversity in target plant and random quadrats in each tract.

My research design imposed limitations on the extent of inferences to be made from the data set. The analysis is valid for the design, however, my results cannot extend beyond direct comparisons between these two systems.

RESULTS

Species richness was greater in the old field (47 species) than in the native prairie (31 species) and the number of species increased with area size for both habitats (Fig. 3). The species-area relationship, i.e., the increase in number of species per increase in area size, (Fig. 4) was similar between the tracts; the slopes of this relationship were similar for each tract. The higher old-field slope value ($z = 0.3449$) indicates that species richness in the old-field tract had a greater increase with area size.

When plants were grouped into perennial grass cover classes, percent cover by *A. gerardii* and *S. nutans* was greater in the native prairie and percent cover by all other perennial grasses was greater in the old field (Fig. 5). *A. scoparius* did not seem to be as extensive a cover component of either tract, as previously observed, but did occupy slightly more area in the old field. When cover variables were grouped into cover classes, coverage by the three target species, standing dead target grasses, and

FIG. 3. Cumulative species richness versus area size as determined from 100 contiguous one m^2 quadrats for old field and native prairie.

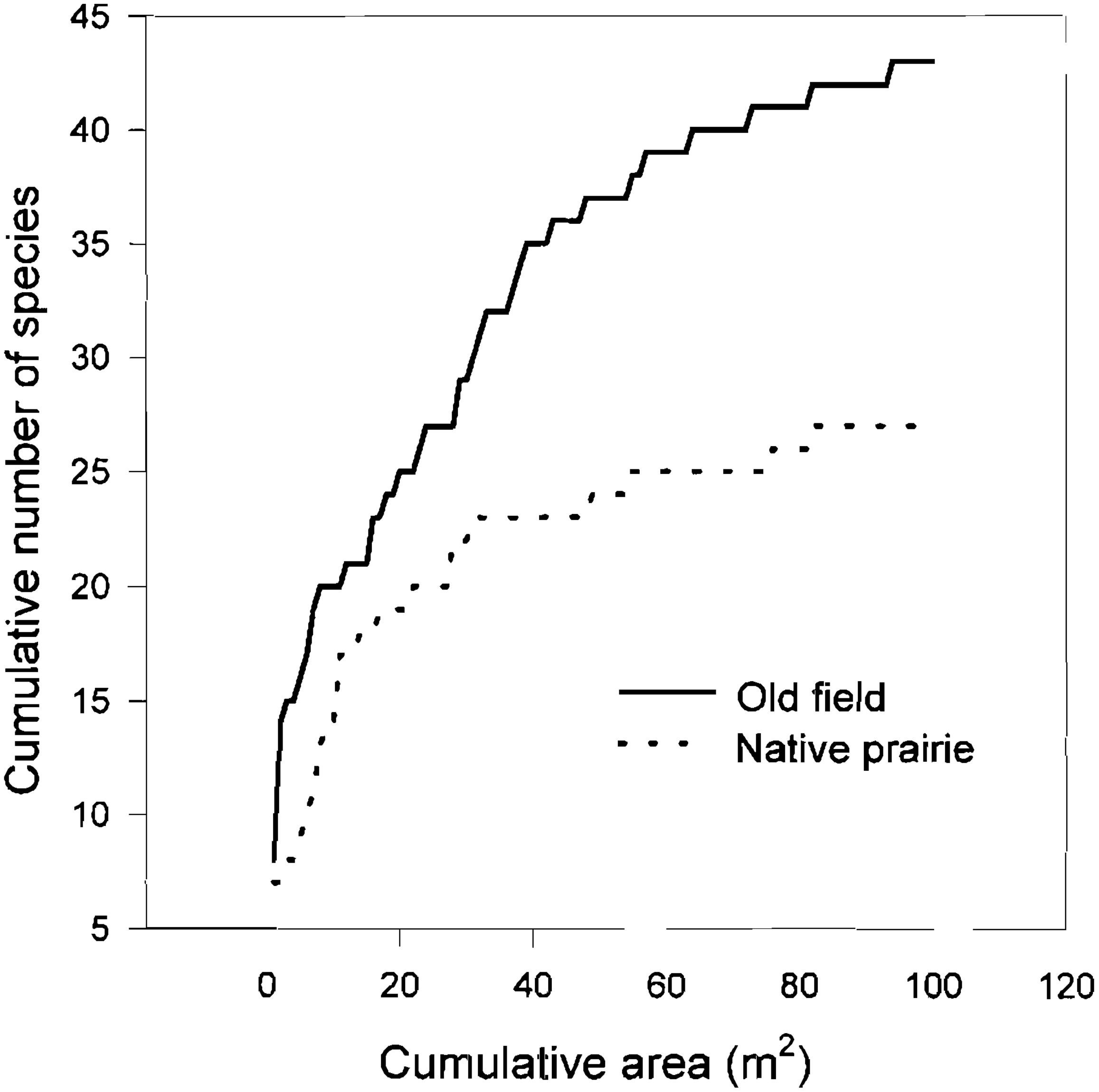

45
40
35
30
25
20
15
10
5
Cumulative number of species
0
20
40
60
80
100
120
Cumulative area (m^2)
Old field
Native prairie

FIG. 4. Common log species richness versus common log area size for old field ($\log S = 0.3449 \log A + 0.9641$) and native prairie ($\log S = 0.3148 \log A + 0.8369$).

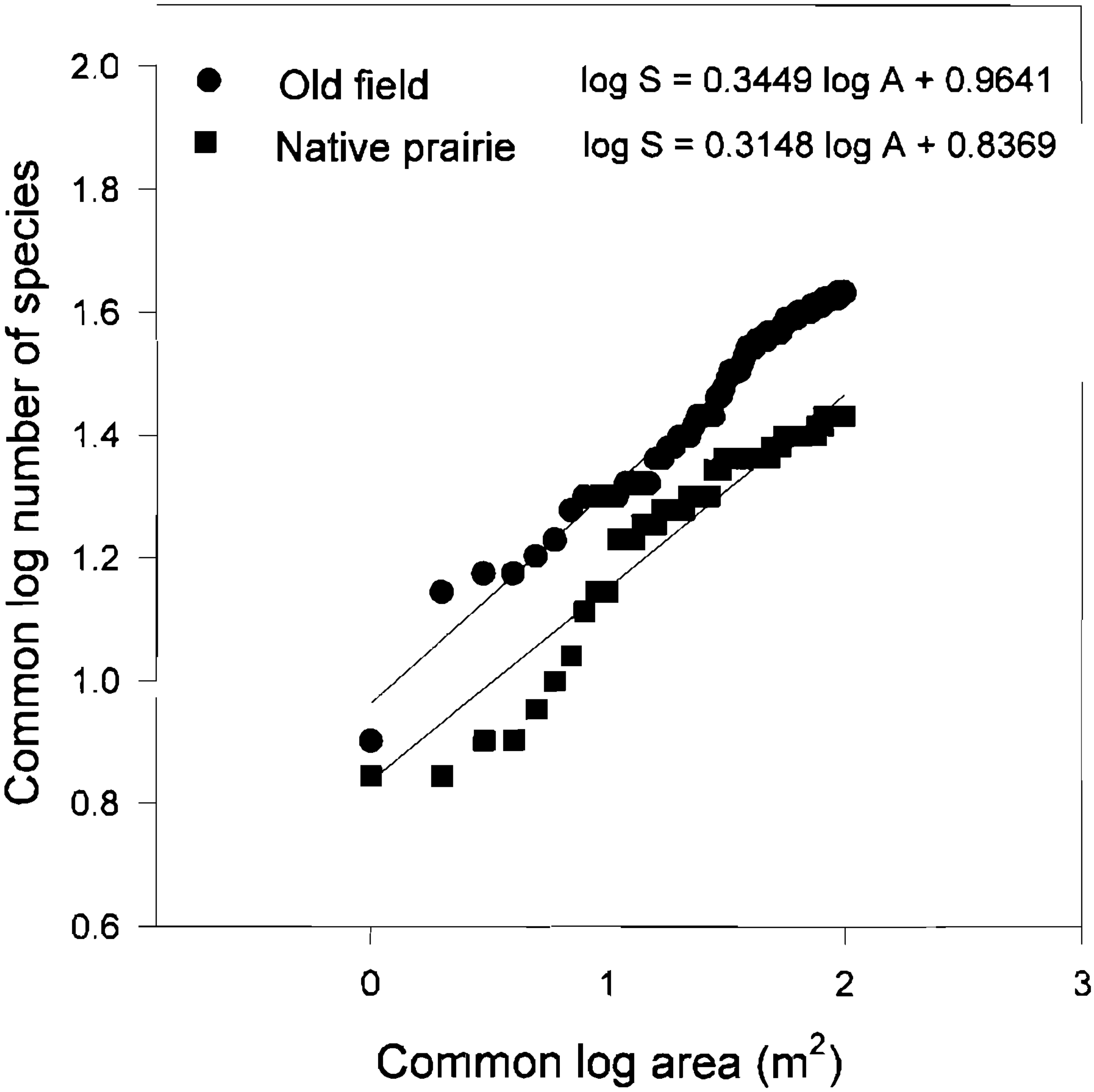
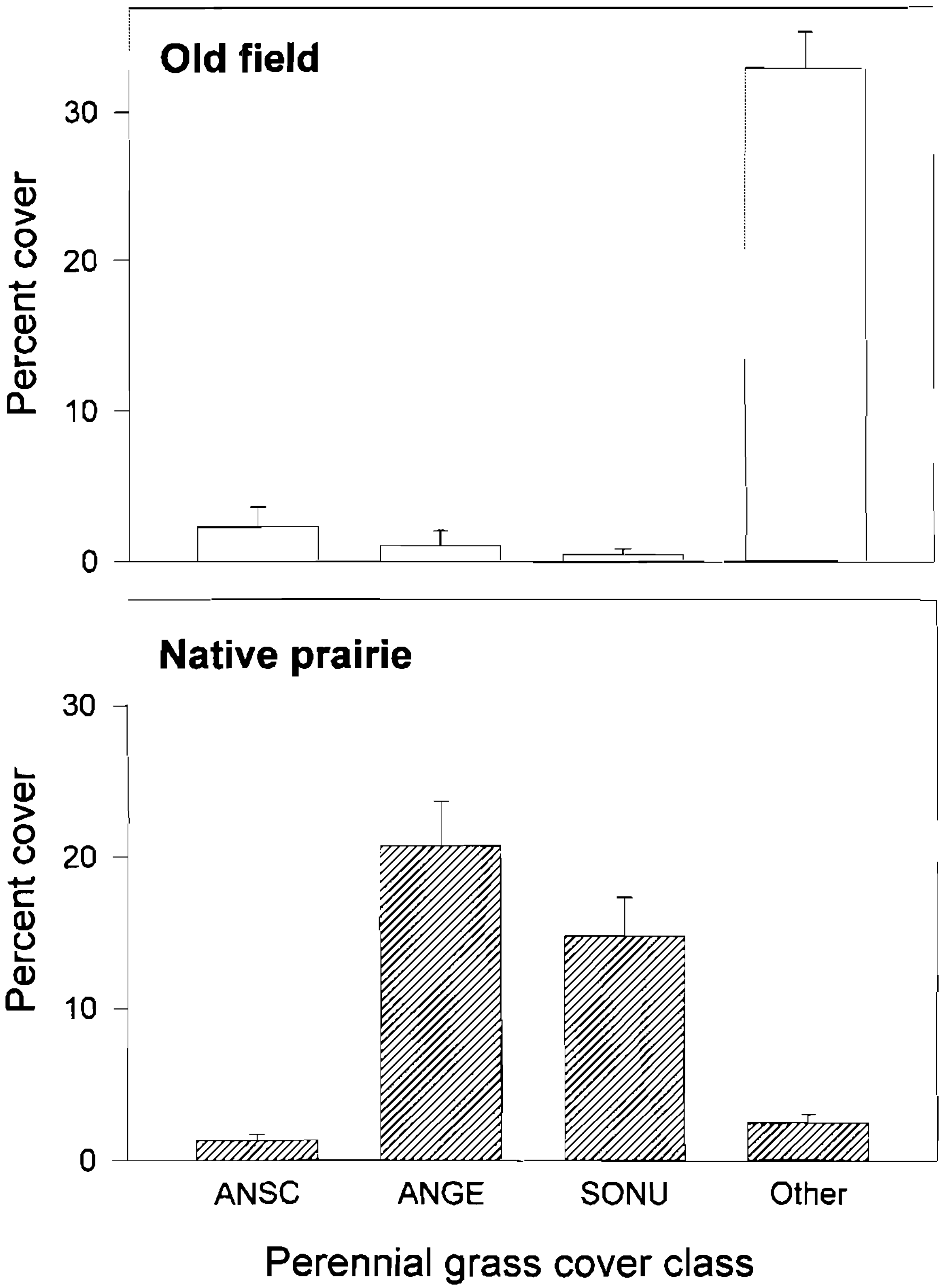

● Old field log S = 0.3449 log A + 0.9641
■ Native prairie log S = 0.3148 log A + 0.8369
Common log number of species
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0
1
2
3
Common log area (m^2)

FIG. 5. Percent coverage by perennial grass cover classes for old field and native prairie. Cover classes are for target species (*A. scoparius*, *A. gerardii*, and *S. nutans*) and for other grouped perennial grasses.


Old field
Native prairie
Percent cover
Percent cover
0
10
20
30
ANSC
ANGE
SONU
Other
Perennial grass cover class

litter was greater in the native prairie while non-target grass species and bareground coverage was greater in the old field (Fig. 6).

The presence of a target plant was correlated with decreased species richness in the old field but not in the native prairie (Fig. 7). Tract had a highly significant effect on species richness in both target plant ($F = 20.61$; $df = 1,54$; $P < 0.001$) and random quadrats ($F = 74.82$; $df = 1,54$; $P < 0.001$) (Table 1). A significant tract by grass species interaction for random quadrats $F = 3.23$; $df = 2,54$; $P < 0.05$) and a marginally significant interaction for quadrats with target plants ($F = 2.873$; $df = 2,54$; $P < 0.1$) indicated species richness may be responding more to the presence of *S. nutans* than to *A. scoparius*. In the old field, there were significantly fewer species in target quadrats with *A. scoparius* ($T = 3.47$; $df = 9$; $P < 0.01$) and *S. nutans* ($T = 4.25$; $df = 9$; $P < 0.01$) (Table 2). There were no differences between paired quadrats in the native prairie.

The presence of a target plant of all three species also was correlated with decreased species diversity in the old field but not in the native prairie (Fig. 8). Tract had a highly significant effect on species diversity in both target plant ($F = 26.283$; $df = 1,54$; $P < 0.001$) and random quadrats ($F = 99.59$; $df = 1,54$; $P < 0.001$) (Table 3). The tract by grass species interaction was significant for random quadrats ($F = 7.04$; $df = 2,54$; $P < 0.002$) but not for the target plant quadrats. There was lower species diversity in target plant quadrats with *A. scoparius* ($T = 2.434$; $df = 9$; $P < 0.05$) and *S. nutans* ($T = 5.54$; $df = 9$; $P < 0.001$) in the old field than in the native prairie (Table 4). Percentage of cover by *A. gerardii* and *S. nutans*, standing dead grasses, and litter was greater in the native prairie and percentage of perennial grasses other than the target species was greater in the old field for both target plant and random quadrats (Fig. 9).

FIG. 6. Percent coverage by all cover classes for old field and native prairie. Cover classes include perennial grasses, annual grasses, perennial forbs, annual forbs, shrubs, litter, standing dead grasses, rock, and bareground.

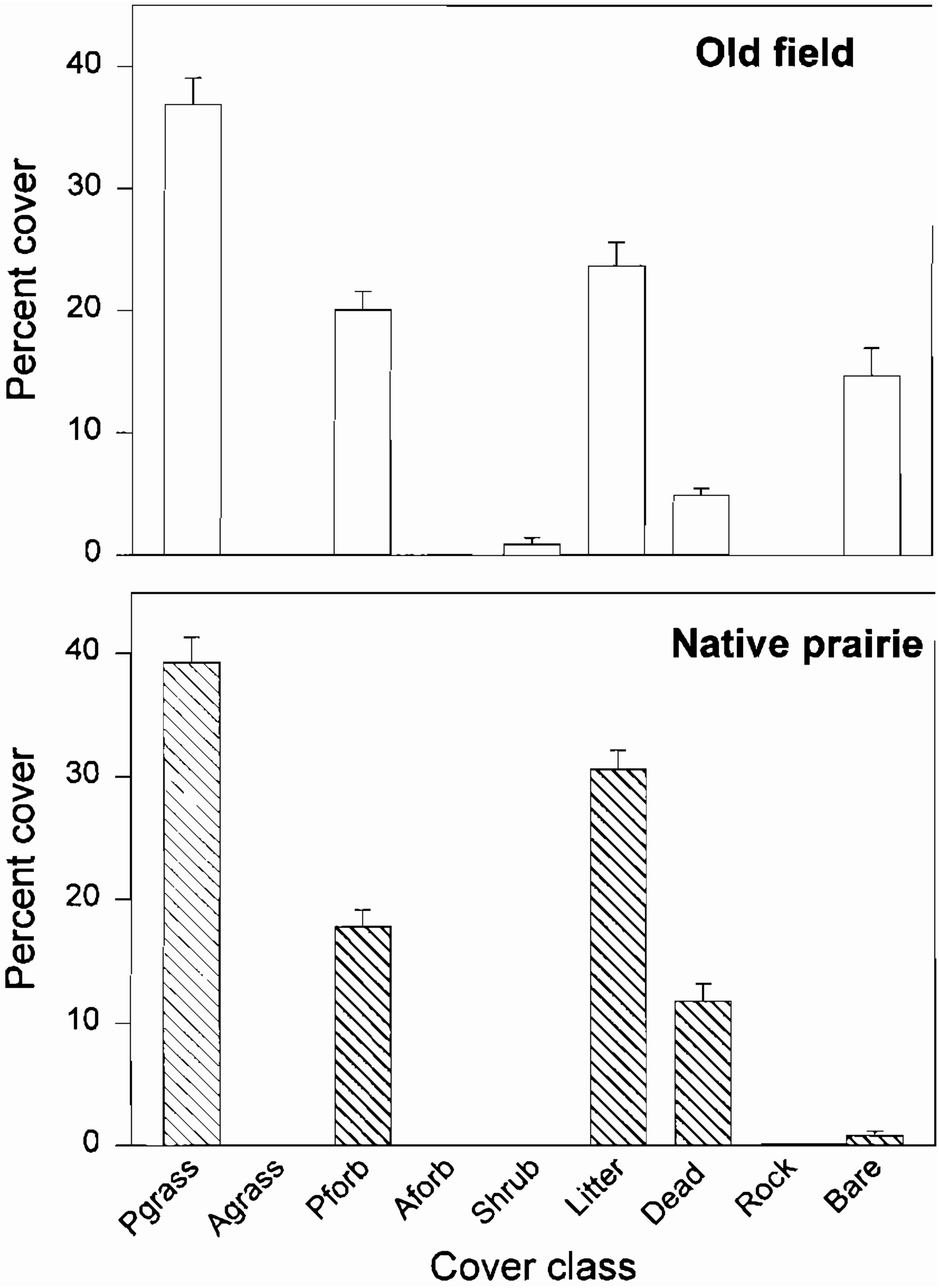

Old field
Native prairie
Percent cover
Percent cover
0
10
20
30
40
Pgrass
Agrass
Pforb
Aforb
Shrub
Litter
Dead
Rock
Bare
Cover class

FIG. 7. Effect of tract on species richness in target plant and random quadrats for *A. scoparius*, *A. gerardii*, and *S. nutans*. See Table 1 for significant P values and Table 2 for significant multiple comparisons.

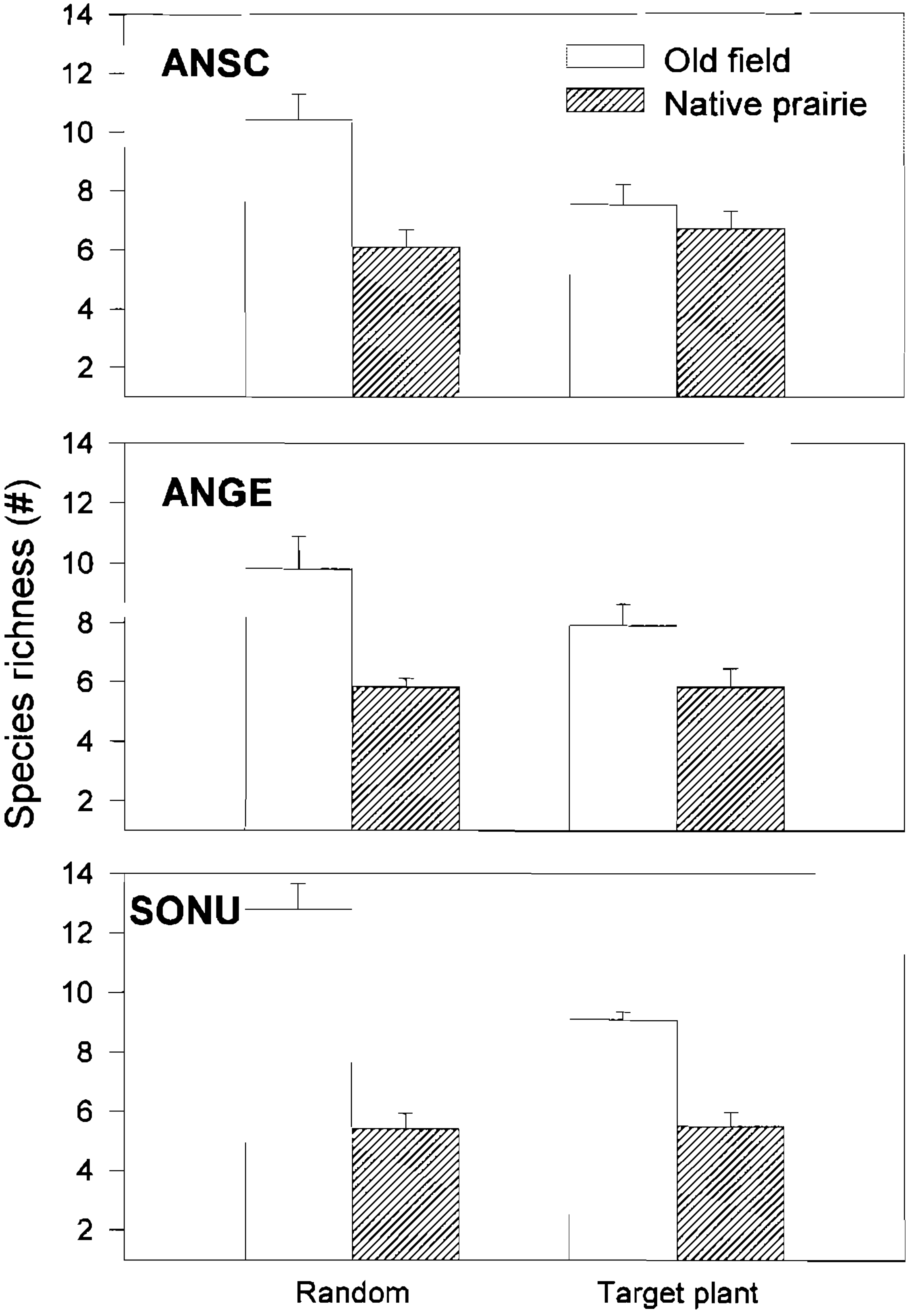

ANSC
ANGE
SONU
Old field
Native prairie
Species richness (#)
14
12
10
8
6
4
2
Random
Target plant

Table 1. Two-level ANOVA of species richness (species #) for random and target quadrats.

Source of variation	df	SS	MS	F	P
Random					
Tract	1	410.817	410.817	74.820	< 0.001***
Grass species	2	17.433	8.717	1.588	0.214 ns
Tract X Species	2	35.433	17.717	3.227	0.047 *
Error	54	296.500	5.491		
Target plant					
Tract	1	70.417	70.417	20.610	< 0.001***
Grass species	2	2.033	1.017	0.298	0.744
Tract X Species	2	19.633	9.817	2.873	0.065 +
Error	54	184.500	3.417		

ns = non-significant, + P < 0.100, * P < 0.050, ** P < 0.010, *** P < 0.001

Table 2. Paired t-test for species richness (species #) for each grass species in each tract.

Tract	Species	Mean difference	df	T	P
Old field	ANSC	2.900	9	3.469	0.007 **
	ANGE	1.900	9	1.272	0.235 ns
	SONU	3.700	9	4.254	0.002 **
Native prairie	ANSC	-0.600	9	-0.709	0.496 ns
	ANGE	0.000	9	0.000	1.000 ns
	SONU	-0.100	9	-0.176	0.864 ns

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 8. Effect of tract on species diversity (Brillouin H) in target plant and random quadrats for *A. scoparius*, *A. gerardii*, and *S. nutans*. See Table 3 for significant P values and Table 4 for significant multiple comparisons.

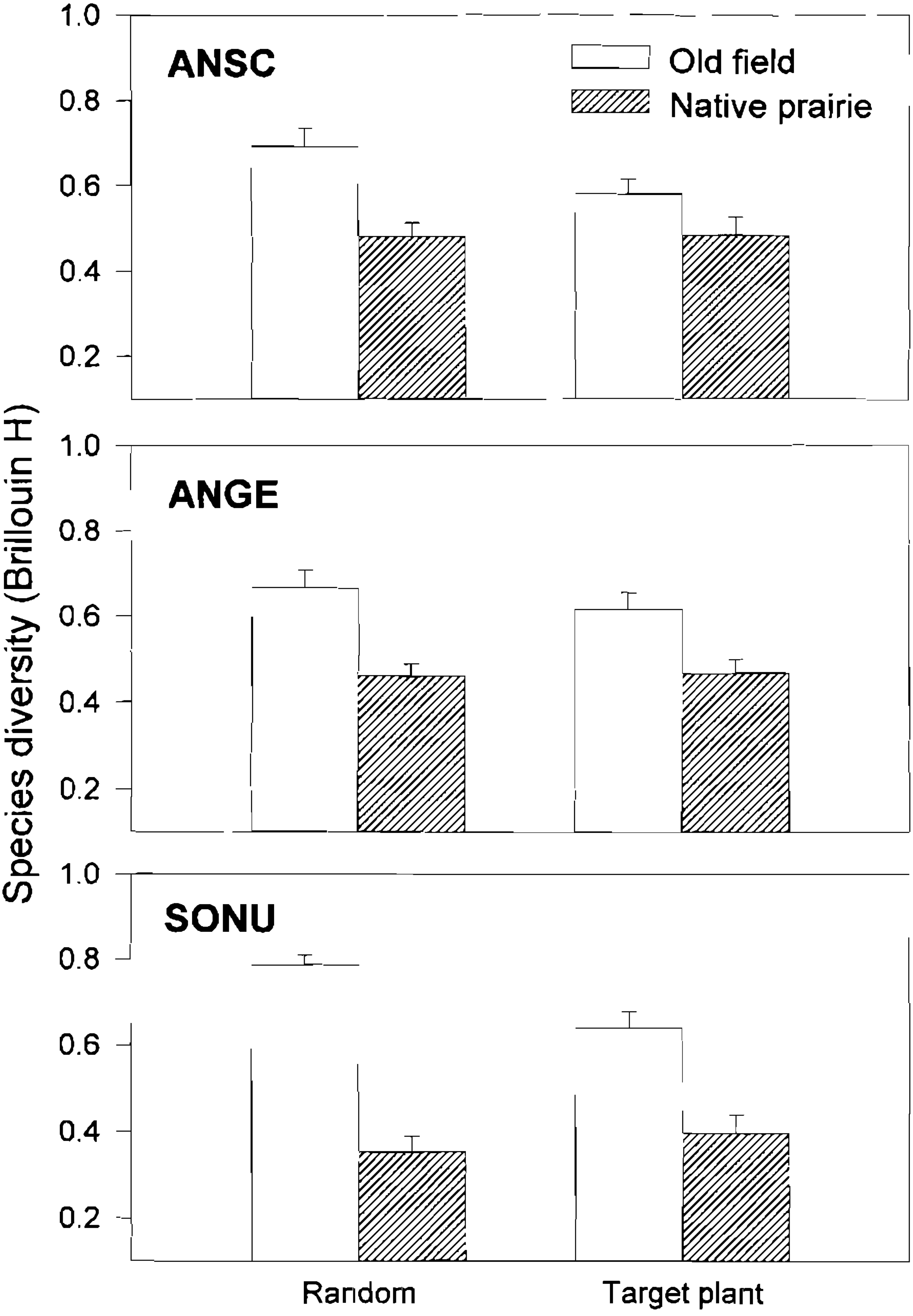

ANSC
ANGE
SONU
Old field
Native prairie
Species diversity (Brillouin H)
1.0
0.8
0.6
0.4
0.2
Random
Target plant

Table 3. Two-level ANOVA of species diversity (Brillouin H) for random and target quadrats.

Source of variation	df	SS	MS	F	P
Random					
Tract	1	1.210	1.210	99.588	< 0.001***
Grass species	2	0.006	0.003	0.227	0.798 ns
Tract X Species	2	0.171	0.086	7.042	0.002 **
Error	54	0.656	0.012		
Target plant					
Tract	1	0.402	0.402	26.283	< 0.001***
Grass species	2	0.005	0.003	0.175	0.840 ns
Tract X Species	2	0.057	0.028	1.860	0.166 ns
Error	54	0.826	0.015		

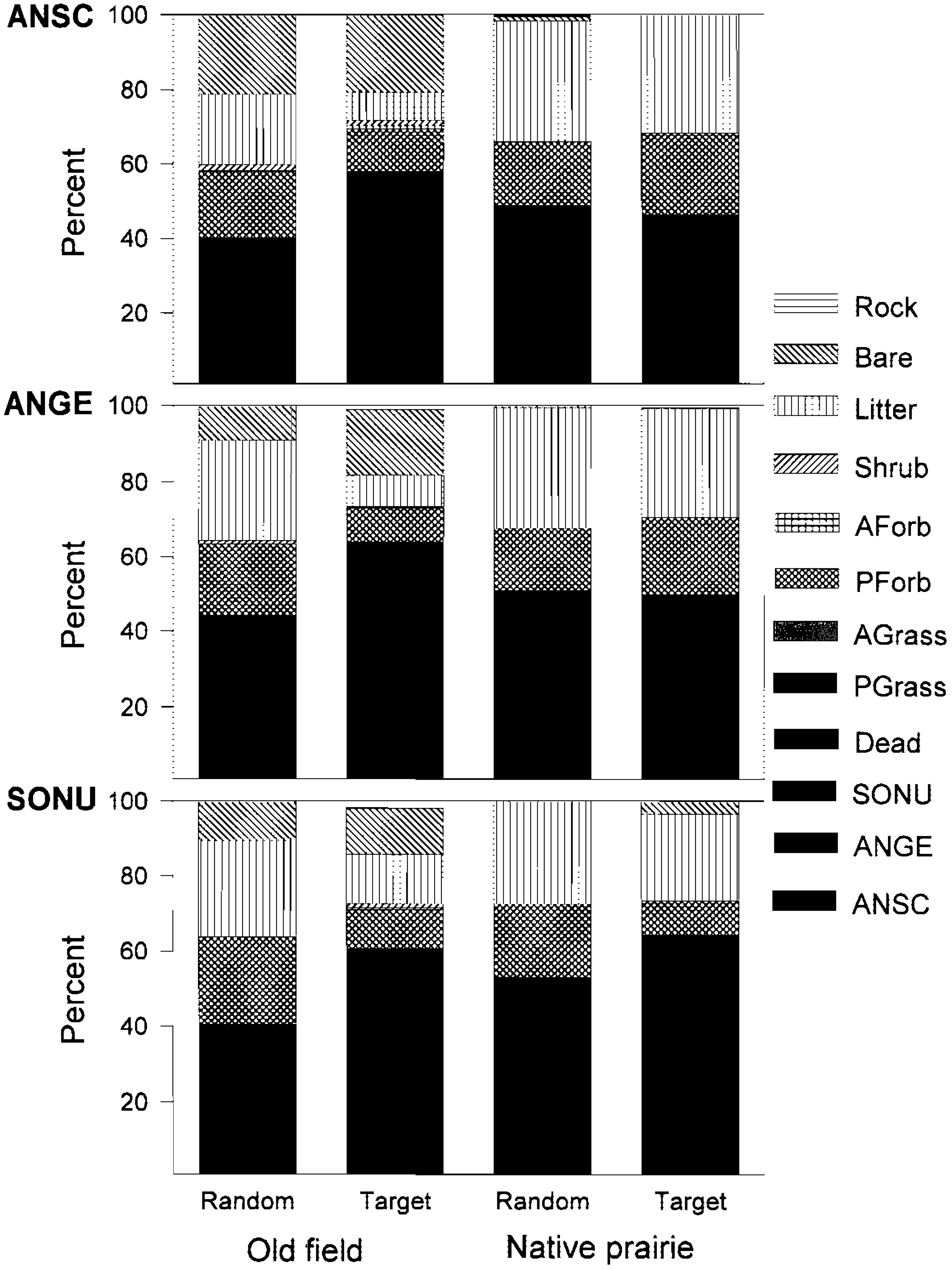
ns = non-significant, + P < 0.100, * P < 0.050, ** P < 0.010, *** P < 0.001

Table 4. Paired t-test for species diversity (Brillouin H) for each grass species in each tract.

Tract	Species	Mean difference	df	T	P
Old field	ANSC	0.112	9	2.434	0.038 *
	ANGE	0.051	9	0.695	0.505 ns
	SONU	0.145	9	5.535	< 0.001***
Native prairie	ANSC	-0.002	9	-0.034	0.973 ns
	ANGE	-0.006	9	-0.132	0.898 ns
	SONU	-0.044	9	-0.753	0.470 ns

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 9. Percent coverage by all cover classes in target plant quadrats with *A. scoparius*, *A. gerardii*, or *S. nutans* and random quadrats for old field and native prairie.


ANSC
ANGE
SONU
Percent
100
80
60
40
20
Rock
Bare
Litter
Shrub
AForb
PForb
AGrass
PGrass
Dead
SONU
ANGE
ANSC
Random
Target
Random
Target
Old field
Native prairie

DISCUSSION

The change in species composition from old field to native prairie suggests changes in patterns of species richness and abundance over time. I found more species and greater abundance per species in the old field, however, I also found fewer species in the presence of target plants. These target-plant competitors may be able to influence species richness in the old field community. As better-competitors are introduced in a succession they may affect the ability of other plants to grow and survive (Wilson and Keddy 1986; Goldberg 1987) and may be an important force in structuring plant communities. Plant diversity increases over successional time (Bazzaz 1975; Tilman 1988), but eventually must give way to the greater productivity of dominant species in a later-stage environment (Tilman et al.1996).

Higher species richness in the old field may have been due to less influence from some competitors in a mid-successional stage. Mid-successions may retain aspects of the disturbances that initiated and structured them, and thus may be a stressful environment for plants (Grime 1979). Mid-successions are also a spatially-patchy environment where colonizers are under less competitive influence (Grime 1977; Wilson and Keddy 1986). *Solidago* spp. were poorer competitors in a mid-successional old field than they were in a late-successional prairie (Werner and Platt 1976). In early successions, Miller and Werner (1987) and Miller (1994) found differential competitive effects and responses of plants resulted from hierarchies of competitive ability in which competitive influence varied by species.

The species unit increase with area size, was similar for each habitat, but the higher species richness in the old field, indicates that colonizing species were being added. Species composition of grasses, forbs, and shrubs varied between the two tracts. Old-field species were disturbance-prone range increasers, as well as, some of the prairie species. In contrast, native-prairie species were only those associated with a near-climax tallgrass prairie. Species richness differences were probably due to the higher number of perennial forbs and shrubs coming into the old field.

The species-area relationship may not be the most appropriate way to describe these changes (Connor and McCoy 1979) because different successions represent different time scales. Species richness may have declined over a much longer time in the native prairie. The relationship of species number to area size may indicate that species richness increases in a succession and then eventually levels off resulting in fewer species because the abundance of individuals has increased (Bazzaz 1975; Tilman 1988). However, the species-ecological time relationship has not been applied to succession data to determine these patterns for North American grasslands (Rosenzweig 1995; Arenz and Joern 1996).

The calculated z values for both sites fall within the range for habitat islands (0.17-0.72) (Begon et al.1996). Mainland z values should be lower (0.10-0.16). Rosenzweig (1995) suggests that small tract size creates problems in interpreting species-area data and that m^2 quadrats used by plant researchers may not be large enough to adequately include all species present in a community and certainly not all those represented on a regional scale. Adjacent disturbed areas, e.g., roads, residential property, and agricultural land, may also influence species richness by limiting recruitment possibilities for plants.

Greater cover by two of three target grasses in the native prairie and by other perennial grasses in the old field is consistent with predicted patterns of more colonizing species with fewer competitive interactions in a mid-successional stage. *A. scoparius*, the third target species, was not highly abundant in the native prairie but was a slightly more abundant colonizer in the old field in my study. Abundance of perennial-grass and perennial-forb cover classes was high, but the species composition of the most abundant species varied between the tracts. In an old-field study in Minnesota, proportion of species in the highest abundance category declined with field age and the presence of *A. scoparius* and *A. gerardii* reduced the abundance of other species (McGinley and Tilman, in press).

Cover by the more abundant non-target grasses in a mid-successional stage may be due to fewer direct interactions between plants or low nitrogen availability in soils which limits plant growth, both characteristics of disturbed habitats (Grime 1979). Basal cover, in terms of biomass of seven grasses, was suppressed in disturbed or infertile habitats and competition declined along a gradient of increased disturbance in pure-stand and additive experimental plots (Campbell and Grime 1992).

Cover by other perennial species in the native prairie may be reduced by the abundance of the target species, *A. gerardii* and *S. nutans*. These plants also inhibit the biomass of other species by senescing into standing dead stems and litter that remain on the prairie until removed by fire or recycled by slow decomposition (Kucera et al. 1967; Abrams et al. 1986). Knapp and Seastedt (1986) studied the effects of fire on the tallgrass prairie in Kansas and found litter and standing dead grasses limited species richness and abundance. Productivity was also reduced because soil temperatures under dead plant material were low enough to slow growth (Rice and Parenti, 1978).

The presence of a target grass was correlated with a less species-rich neighborhood in the old field but not in the native prairie. Old-field target plants had large crowns, but they gained competitive effect from their higher proportion of roots to tillers. Root:shoot ratios increased with old-field age in studies by Mellinger and McNaughton (1975) and Newell and Tramer (1978). Target species probably allocate more of their nutrient resources to root development (Gleeson and Tilman 1990) and have increased capacity for carbohydrate and mineral storage. The ability to maintain seasonal storage of nitrogen and carbohydrates enhances productivity the following year (McKendrick et al. 1975; Woodmansee et al. 1978). Early spring growth is supported by carryover reserves, giving these grasses a competitive advantage with C_3 grasses.

Native C_4 grasses may be superior competitors in nitrogen-poor soils; *A. scoparius* and *A. gerardii* were competitive dominants for nitrogen on impoverished soils at Cedar Creek Natural History Area in Minnesota (Tilman and Wedin 1991 a,b). Prairie grasses have conservative mechanisms for nitrogen uptake and may be successful in low nitrogen environments. Turner and Knapp (1996) found C_4 dominant grasses had low water and nitrogen requirements. Rice and Pancholy (1972) reported more energy-efficient use of nitrogen by tallgrass prairie grasses. C_4 grasses use ammonium nitrogen directly in a chemical short-cut process of assimilation that saves four conversion steps.

Prairie grasses may also secure nitrogen through association with free-living bacteria on or near their root surfaces. High numbers of these nitrogen-fixing bacteria may be present in the rhizosphere, particularly in the early spring under near-saturated moisture conditions. In testing for nitrogenase, the enzyme system that mediates bacterial reduction of atmospheric nitrogen to ammonium for plant use, Blew (1984) found activity was enhanced eight fold under low oxygen levels for *A. gerardii*. Additional nitrogen, early in the growing season, may partially explain high productivity in these dominant grasses.

These grasses may gain an additional competitive edge because they produce allelopathic tannins. Rice and Pancholy (1973) found that tannins inhibit nitrifying bacteria that convert ammonium nitrogen to nitrate and lower the availability of nitrogen for plants that require nitrate.

The presence of a target grass was also correlated with lower neighborhood species diversity in the old field. Ecological diversity adds the component of the eveness with which individuals are apportioned as a correlate of species richness (Pielou 1977). Competitive ability of plants may be a factor in reducing the diversity of neighbors but it is by no means certain that this had actually happened during my study.

In the old field early colonizers were few, and had been replaced by perennial grasses and forbs characteristic of mid succession. In the late-successional prairie *A. gerardii* and *S. nutans* were far more abundant and the species richness and diversity of other perennials were reduced. If competition drives a nitrogen limited system (Tilman and Wedin 1991a,b), the prairie codominants may be the better competitors because they invest resources in massive root systems (Weaver 1958) and are able to garner light by growing taller than competing species (Tilman 1982).

A decline in species richness and average abundance per species might then be expected as these better competitors begin to take over during a mid-successional stage. *A. gerardii* and *S. nutans* have gained a competitive foothold in the old field but they are not yet widespread. *A. scoparius,* however, is more abundant in the old field than in the native prairie and may be a more successful competitor in a mid-successional environment.

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CHAPTER 2

LIFE HISTORY VARIATION IN THREE PRAIRIE GRASSES

INTRODUCTION

Life history traits include phenotypic traits such as growth rate, age at first reproduction, size at first reproduction, reproductive effort, and life time reproductive success. Such life history traits have a direct influence on the fitness of an individual (Venable 1984; Stearns 1992) and thus, are subject to strong selective pressures that can generate patterns of local adaptation among different populations. Differences in these patterns of life history trait expression among populations may reflect differences in local environments, as well as the history of colonization of the different populations. Plants show variation in all aspects of their life histories. One approach to explain the adaptive nature of differences in life history trait expression among different populations of plants has been to compare traits from populations within a species in different habitats where environmental factors differ (moisture: Teeri 1978; Roy and Mooney 1982; Barnes 1985; Platenkamp 1990; nutrients: Kik et al. 1990; Bazzaz and Sultan 1993a; light: Dudynsky 1983; Bazzaz and Sultan 1993b; land use: Van Tienderen and Van der Toorn 1991; and plant density: Law et al. 1977). If life history traits differ with the environment, they may help to explain patterns seen in plant communities, as well as, changes in those communities over time.

Two genetic explanations exist regarding the evolution of locally adapted life history traits. A single genotype may produce an array of environmentally modified phenotypes (phenotypic plasticity; Wright 1931), whose traits are shaped to different patterns of local adaptation over the course of succession. Within a species, one flexible genotype, with traits that can be maintained over different successional stages, could be expected to establish early on and maintain dominance through later stages.

Alternatively, differences in life history patterns at different stages could be due to genetic differentiation between populations in the different habitats.

To examine patterns of local adaptation, I compared life history trait expression in three perennial grasses growing in an undisturbed prairie and in an old-field succession. Two species, *Andropogon gerardii* and *Sorghastrum nutans* are codominants on the native tallgrass prairie and the third, *Andropogon scoparius,* is considered to be a codominant by some researchers, but is more evident on my prairie site only in dry years. All three species are recolonizers in the old field. Because these species are long-lived iteroparous perennials, and not good candidates for age-specific studies, surrogate measures of fitness were used, e.g., growth rates, proportion of plants flowering, and reproductive effort in these grasses.

In this study, I asked three questions. First, has differentiation of life history traits occurred in these two populations? If prairie grasses exhibit life history traits characteristic of long-term stable environments, do these same grasses growing at a mid-successional stage in the old field, show some traits that would be more characteristic of colonizing species? If the prairie produces good competitors and the more recently disturbed old field produces higher fecundity biotypes, as suggested by Solbrig and Simpson (1974, 1977), then the life history traits of these species should be adaptive at either stage. These plants may be good competitors because they are good competitors in any community.

Second, does reproductive effort differ between these populations? Reproductive success involves resource allocation and timing. Reproductive effort is a measure of the investment a plant makes in reproductive propagules, i.e., seeds and seed structures, per total plant biomass (Harper and Ogden 1970; Thompson and Stewart 1981). Grasses in the native prairie may allocate more resources to growth and vegetative tissue (Grime 1979) because in a competitive regime a ramet (tiller) or a root that receives essential nutrients is more likely to survive than a seedling. Old-field grasses may allocate more plant tissues to reproduction because seedlings are more likely to survive in a more disturbed and open environment (Fenner 1985).

Third, if two populations have different life history traits, are these differences the result of phenotypic plasticity? Traits are the result of phenotypic plasticity if they are environmentally induced. Genetically identical plants may express different traits if their growth environments differ. Traits may also vary because each population contains genetically distinct individuals. I used a common garden design, where plants from both populations were grown under uniform conditions, to determine whether plant response was due to plasticity or genetic differences. If plants from the two populations converge on similar expressions of life history traits in the common garden, this would suggest that differences in these traits measured in the field were due to plasticity rather than strong genetic differentiation between the two populations (Clausen et al. 1948). Alternatively, if the field-observed differences persist among common garden plants, this suggests that genetically-based differences exist between these two populations.

I tested three hypotheses that may explain how plant strategy differs with successional stage. H_{A2}: Grasses in a mid-successional old field have different patterns of life history trait expression than in the near-climax community. H_{02}: These strategies will not vary at either stage. I analyzed growth rate, basal area plant coverage, and proportion of plants flowering in old-field and native-prairie populations. H_{A3}: Grasses in a mid-successional old field have greater reproductive effort than in the near-climax community. H_{03}: Reproductive effort is the same at either successional stage. I compared reproductive biomass per total plant biomass for both populations. H_{A4}: Grasses in a mid-successional old field have different traits than in the near-climax community when grown in a common environment. H_{04}: Life history traits are the same for either population. I measured mass dry-weight of plant, tiller height, and number of tillers for the common garden plants and compared these statistically between the two sites to distinguish between these different hypotheses.

METHODS

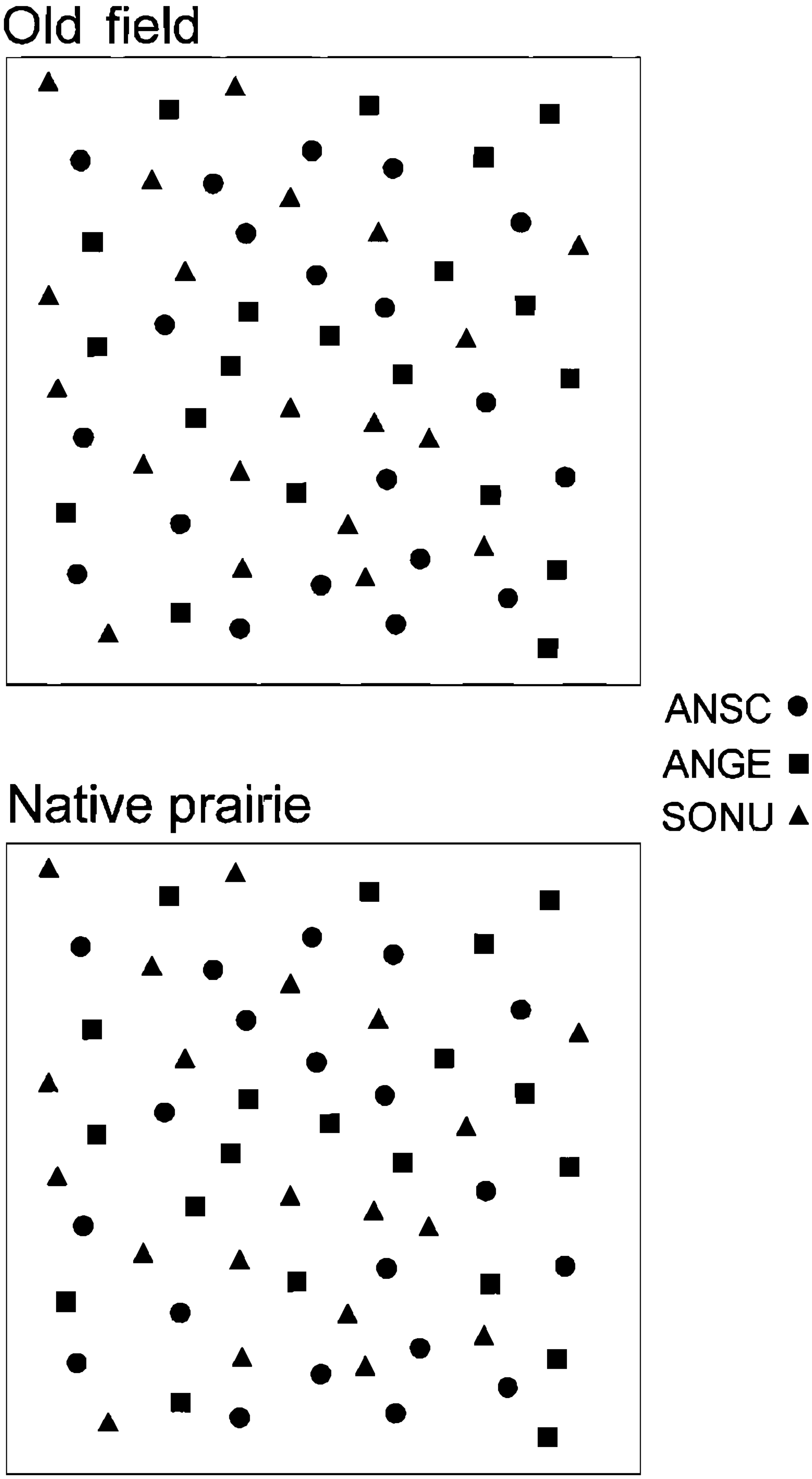
Growth field methods

All traits were measured at the level of the phenotype. A plant was considered to be a discrete crown or module that consisted of all the developmental products of a single apical meristem (Harper and White 1974; Horn 1979; White 1980; Harper 1981). This designation was used because a genet may be extensive in a prairie and the boundaries of a genetic individual are hard to define. The grasses measured in the native prairie formed individual clumps and had no conspecific neighbors closer than one m. The old-field grasses measured were isolated bunch grasses with no near conspecifics. Typically grasses of this type are referred to by range managers, as "wolf plants," because of their lone wolf properties.

I measured life history characteristics of 60 plants chosen randomly from each tract, 20 of each study species, *A. scoparius* (ANSC), *A. gerardii* (ANGE), and *S. nutans* (SONU) (Fig. 10). I monitored these same plants throughout the growing seasons of 1994-1995. Plants were individually marked with 4 x 5 in dayglo orange flags that were 1 m tall for good visibility in dense vegetation. Plants in the prairie were more difficult to relocate and were marked in clusters of three species along a transect line. Each cluster was identified by a 1.30 m wire rod topped by a double dayglo flagging strip secured with duct tape.

Growth rates were determined by measuring the height of individual vegetative tillers using a 2 m stick. Plants were measured at 2 wk intervals from 5 July through 30 September in 1994 and from 4 July through 7 October in 1995. Ten measurements were taken, 6 in a clockwise direction around the outside circumference and 4 from the interior of each plant. The rate of growth was calculated using mean height per

FIG. 10. Research design for growth rates and reproductive effort measurements for old field and native prairie. Target plants are *A. scoparius*, *A. gerardii*, and *S. nutans*.


Old field
Native prairie
ANSC ●
ANGE ■
SONU ▲

measuring interval while the plant was actively growing. These means were compared between tracts for each species. Vegetative growth rates were also compared between years by determining the basal area plant size at the end of a growing season. A diameter was measured from four different directions and the average obtained was used in the equation:

$$A = \pi r^2,$$

where A = area, π = pi, and r = radius, to calculate basal area for each plant.

Flowering status was determined from the proportion of plants that flowered in each tract in 1994 and 1995. The number of plants in flower and the number of reproductive stalks per plant were recorded at each measurement interval for all three species.

Statistical analyses

Growth rates based on height in cm/day were analyzed using a two-level analysis of variance (ANOVA) for each year, to test for effects of tract, grass species, and tract by species interaction (Sokal and Rohlf 1981; SYSTAT 1992). I used Tukey's Honestly Significant Difference (HSD) method as a post-hoc comparison of means for species of grasses. Because growth rates were higher in the native prairie, I wanted to determine which species were growing faster. I analyzed data for both years to compare growth from year to year, using a repeated measures ANOVA where tract and grass species were the main effects and time (year) was the added effect. I also plotted growth curves for each of the three species in the old field and in the native prairie for 1994 and 1995, but because these data were similar between tracts and years, they were not analyzed.

Growth rates based on basal area of plants in cm^2 were analyzed using a two-level ANOVA to compare basal area size difference from 1994 to 1995. Data were natural log transformed to meet the assumptions for normality and homogeneity of variance (Sokal and Rohlf 1981). I tested for the effect of tract, grass species, and their interaction. I omitted 32 plants with negative growth values from the analysis (n = 88). To determine which species exhibited greater growth, I used Tukey's HSD method of multiple comparisons.

I plotted the percentage of plants flowering on each tract in 1994 and 1995. I then compared the results using Fisher's exact test of proportion (two-tailed) for single species per year and for all three species on a tract per year.

Reproductive effort field methods

I harvested aboveground biomass for all study plants on both tracts for 1995, after they had completed flowering and senesced. Plants were clipped at ground level, sorted into sexual and vegetative structures, and tied in bundles. I considered the inflorescence plus the supporting stem down to the first node to be sexual and the remaining stem and leaves to be vegetative (Thompson and Stewart 1981). Each bundle was placed in a paper bag, labeled, and oven-dried at 80^oC for several weeks. Biomass for each part was weighed to the nearest mg on a Mettler P1000 digital balance beam scale.

Statistical analyses

I calculated reproductive effort for each plant, using the equation in Harper and Ogden (1970):

$$RE = \text{Total wt of propagules/Total wt of aboveground biomass},$$

where propagules are sexual reproductive structures (g dry-weight) and biomass is both sexual and vegetative structures (g dry-weight). Effects of tract, reproductive effort of grass species, and interaction of tract by species were tested with a two-level ANOVA. I used Tukey's HSD method to test unplanned means comparisons between species of grasses. To minimize the influence of basal area plant size on biomass, I used a two-level analysis of covariance (ANCOVA) with basal area and mass as covariates. I tested if differences were still due to reproductive effort when I adjusted for the same initial basal plant size.

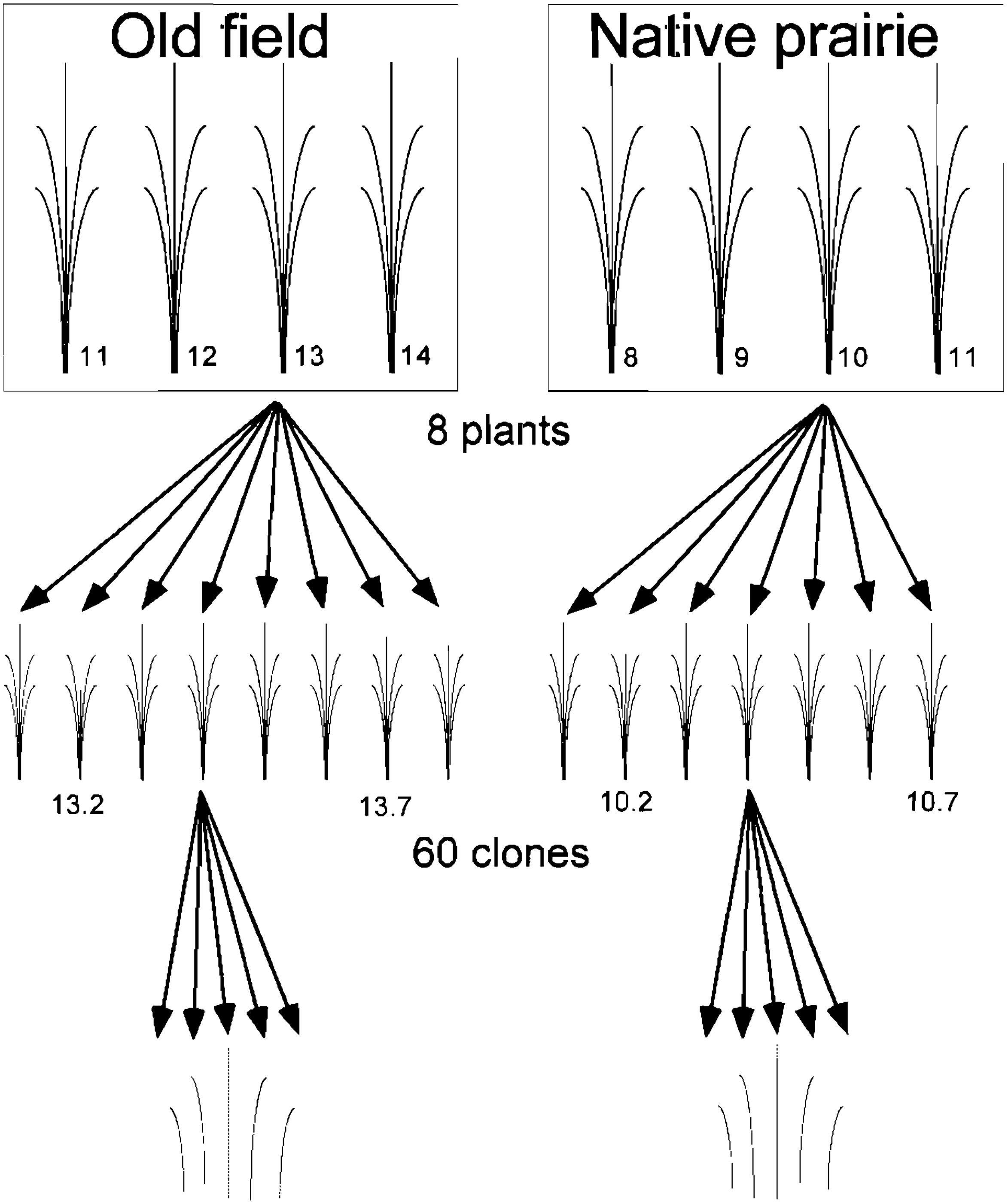
Environmental influence experiment

The purpose of this experiment was to determine if locally adapted populations expressed similar traits when grown in a common environment. I grew tillers cloned from *S. nutans* from both the old field and the native prairie in a greenhouse to simulate the common garden setting. Plants were dug in the field, their roots washed and carefully broken apart. Each tiller was trimmed to 20 cm and planted in Cornell Peat-lite Mix B potting medium in a 6 in pot.

The experimental design (Fig.11) included four plants from each tract, with eight clones of each plant from the old field and seven clones from the native prairie. Each clone was divided into five tillers which served as replicates, however, because some of the tillers died only four tillers for each clone were used in the experiment (n = 60). Pots were placed on a greenhouse bench in a design randomized to include one clone from each plant and each tract for every group. The block design was incomplete, however, and I could not test for a block effect because two groups contained two clones from the same plant.

Environmental conditions on the bench appeared so similar that plants were not rotated during the experiment. Plants were watered twice per week and were not fertilized. They were grown from 20 March until they were harvested on 7 October. I measured final tiller number and tiller height for each plant. I did not harvest roots because, while they were initially selected for uniformity, they were not trimmed to equal size at the start of the experiment. All aboveground biomass was clipped, dried at 80^{o}C, and weighed to the nearest mg.

FIG. 11. Research design for environmental influence experiment for old field and native prairie. Eight *S. nutans* plants were divided into eight old-field clones and seven native-prairie clones with five tillers from each clone as replicates in an incomplete randomized block design. Fifteen tillers died, leaving four replicates per clone (n = 60).


Old field
Native prairie
11
12
13
14
8
9
10
11
8 plants
13.2
13.7
10.2
10.7
60 clones

Statistical analyses

I analyzed final plant biomass, average tiller height, and number of tillers produced, each as a dependent variable in a two-level nested ANOVA with unequal sample sizes (Sokal and Rohlf 1981; SYSTAT 1992). I compared variation between tracts, among plants, and among clones, with clones nested within plants. All data were natural log transformed to meet the assumptions of normality and homogeneity of variance.

RESULTS

Field growth

Growth rates based on height for *A. gerardii* and *S. nutans* were higher in the native prairie than in the old field in 1994, but not in 1995 (Fig. 12). Growth rates for both species in the old field were lower in the dry season of 1994 than in the relatively wetter year of 1995. *A. scoparius* had a lower overall rate of growth on both tracts and showed little difference in growth rate between the two years. Tract had a significant effect on growth rate in 1994 ($F = 4.631$; df = 1,114; $P < 0.05$) but not in 1995 (Table 5). Grasses were growing at significantly different rates in 1995 ($F = 5.23$; df = 2,114; $P < 0.01$) (Table 5). Comparisons of means showed both *A. gerardii* and *S. nutans* grew at significantly faster rates ($P < 0.05$) than *A. scoparius* in 1995 (Table 5). Results of the repeated measures ANOVA (Table 6) confirmed tract had a similar effect on all species, all three species grew at significantly different rates ($P < 0.01$), and native prairie species grew marginally faster. Growth curves for the three species for 1994 and 1995 show native prairie grasses were taller than their counterparts in the old field in 1994, but not in 1995 (Fig. 13).

Basal area plant size for the three species was greater in the old field than in the native prairie for both years (Fig. 14). Old-field plants increased in base size from 1994 to 1995. Tract had a highly significant ($F = 13.08$; df = 1,82; $P < 0.001$)

FIG. 12. Effect of old field versus native prairie on mean growth rates based on plant height for *A. scoparius*, *A. gerardii*, and *S. nutans*. See Table 5 for significant tract effect P values and significant multiple comparisons.

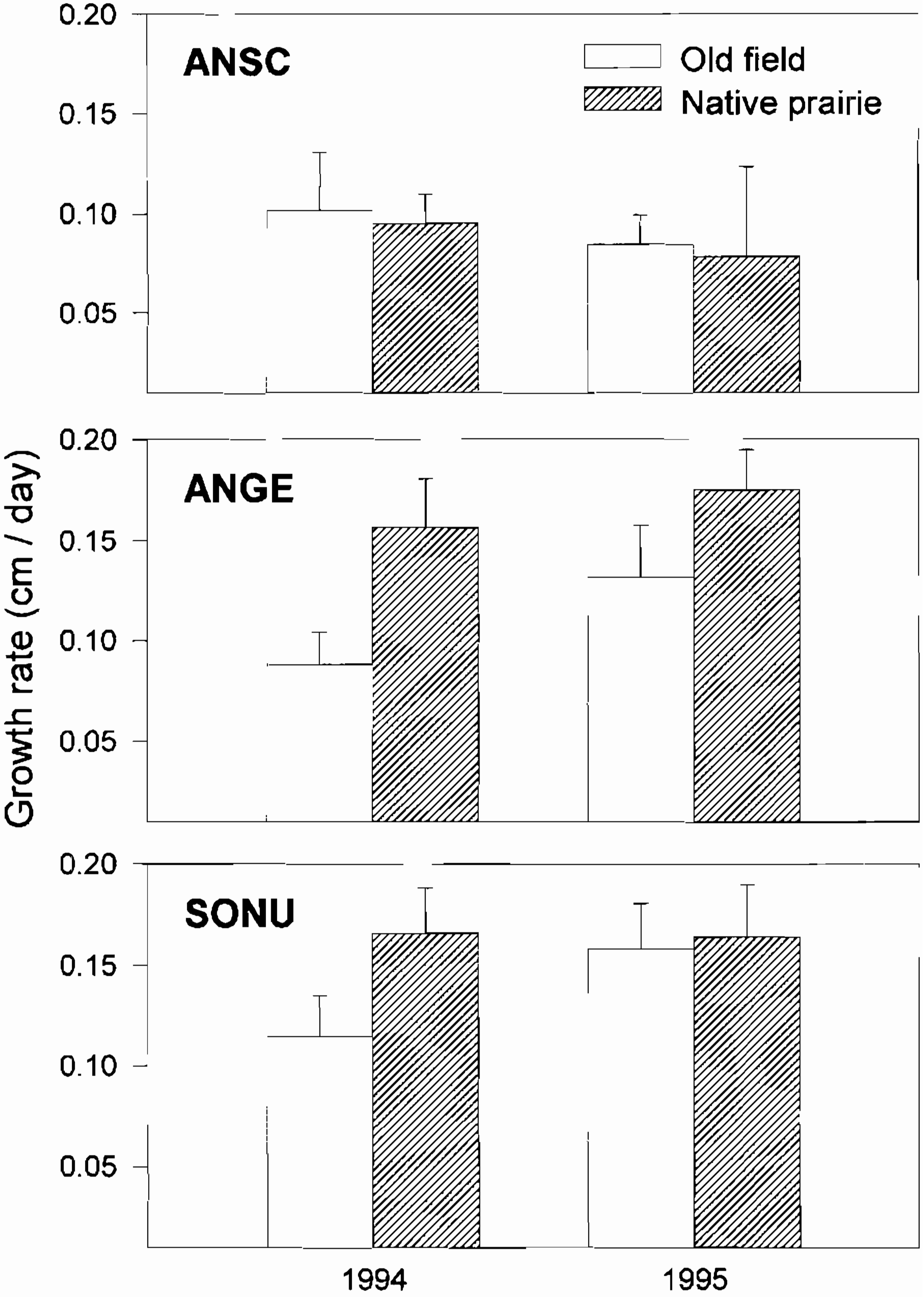

ANSC
ANGE
SONU
Old field
Native prairie
Growth rate (cm / day)
0.20
0.15
0.10
0.05
1994
1995

Table 5. Two-level ANOVA of growth rate (cm /day).

Source of variation	df	SS	MS	F	P
1994					
Tract	1	0.043	0.043	4.631	0.034 *
Grass species	2	0.035	0.018	1.920	0.151 ns
Tract X Species	2	0.031	0.015	1.659	0.195 ns
Error	114	1.052	0.009		
1995					
Tract	1	0.006	0.006	0.422	0.517 ns
Grass species	2	0.155	0.078	5.226	0.007 **
Tract X Species	2	0.013	0.007	0.450	0.638 ns
Error	114	1.695	0.015		

Tukey HSD Multiple Comparison for 1995 growth rate.

Comparison	Mean difference	P
ANGE vs ANSC	-0.072	0.025 *
ANGE vs SONU	0.008	0.954 ns
ANSC vs SONU	0.080	0.011 *

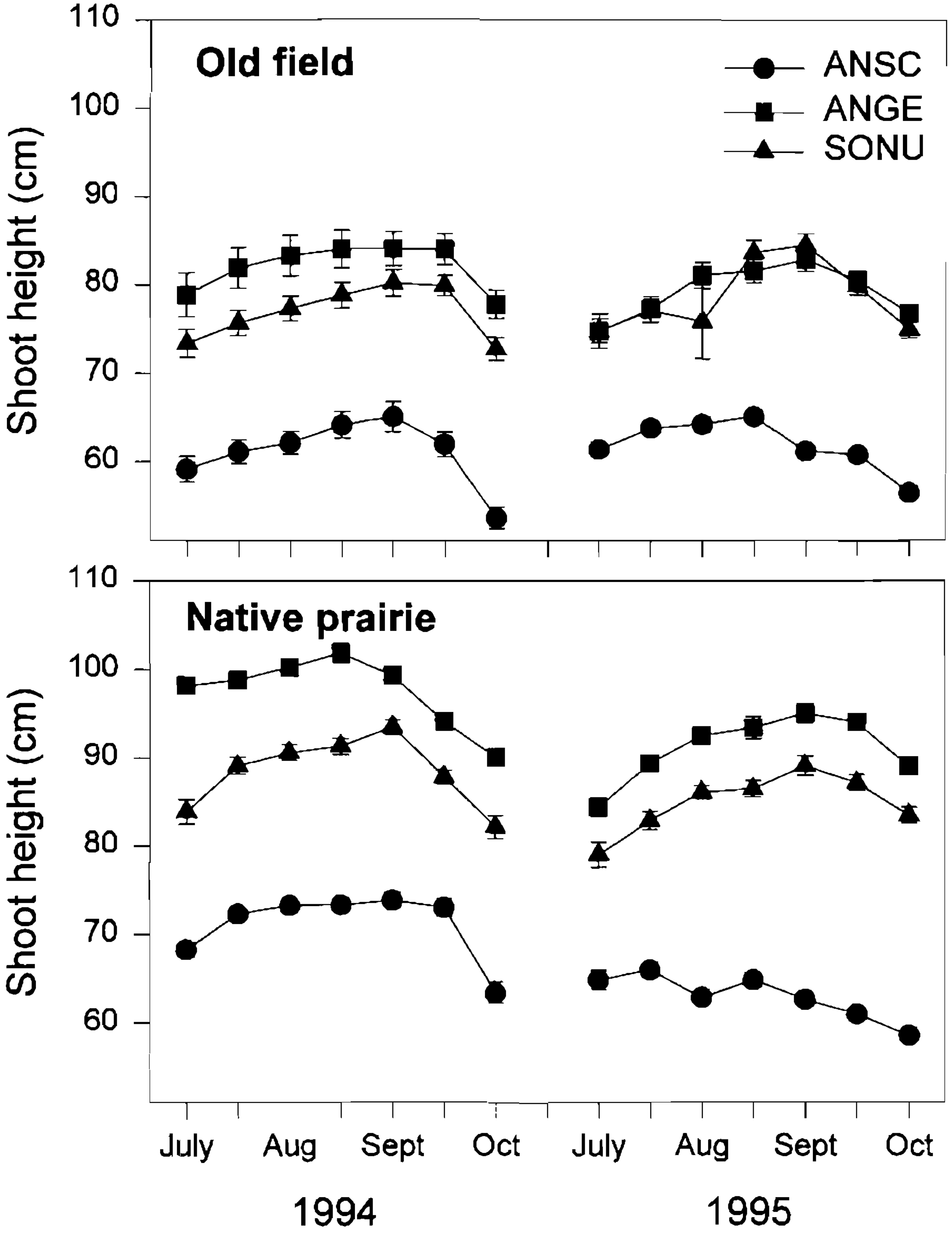
ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

Table 6. Two-level repeated measures ANOVA of growth rate (cm /day).

Source of variation	df	SS	MS	F	P
Between subjects					
Tract	1	0.041	0.041	3.358	0.070 +
Grass species	2	0.165	0.082	6.776	0.002 **
Tract X Species	2	0.039	0.019	1.594	0.208 ns
Error	114	1.388	0.012		
Within subjects					
Year	1	0.008	0.008	0.676	0.413 ns
Year X Tract	1	0.008	0.008	0.681	0.411 ns
Year X Species	2	0.026	0.013	1.084	0.342 ns
Year X Tract X Species	2	0.005	0.003	0.218	0.804 ns
Error	114	1.359	0.012		

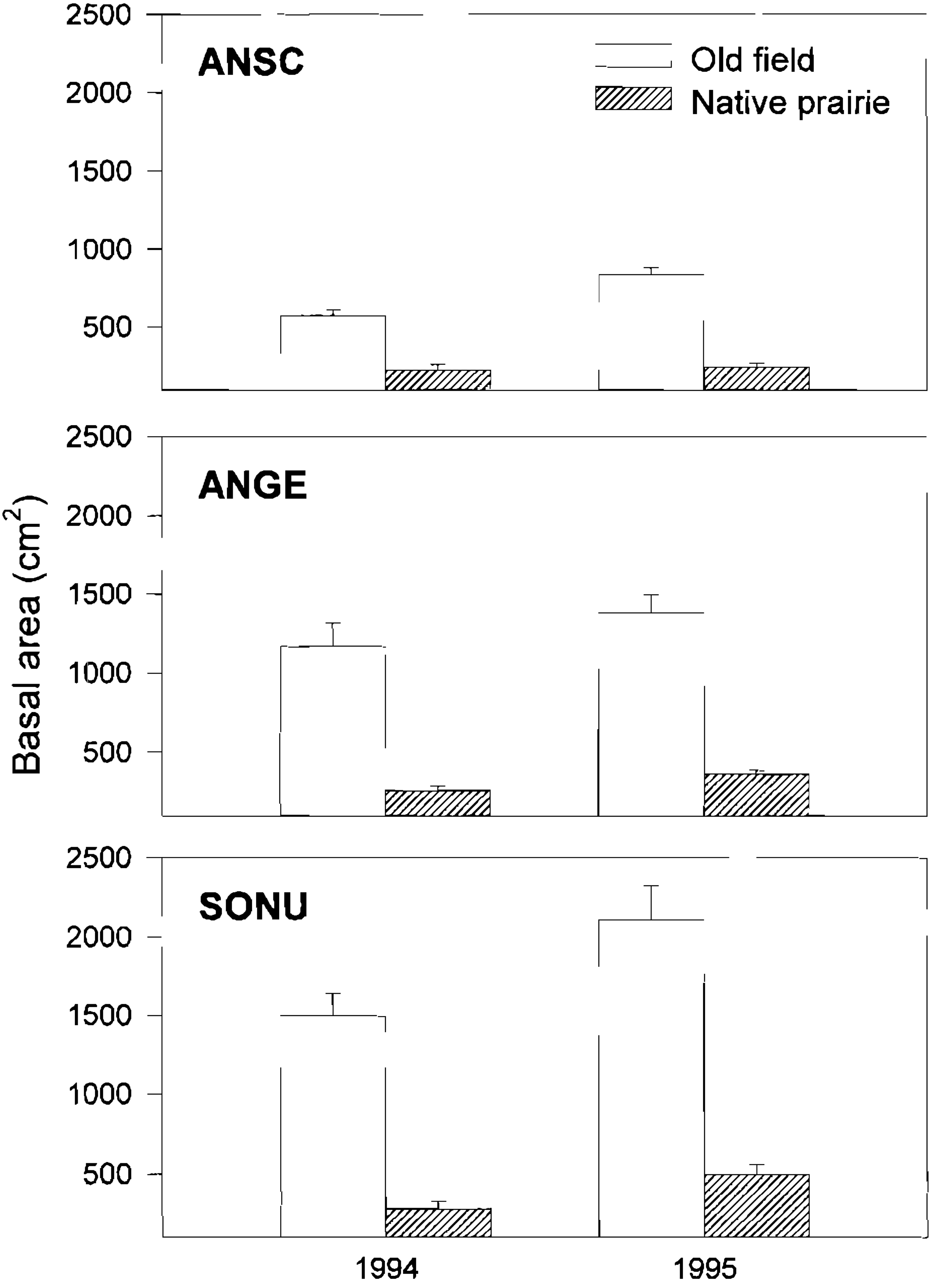
ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 13. Mean shoot height of old-field and native-prairie plants for *A. scoparius*, *A. gerardii*, and *S. nutans* for 1994 and 1995 growing seasons.



Old field
Native prairie
ANSC
ANGE
SONU
Shoot height (cm)
110
100
90
80
70
60
July
Aug
Sept
Oct
July
Aug
Sept
Oct
1994
1995

FIG. 14. Effect of old field versus native prairie on growth rate based on mean basal area plant size increase for *A. scoparius*, *A. gerardii*, and *S. nutans*. See Table 7 for significant tract effect P values.


ANSC
ANGE
SONU
Old field
Native prairie
Basal area (cm^2)
2500
2000
1500
1000
500
1994
1995

effect on basal plant growth (Table 7), however, individual species grew at marginally different rates ($P < 0.1$). Multiple comparisons showed marginal differences in growth rate between *S. nutans* and the other two species (Table 7).

Field reproductive effort

The percentage of plants that flowered varied by species (Fig. 15) in the native prairie, but not in the old field. More *S. nutans* flowered in the native prairie than the other two species in both years, but especially in 1994. *A. gerardii* had fewer plants that flowered in the native prairie in the dry year of 1994, but rebounded in the wet year (1995). *A. scoparius* had fewer plants that flowered in the native prairie in both years. This difference was highly significant in the wet year of 1995 using the Fisher's exact test of proportion ($P < 0.001$) in Table 8. Greater than 95% of *S. nutans* plants flowered in the old field and the native prairie during both wet and dry years, however, the percentage of *A. gerardii* plants that flowered during the drought (1994) was 70% in the old field and 45% in the native prairie.

Reproductive effort was greater for *A. gerardii* and *S. nutans* in the native prairie, but greater for *A. scoparius* in the old field (Fig.16). Reproductive effort was only measured in 1995 because in the drought year of 1994 a number of *A. gerardii* and *A. scoparius* plants failed to flower. All three grasses were differentially allocating resources to reproduction ($F = 4.02$; df = 2,114; $P < 0.05$) which contributed to a highly significant ($F = 16.69$; df = 2,114; $P < 0.001$) plant species by environment (tract) interaction (Table 9). Means comparisons indicated this was due to a significant difference ($P < 0.05$) in reproductive output between *S. nutans* and *A. scoparius* (Table 9). The ANCOVA showed biomass devoted to reproduction was not significantly dependent on plant basal area size when the plants were measured (Table 10). Mass was marginally significant ($F = 3.08$; df = 1,112; $P < 0.1$) and the strong plant species by tract interaction ($F = 13.774$; df = 2,112; $P < 0.001$) was upheld.

Table 7. Two-level ANOVA of natural log transformed basal area difference from 1994-1995 (cm^2).

Source of variation	df	SS	MS	F	P
Tract	1	22.881	22.881	13.084	0.001***
Grass species	2	10.773	5.387	3.080	0.051 +
Tract X Species	2	1.788	0.894	0.511	0.602 ns
Error	82	143.402	1.749		

Note: 32 individuals with negative growth not included.

Tukey HSD Multiple Comparison for basal area difference.

Comparison	Mean difference	P
ANGE vs ANSC	-0.006	1.000 ns
ANGE vs SONU	0.747	0.087 +
ANSC vs SONU	0.752	0.087 +

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 15. Effect of tract on percentage of plants that flowered in 1994 and 1995 for *A. scoparius*, *A. gerardii*, and *S. nutans*. Significant for *A. scoparius* in 1995.

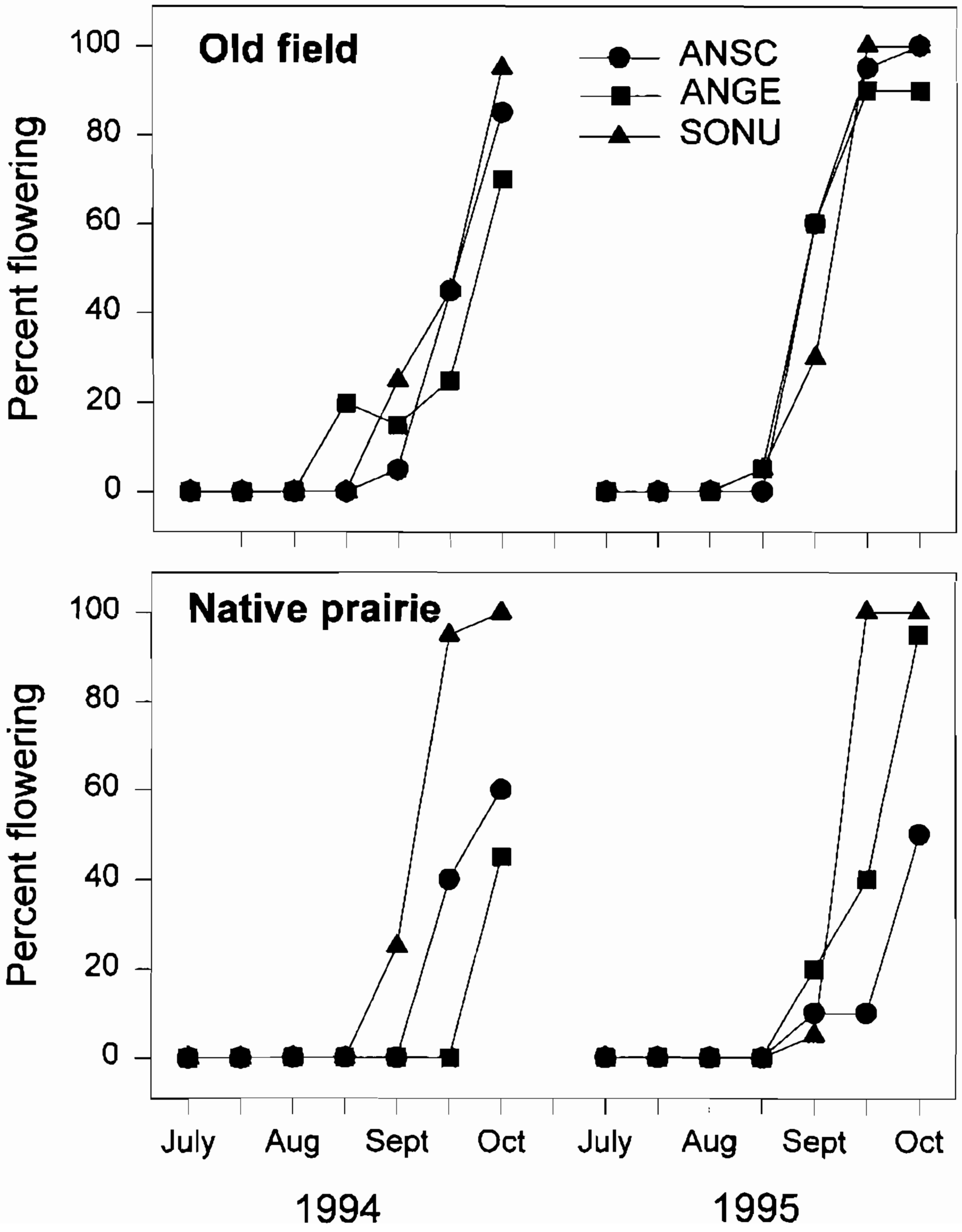

Old field
Native prairie
ANSC
ANGE
SONU
Percent flowering
0
20
40
60
80
100
July
Aug
Sept
Oct
1994
1995

Table 8. Fisher's exact test of proportion of plants flowering by tract.

		Old Field		Native Prairie			
Year	Species	N	Y	N	Y	df	P
1994	ANSC	3	17	8	12	1	0.155 ns
	ANGE	6	14	11	9	1	0.200 ns
	SONU	1	19	0	20	1	1.000 ns
1995	ANSC	0	20	10	10	1	< 0.001***
	ANGE	2	18	1	19	1	1.000 ns
	SONU	0	20	0	20	1	1.000 ns

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 16. Effect of old field versus native prairie on reproductive effort (RE = sexual biomass / total biomass) for *A. scoparius*, *A. gerardii*, and *S. nutans*. See Table 9 for significant tract effect and tract by species interaction and significant multiple comparisons.

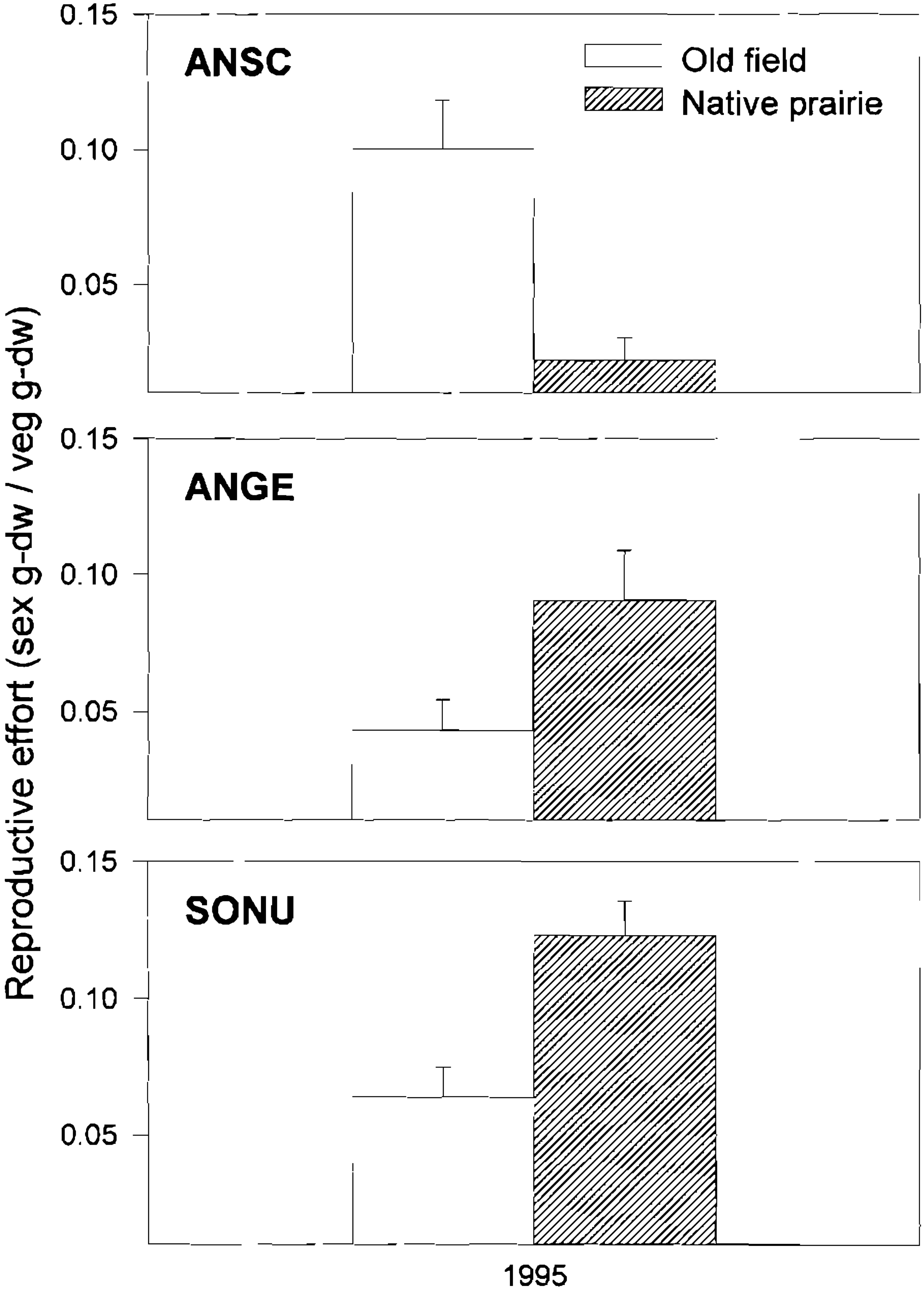

ANSC
ANGE
SONU
Old field
Native prairie
Reproductive effort (sex g-dw / veg g-dw)
0.15
0.10
0.05
1995

Table 9. Two-level ANOVA of reproductive effort (g dry-weight of sexual reproductive structures / g dry-weight total).

Source of variation	df	SS	MS	F	P
Tract	1	0.002	0.002	0.656	0.420 ns
Grass species	2	0.020	0.010	4.016	0.021 *
Tract X Species	2	0.082	0.041	16.690	< 0.001***
Error	114	0.280	0.002		

Tukey HSD Multiple Comparison for reproductive effort.

Comparison	Mean difference	P
ANGE vs ANSC	-0.005	0.881
ANGE vs SONU	0.024	0.079 +
ANSC vs SONU	0.029	0.024 *

ns = non-significant, + P < 0.100, * P < 0.050, ** P < 0.010, *** P < 0.001

Table 10. Two-level ANCOVA of reproductive effort (g dry-weight of sexual reproductive structures / g dry-weight total) with basal area (cm^2) and total mass (g dry-weight) as covariates.

Source of variation	df	SS	MS	F	P
Area	1	0.006	0.006	2.666	0.105 ns
Mass	1	0.007	0.007	3.080	0.082 +
Tract	1	0.000	0.000	0.204	0.652 ns
Grass species	2	0.019	0.009	3.892	0.023 *
Tract X Species	2	0.067	0.033	13.774	< 0.001***
Error	112	0.272	0.002		

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

Environmental influence experiment

Overall, little difference was detected for any trait measured between clones of *S. nutans* from native-prairie plants and old-field plants when grown under the common garden environmental conditions. Neither mass dry-weight (Fig. 17, Table 11) nor number of tillers (Fig. 18, Table 12) were significantly different between clones from the native-prairie and the old-field tracts. Average height of tillers produced by clones from the two tracts did differ significantly ($F = 7.159$; $df = 1,52$; $P < 0.05$) (Fig 19, Table 13), but the effect of taller old-field tillers in the garden was opposite to the pattern I observed in the field and does not suggest a genetically based difference.

DISCUSSION

Vegetative growth variation

Growth rates differed substantially between old-field and native-prairie grasses, for two of the three species, especially in the dry year of 1994. Old-field *A. gerardii* and *S. nutans* grew more slowly and were shorter than their counterparts in the native prairie. They allocated more resources to vegetative tillers and had a greater year-to-year increase in basal area size. In contrast, plant height, basal size, and increase in basal area were lower, than the other two species, for *A. scoparius* in both old field and native prairie and little variation was detected either between tracts or between years. Thus, the species appeared to differ in their pattern of response to differences in the two environments.

Local environments change over the course of a succession. After 22 years, the study old field still maintained a carryover of disturbance and low soil fertility (Barber 1985; Crandall 1987), although soil fertility may have increased since the field was abandoned (Inouye et al. 1987; Tilman 1988). Infertile habitats support plants with slower growth rates (Chapin III 1980). The history of colonization of any species is limited by its dispersal opportunities, however, all three species have slowly

FIG. 17. Effect of old field versus native prairie on mean aboveground biomass of *S. nutans* clones in the environmental influence experiment.

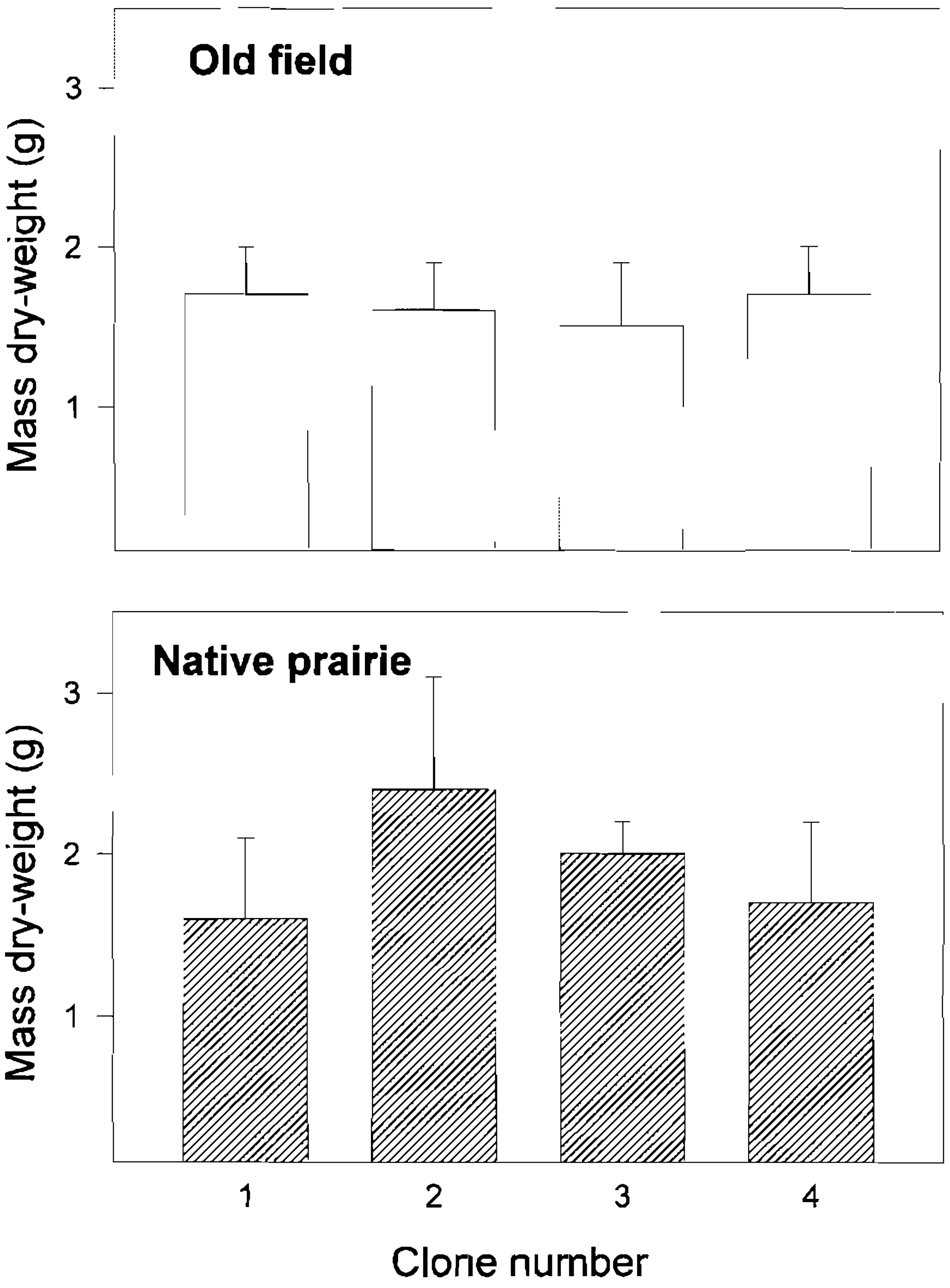

Old field
Mass dry-weight (g)
3
2
1
Native prairie
Mass dry-weight (g)
3
2
1
1
2
3
4
Clone number

Table 11. Two-level nested ANOVA with unequal sample sizes of natural log mass (g).

Source of variation	df	SS	MS	F	P
Among tracts	1	0.001	0.001	0.003	> 0.750 ns
Among plants	6	2.297	0.383	0.425	> 0.750 ns
Among clones	52	46.838	0.901		

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 18. Effect of old field versus native prairie on mean number of tillers of *S. nutans* clones in the environmental influence experiment.

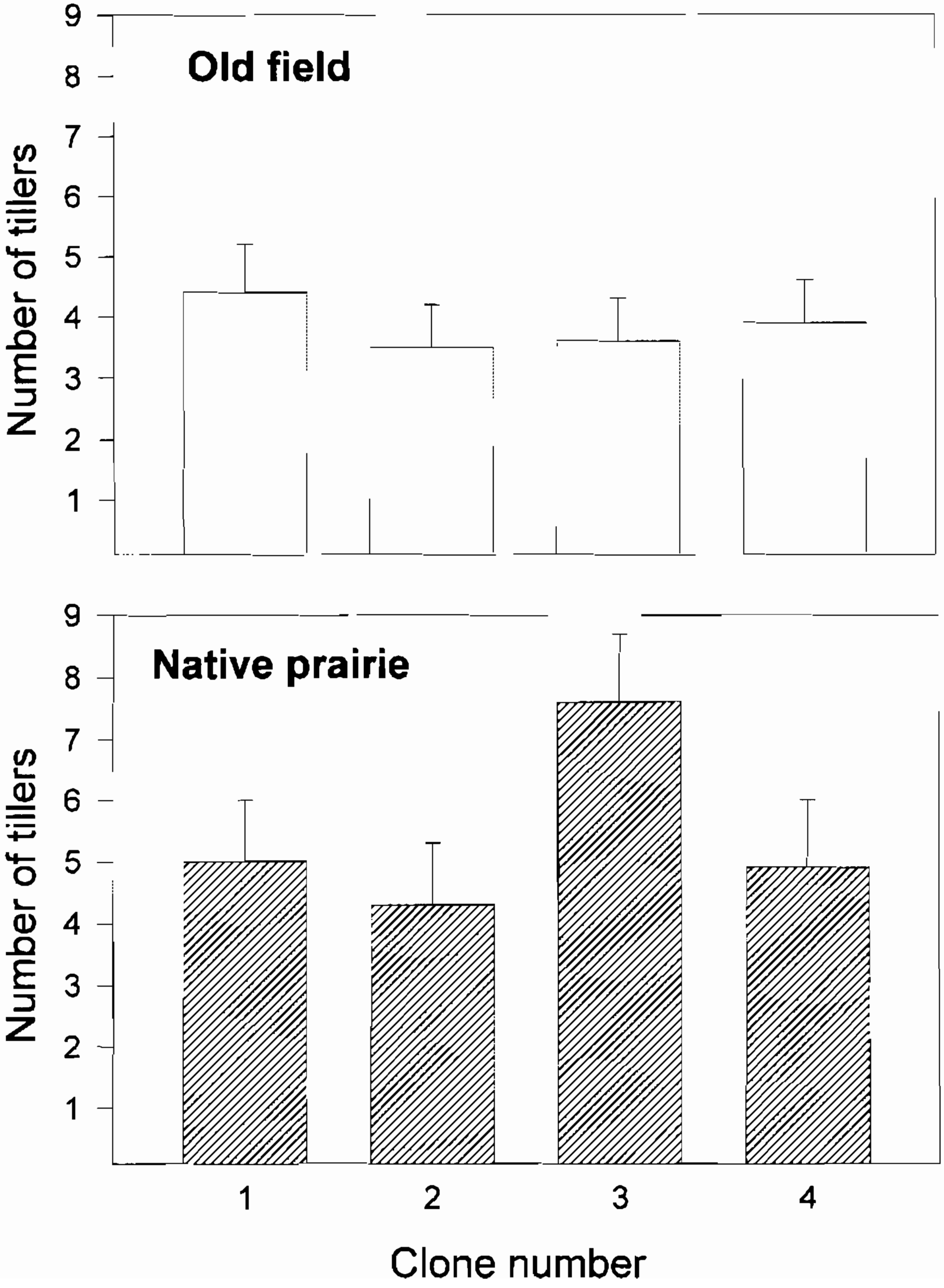

Old field
Native prairie
Number of tillers
Number of tillers
9
8
7
6
5
4
3
2
1
1
2
3
4
Clone number

Table 12. Two-level nested ANOVA with unequal sample sizes of number of tillers.

Source of variation	df	SS	MS	F	P
Among tracts	1	37.507	37.507	4.645	< 0.100 +
Among plants	6	48.451	8.075	1.435	> 0.100 ns
Among clones	52	292.625	5.627		

ns = non-significant, + P < 0.100, * P < 0.050, ** P < 0.010, *** P < 0.001

FIG. 19. Effect of old field versus native prairie on mean tiller height of *S. nutans* clones in the environmental influence experiment.

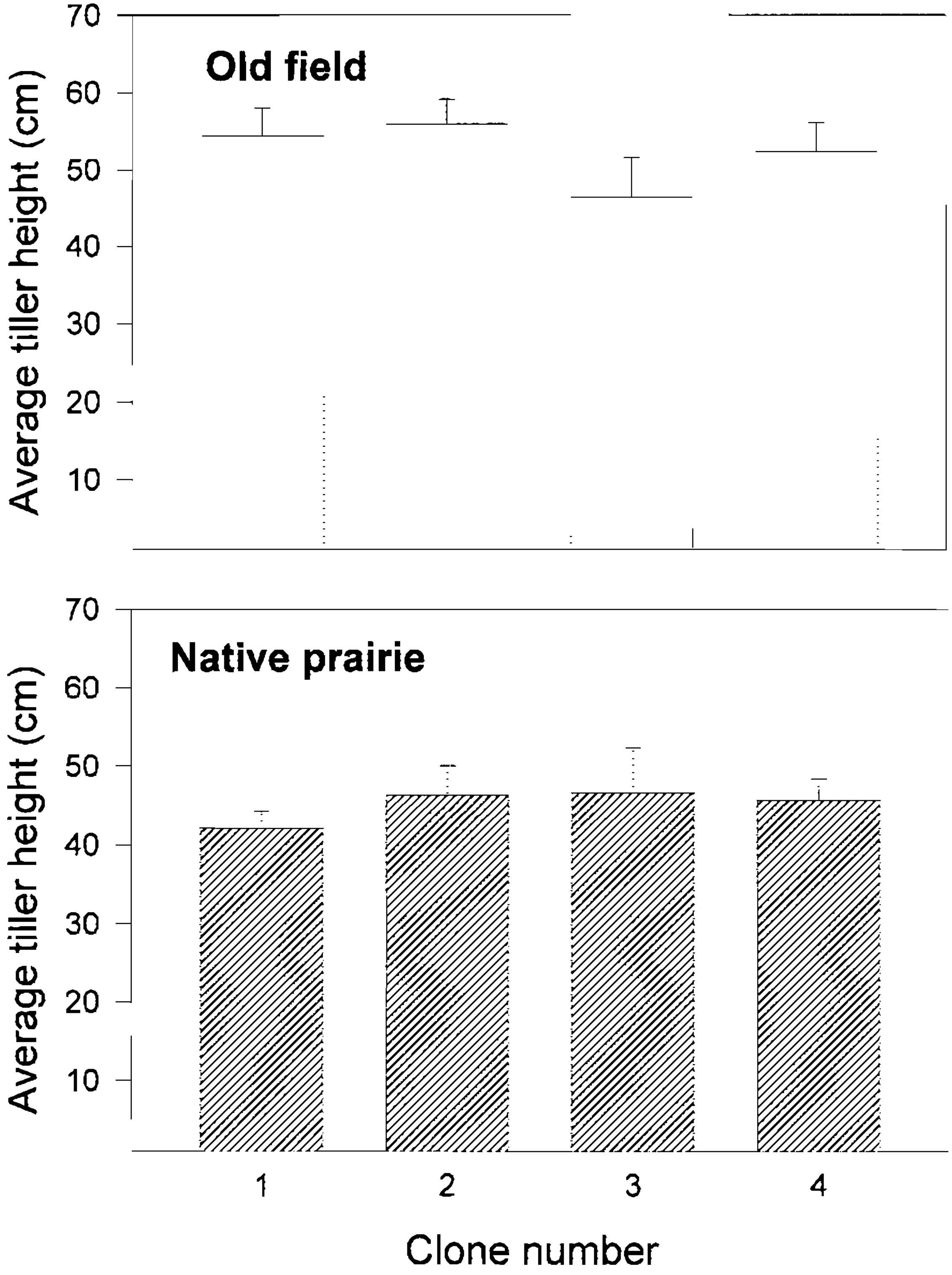

Old field
Native prairie
Average tiller height (cm)
70
60
50
40
30
20
10
1
2
3
4
Clone number

Table 13. Two-level nested ANOVA with unequal sample sizes of natural log average tiller height (cm).

Source of variation	df	SS	MS	F	P
Among tracts	1	0.315	0.315	7.159	< 0.050 *
Among plants	6	0.264	0.044	0.657	> 0.500 ns
Among clones	52	3.480	0.067		

ns = non-significant, + P < 0.100, * P < 0.050, ** P < 0.010, *** P < 0.001

colonized the old field and appear to be successful in an environment with a low intensity of disturbance and fairly poor soil.

A. gerardii and *S. nutans* growth rates may have been slowed by an allocation trade-off to roots, tiller expansion, or defensive compounds (Tilman 1988), which could make them superior competitors for any available nitrogen (Tilman and Wedin 1991a) and insure their continued presence. Gleeson and Tilman (1990) found that slow growth rates in prairie grasses were correlated with higher relative allocation to belowground biomass of roots. In the native prairie, these same grasses are more constrained by the competitive presence of neighbors and thus may grow at a faster rate to obtain more light (Tilman 1988). *A. scoparius* grew at a lower rate, than either of the tallgrasses, in both tracts and may have been exchanging less growth in height for more reproductive effort in the old field, but not in the native prairie. Such a trade-off may be a colonizing strategy that could be maintained into mid-succession once super-competitor status is achieved. Wedin and Tilman (1993) found *Schizachyrium scoparium* (*A. scoparius*) dominated other species in comparison plots in a five year study, indicating that this species has both colonizing and competitive abilities.

Differences in growth rates for *A. gerardii* and *S. nutans* may have been due to yearly patterns of rainfall. Old-field plants increased growth rate with increased moisture in 1995 but native-prairie plants did not. Plants of both species had higher reproductive effort in the native prairie than in the old-field in 1995, suggesting that a trade-off of growth rate for sexual reproduction was made by the native-prairie plants. *A. scoparius* plants decreased their growth rate slightly in the wetter year (1995) indicating that they may be more drought resistant and compete more successfully in a drier environment.

Basal area was greater for all three species in the old field than in the native prairie where the plants were taller. Plants colonizing the old field may invest in vegetative expansion to gain a good position with regard to competitors before growing taller. Tilman (1988) has argued light is not a limiting factor in an old field and old-field grasses may trade growth rate in height in favor of producing more tillers to support a developing root system. Ramet (tiller) density was shown to increase with light intensity by Kays and Harper (1974). In the native prairie, the constraints of neighbors may make these plants grow taller as light becomes more limiting. Rapid grass production resulted in low light conditions within the tallgrass prairie canopy (Knapp 1984). Briske and Butler (1989) found clone size was regulated by neighbor density in *S. scoparium* (*A. scoparius*) in a Texas grassland.

Growth-related trait differences in the old-field plants did not resemble the characteristic rapid growth and rapid turnover traits of early colonizers in a succession (Lewontin 1965; MacArthur and Wilson 1967; Pianka 1970). These plants have preempted space, have maintained successfully, and appear to be expanding by vegetative tillering. Plant size is a trait that typically responds to the environment by phenotypic plasticity (Silvertown and Lovett Doust 1993), as well as, by genetic influence. Vegetative expansion is favored in productive or unproductive environments with a low intensity of disturbance (Grime 1979), which is descriptive of an old field and supports my results for old-field plants.

Life history traits for plants are often a trade-off between increased benefits in one environment over another and are shaped by ongoing abiotic and biotic processes. Nutrient levels, particularly nitrogen, may be lower in the old field, but competition from neighbors may be the greater factor in the native prairie. Natural selection can change life history traits in long time occupants of different communities and could enable these plants to compete successfully at more than one successional stage.

Reproductive growth variation

A high percentage of *S. nutans* plants flowered in both tracts in both the dry (1994) and wet (1995) years. Fewer *A. gerardii* plants flowered during the drought but they recovered in the wet year in both tracts. *A. scoparius* was the only one among the study species to show a site-related effect on flowering. More *A. scoparius* plants flowered and they produced more flowering stems in the old field. Higher reproductive output is characteristic of the high fecundity biotype of Grime (1979) and suggests that seed production may be an advantage in earlier successional stages (Fenner 1985). However, *A. scoparius* experienced a 50 % reduction in the number of plants that flowered in the native prairie during the relatively wet year of 1995. The species may not be as successful on the native prairie during years of excess rainfall, but can rebound to some extent during dry years.

A. scoparius also invested a higher percentage of its total biomass in reproductive structures in the old field than in the native prairie. A number of studies have found plants make higher reproductive investment at earlier successional stages or in more disturbed habitats (Abrahamson and Gadgil 1973; Gaines et al.1974; Solbrig and Simpson 1974; Pitelka 1977; Primack 1979; Kik et al. 1990). Investing more resources in reproductive effort is a colonizing strategy that could persist into mid succession.

The prairie codominant grasses, *A. gerardii* and *S. nutans*, on the other hand, invested less in reproduction in the old field and more in reproduction in the native prairie. Lower reproductive effort in the old field may be explained by resource allocation trade-offs. A plant must allocate to alternate demands in a resource-limited environment. Nitrogen limitation in the old field may result in a trade-off between reproduction and growth. Reproductive effort must be balanced against vegetative expansion for both of the old-field tallgrasses. High reproductive output in one year can reduce plant size the following year (Law 1979). The cost of competition may also lower future reproductive effort.

Higher reproductive effort for these same grasses in the native prairie is less easily explained. In the native prairie, vegetative expansion costs must be balanced against the costs of competition with neighbors. Competition could limit vegetative expansion or force the plant to expand by sending out rhizomes. A superior competitor may then be able to switch more resources to sexual reproduction. In a comparison of 26 clonal plants, that included perennial species, Silvertown et al. (1993) found a negative correlation between vegetative growth and a shift to sexual reproduction. A trade-off between growth rate and sexual reproduction in native-prairie codominants could favor increased reproductive effort in years when moisture was abundant. High reproductive effort may be episodic for the tallgrasses. Reproductive effort was measured for the 1995 season, which followed a season of low rainfall when presumably reproductive effort for these plants was low.

Phenotypic vs genetic variation

Under common garden conditions, *S. nutans* exhibited similar life-history traits thus suggesting plastic responses by plants in the old-field and native-prairie environments. While the common garden experiment may not have included enough plants to completely rule out the possibility of genetic-based population differences between individuals from the two habitats, the lack of significant differences between old-field and native-prairie clones for two of the three traits measured, argues against strong genetic differentiation. Even for the one trait that did differ between native-prairie and old-field clones (tiller height), all of the variation was attributed to a between field difference in plant height which was counter to the pattern observed in the field. This suggests that this effect may have been due to an artifact of the experiment. Possibly growing the plants in six inch pots, restricted the number of vegetative tillers and old-field plants were able to allocate more resources to tiller height.

Phenotypic plasticity in response to environmental differences is not uncommon in plants. A number of plant studies have found similar plastic responses to environmental variation (in *Ranunculus repens*, Lovett Doust 1981; in *Plantago lanceolata*, Antonovics and Primack 1982; in *Danthonia spicata*, Scheiner and Goodnight 1984; in *Plantago major*, Lotz and Blom 1986). A phenotype which expresses certain life-history traits is the result of interaction between the genotype and its environment. Phenotypic plasticity is an adaptation to environmental heterogeneity (Bradshaw 1965; Marshall and Jain 1968; Schlicting 1986) and the environment can be the stronger force in shaping phenotypic life-history traits (Price and Schluter 1991). Natural selection acts on the phenotype to modify these traits and plants from the old field and the native prairie may represent locally modified phenotypes.

My study could not rule out entirely that life-history trait differences observed in the field study had a genetic component. I only measured differences between four clones of each habitat type in the common garden and it is possible that some genotypes present in these populations were not sampled. Different genotypes in a population have explained life history variation in a number of plant species (in *Achillea lanulosa*, Clausen et al.1948; in *Poa annua*, Law et al. 1977; in *Anthoxanthum odoratum*, Grant and Antonovics 1978; in *Spartina patens*, Silander and Antonovics 1979; in *Trifolium repens*, Burdon 1980). Also plastic responses in some traits can keep natural selection from operating directly on certain genes by covering over genetic differences (Sultan 1987). Thus, plants could be genetically distinct individuals with their variation masked by the demands of their environment.

Understanding the mechanisms that produce local adaptation, whether by plasticity or genetic variance, is beyond the scope of my study. However, perennial plant species must over time endure environmental variation that genetic change is not flexible enough to meet. Prairie grasses may have evolved phenotypic plasticity to compete in a changing successional environment.

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CHAPTER 3

VARIATION IN COMPETITIVE RESPONSE IN *SORGHASTRUM NUTANS*

INTRODUCTION

Competition from neighbors has a significant impact on the evolution of life-history traits in plants, such as survival, growth, and reproduction, as well as, playing a role in community structure (Goldberg 1988; Grace and Tilman 1990). Successful competitors acquire their most limiting resource and resist the inhibiting effects of neighbors, grazers, and pathogens. Competitive interactions can determine which plants persist in a community (Parrish and Bazzaz 1982; Connell 1983; Schoener 1983; Tilman 1985). A plant that achieves long-term status can persist even as the community changes over more than one successional stage. If species differ in their competitive abilities, intensity of competition should vary with successional stage or remain the same as amounts of limiting resources change.

Two models reflect these contrasting views. First, the plant strategy theory proposes that competition increases in intensity as plant biomass increases and the resulting higher density creates greater demand for limiting resources (Grime 1973, 1977; Huston 1979; Keddy 1989). Consistent with this hypothesis, competitive intensity increased with increased biomass in studies on a lakeshore (Wilson and Keddy 1986) and in an old field (Reader and Best 1989). Plants in later successional stages are predicted to undergo more intense competition and should respond to neighbor removal with increased growth.

Second, Tilman (1980; 1985; 1986), in the resource-ratio hypothesis of succession, argues competition is equally intense along productivity gradients, i.e., all successional stages, although the limiting resource may change over time. The hypothesis, summarized in Begon et al. (1996), emphasizes the relative change in the competitive abilities of plants as limiting resources slowly change in a succession. In support of this hypothesis, two studies demonstrated that the intensity of competition did not vary with added fertilizer or increased standing crop in a prairie (Wilson and Shay 1990) and in an old field (Wilson and Tilman 1991). Under this hypothesis plants in earlier successional stages or unproductive habitats are predicted to be under intense competition (Newman 1973; Tilman 1982, 1988) due to extreme resource limitations and plants from both successional stages should respond to neighbor removals.

In an additive experiment to test both models, Turkington et al. (1993) demonstrated competition as a structuring force in a pasture community by predicting competitive intensity should increase as productivity increased and decline with increased disturbance. Addition of neighbors in garden plots along nutrient and disturbance gradients produced effects beyond those due to gradient level, which were attributed to competition. Results for the most part supported Grime (1977) and Campbell and Grime (1992), however, the effects on grasses, when standardized for pure stand performance, were consistent with Tilman (1988).

To test these alternative models, I asked, do populations from a mid-successional old field (recovering from high disturbance) and a late-successional prairie (in high productivity) differ in their response to competitors? If competitors are removed will a plant respond with increased vegetative expansion, biomass, or reproductive effort? Studies that have closely examined growth patterns of tillers (ramets) in grasslands have found differences in competitive ability among species (Briske and Butler 1989; Pyke 1990). Tilman (1989) reported a 3.8 fold increase in plant biomass for *Schizachyrium scoparium* (*Andropogon scoparius*) when all neighboring plants were removed. On the tallgrass prairie, Hartnett (1993) showed *Panicum virgatum* L. increased growth when experimental plants were released from neighborhood competition.

I manipulated *Sorghastrum nutans* (L.) Nash (SONU) plants in the field by removing one-half of their surrounding vegetation to test the effect of competitor removal on life history trait expression in the experimental plants. *S. nutans* was chosen for the experiment because it is one of the tallgrass prairie dominants and because it forms discrete and well-defined crowns on both the old-field and native-prairie study tracts. To compare responses between tracts, between plants within a tract, and between halves of manipulated plants, I predicted (H_{A5}), grasses in a mid-successional old field have less competition than grasses in a later-successional prairie and therefore should show less response to release from competition than grasses in the native prairie tract. I tested the null hypothesis (H_{05}) that these two populations are subject to the same competitive effects and will show equal responses to release from competition.

METHODS

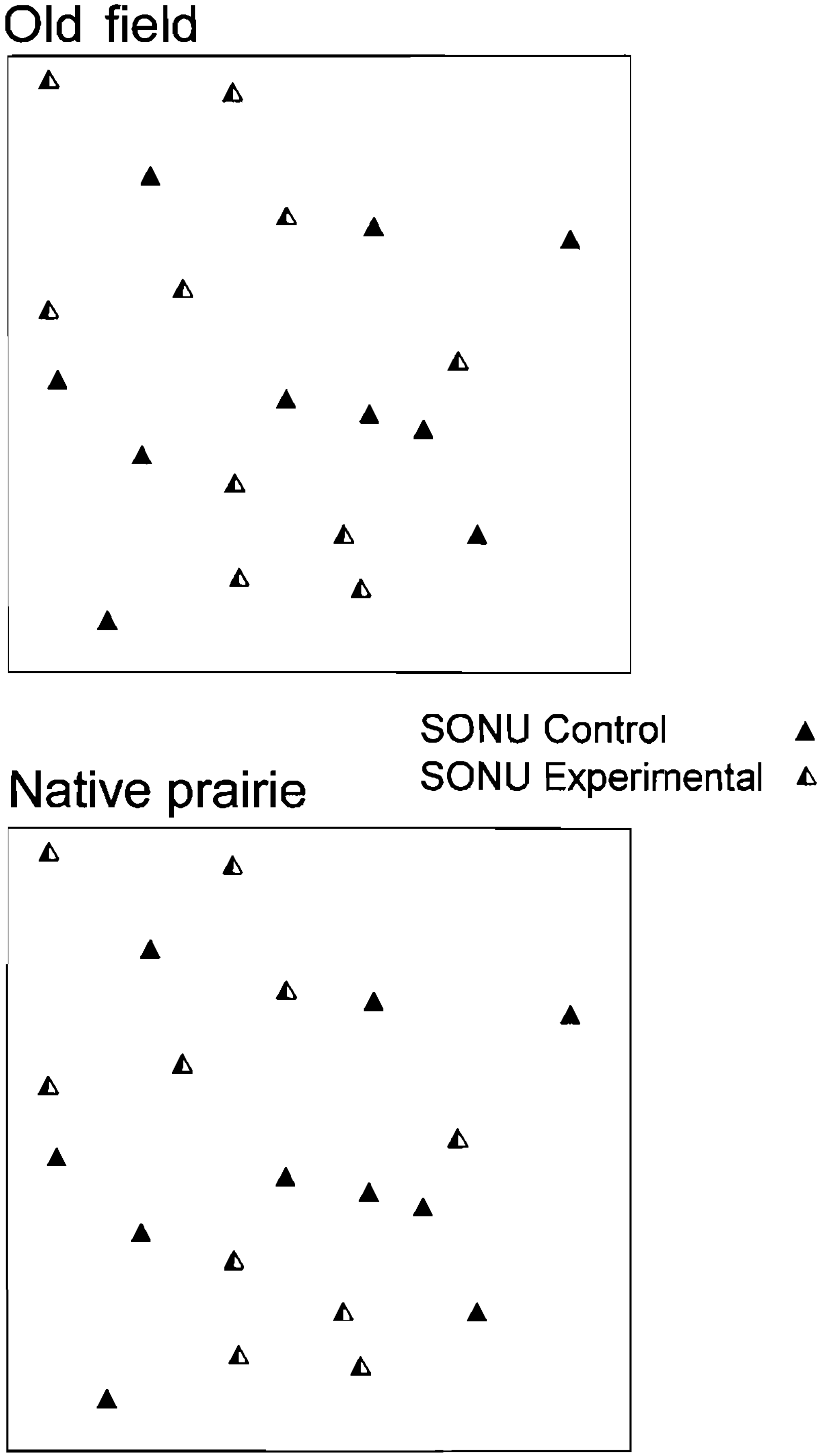
Field experiment

The removal experiment was conducted during 1996 from 1 June to 30 September. *S. nutans* plants naturally growing in a 22-year old field and an undisturbed tallgrass prairie were used in the experimental design (Fig. 20). Twenty plants in each tract were chosen for the experiment. These same plants were randomly selected, marked, and monitored previously in 1994 and 1995 and baseline measurements were available for them. Each plant was clipped at ground level in October 1995 and was free of dead plant material at the start of the experiment.

Basal area plant size was determined from diameter measurements taken in N-S and E-W directions through a center point. I used a compass to align the diameters. Each diameter was delineated by tying a heavy cotton cord between two plant label sticks that were driven into the ground and the plant center was marked with a wire rod.

I divided the plants in a tract into two groups. One group received the neighbor removal treatment on 3 June by applying 5% N-(phosphonomethyl) glycine (Roundup),

FIG. 20. Research design for neighbor-removal experiment for old-field and native-prairie *S. nutans* plants. Ten experimentals had one-half of all potential competitors removed from around a target plant and ten controls were undisturbed.


Old field
Native prairie
SONU Control ▲
SONU Experimental △

a short-lived, biodegradable herbicide. A 4 x 5 ft cardboard sheet shielded the experimental plant from the spray. The impact of Roundup on plant roots was not assessed but every effort was made to protect the experimental plants. All neighboring vegetation within a one m distance around one-half of a plant was removed. Orientation of the treatment side was randomly rotated. The treated area was cleared of all debris and kept free of potential competitors. Natural vegetation on the untreated side was undisturbed. Competition intensity was normal for one-half of a plant, while it was minimal for the experimental half. The second group of ten plants received no treatment and were used as controls.

I measured all plants at the start and end of the experiment and used plant diameter averages in the equation:

$$A = \pi r^2,$$

where A = area, π = pi, and r = radius, to calculate basal area. Vegetative expansion for a season was the difference between pre-experiment and post-experiment basal area plant size. I also calculated basal area differences for each one-half of each experimental plant.

Aboveground biomass was harvested after seed production for both control and experimental plants. Biomass was divided into sexual and vegetative structures for each one-half of a plant and all parts were dried separately at 80^{o}C. I used the ratio of sexual mass dry-weight (g) to total mass dry-weight (g) to calculate reproductive effort (Harper and Ogden 1970):

RE = Total weight of propagules/Total weight of aboveground biomass,

where propagules are sexual structures above the first node in a grass (Thompson and Stewart 1981) and total biomass equals sexual plus vegetative structures.

Statistical analyses

For basal area size of control vs experimental plants for the two years prior to removal treatment and one year following removal, a two-level analysis of variance (ANOVA) with interaction was used to determine whether plants increased in vegetative size after treatment. Examination of residual plots showed natural log (ln) transformed data better met the assumptions of normality and homogeneity of variance so transformed data were used in all analyses. I used a two-level repeated measures ANOVA, to compare the main effects of tract and treated plant with the added effect of time (year).

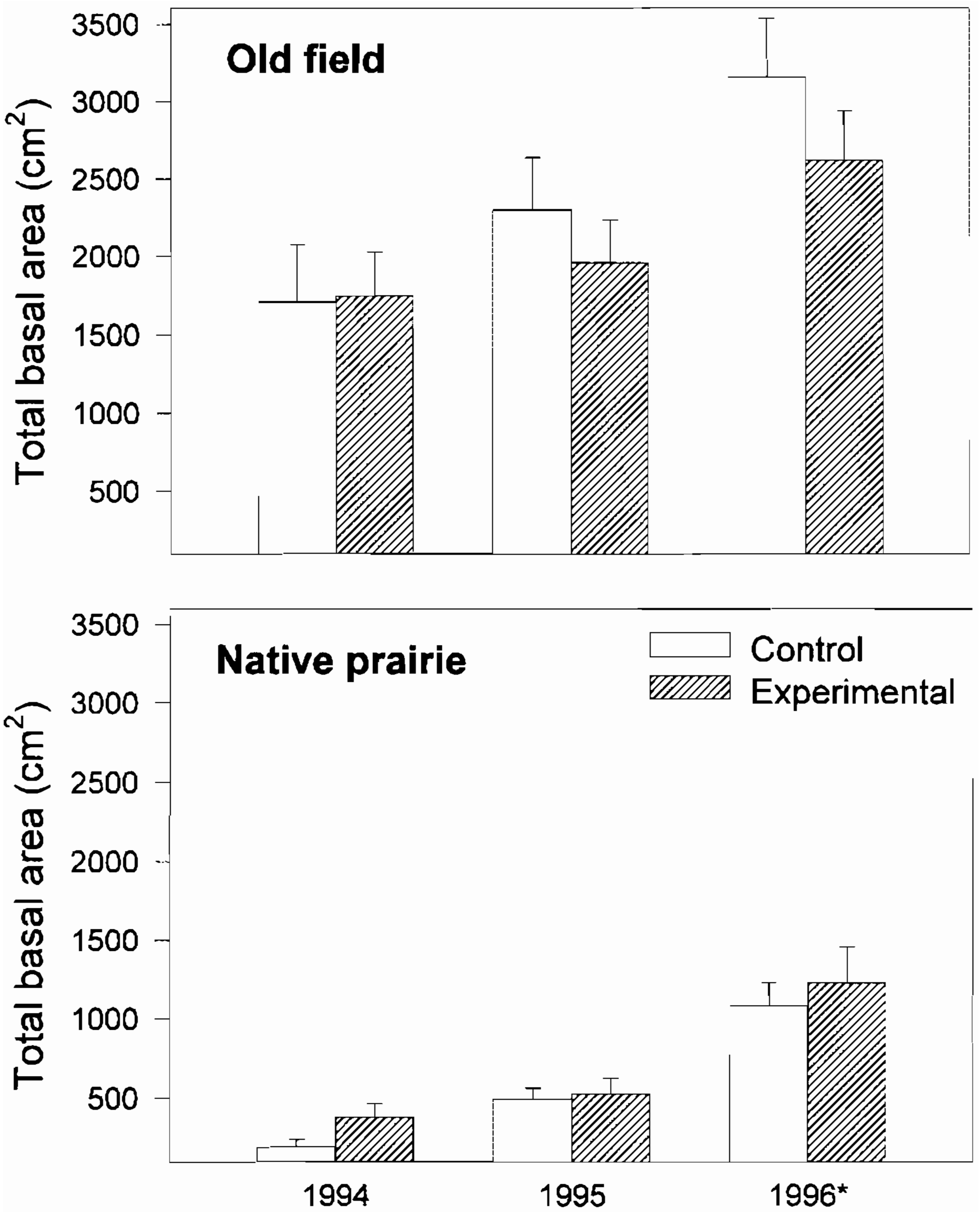
I analyzed difference in basal area size of plants from June to October with a two-level ANOVA with interaction of tract and treated plant. I used a natural log transformation on the data to meet the assumptions of normality and homogeneity of variance.

I compared basal area for treated and untreated sides of individual plants with a paired t-test on ln transformed data. I then used an ANOVA of ln transformed basal area to test for a within plant position effect to determine if the data were biased by position of the treated side. Mass dry-weight (g) and reproductive effort differences in individual plant sides were compared with paired t-tests.

RESULTS

Mean basal area plant size increased in 1994 and 1995 prior to neighbor removal and in 1996 following removal for control and experimental plants on both the old-field and native-prairie sites (Fig. 21). Control and experimental plants were similar in size prior to competitor removal in both old-field and native-prairie tracts. After competitor removal, control plants were slightly larger in the old field, but no difference was detected between control and experimentals in the native prairie. Tract had a highly significant ($F = 75.182$; $df = 1,36$; $P < 0.001$) effect on basal area plant

FIG. 21. Effect of tract on basal area plant size for control and experimental *S. nutans* plants for two years prior to (1994 and 1995) and one year (1996) following neighbor-removal treatment. See Table 14 and Table 15 for significant P values.


Old field
Native prairie
Control
Experimental
Total basal area (cm^2)
3500
3000
2500
2000
1500
1000
500
1994
1995
1996*

size both before and after treatment (Table 14). Results of the repeated measures ANOVA (Table 15) confirmed tract had a similar effect on basal area plant size ($F = 169.129$; $df = 1,36$; $P < 0.001$) and contributed to a marginally significant tract by treatment interaction. When the effect of year was added to the analysis, there was a highly significant ($F = 9.385$; $df = 2,72$; $P < 0.001$) year by tract interaction that explained the variance in mean plant size among the years.

Basal area plant size increased from June to October in both old-field and native-prairie plants (Fig. 22). Old-field controls showed greater, but non-significant increase than experimentals, but they were also larger plants when the experiment started. Native-prairie controls were similar in size to the experimentals. Basal area plant size differences between control and experimental plants in both tracts were not significantly different (Table 16).

The ANOVA for position of the removal treatment effect showed the side on which the treatment was applied did not affect the results (Table 17). Neighbor removal from one-half of each plant resulted in increased vegetative expansion on the treatment side of the plant in both old-field and native-prairie plants (Fig. 23). Old-field plants had the greater amount of expansion on the competitor-free side. A pairwise comparison for each one-half of a plant showed a significant difference for old-field plants ($T = -3.659$; $df = 9$; $P < 0.05$), but not for native-prairie plants (Table 18).

Neighbor removal also increased aboveground biomass on the treated side of a plant in the old field, but there was no difference between control side and removal side in the native prairie (Fig. 24). A paired t-test for mass dry-weight (g) for each side of a plant was significant ($T = -8.012$; $df = 9$; $P < 0.001$) for old-field plants but not for native-prairie plants (Table 19).

Table 14. Two-level ANOVA of natural log transformed basal area (cm^2) for two years (1994-95) prior to and one year (1996) following removal of potential competitors.

Source of variation	df	SS	MS	F	P
1994					
Tract	1	40.240	40.240	75.182	< 0.001***
Treatment	1	1.367	1.367	2.555	0.119 ns
Tract X Treatment	1	1.399	1.399	2.613	0.115 ns
Error	36	19.268	0.535		
1995					
Tract	1	21.259	21.259	90.726	< 0.001***
Treatment	1	0.067	0.067	0.285	0.597 ns
Tract X Treatment	1	0.053	0.053	0.226	0.637 ns
Error	36	8.435	0.234		
1996					
Tract	1	9.211	9.211	46.113	< 0.001***
Treatment	1	0.026	0.026	0.130	0.721 ns
Tract X Treatment	1	0.177	0.177	0.885	0.353 ns
Error	36	7.191	0.200		

ns = non-significant, + P < 0.100, * P < 0.050, ** P < 0.010, *** P < 0.001

Table 15. Two-level repeated measures ANOVA of natural log transformed basal area (cm^2) for two years (1994-95) prior to and one year (1996) following removal of potential competitors.

Source of variation	df	SS	MS	F	P
Between subjects					
Tract	1	65.233	65.233	169.129	< 0.001***
Treatment	1	0.187	0.187	0.486	0.490 ns
Tract X Treatment	1	1.121	1.121	2.905	0.097 +
Error	36	13.885	0.386		
Within subjects					
Year	2	24.736	12.368	42.385	< 0.001***
Year X Tract	2	5.477	2.739	9.385	< 0.001***
Year X Treatment	2	1.273	0.636	2.181	0.120 ns
Year X Tract X Treatment	2	0.508	0.254	0.870	0.423 ns
Error	72	21.010	0.292		

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 22. Effect of tract on basal area plant size for control and experimental *S. nutans* plants before (June) and after (October) neighbor-removal treatment.

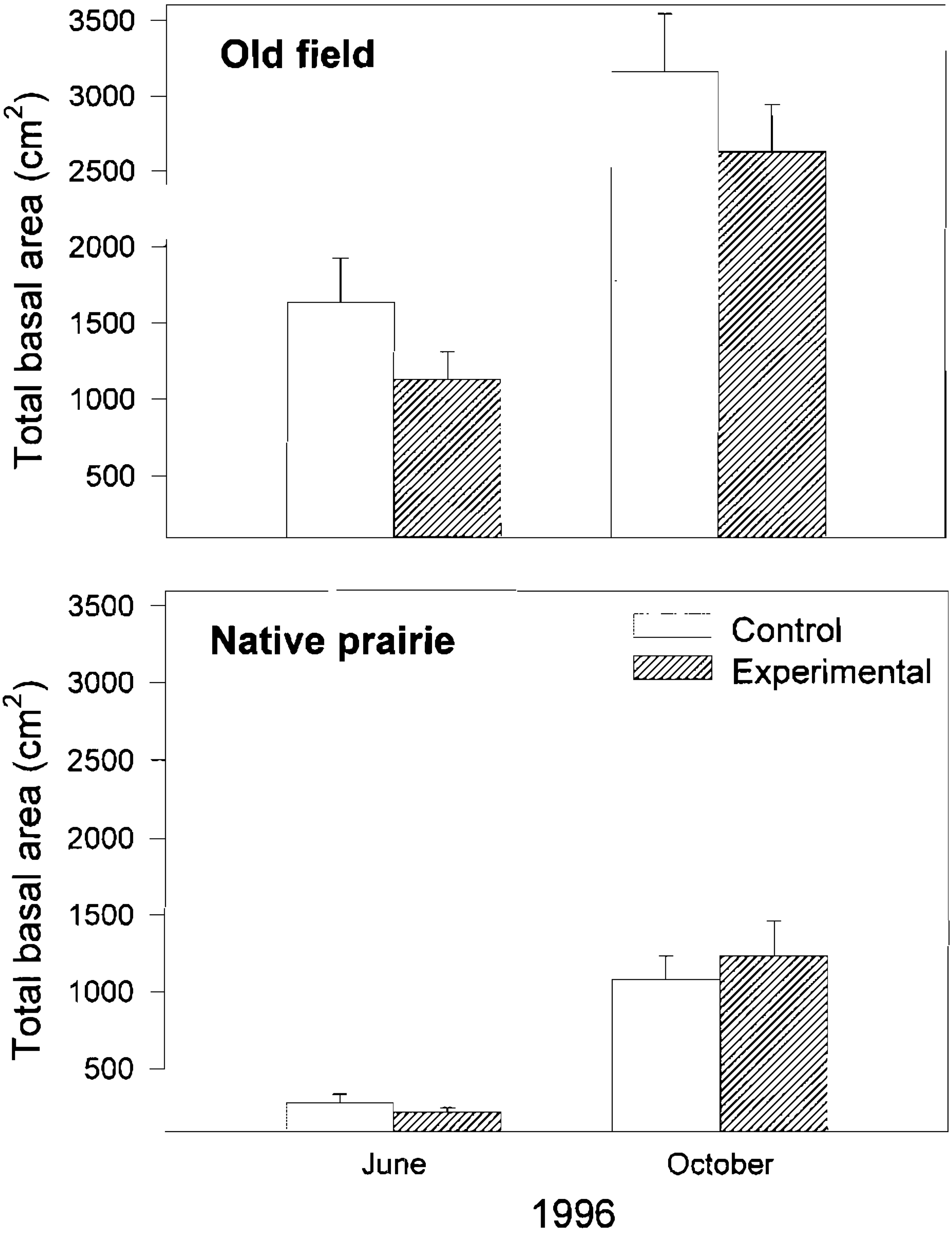

Old field
Total basal area (cm^2)
3500
3000
2500
2000
1500
1000
500
Native prairie
Control
Experimental
Total basal area (cm^2)
3500
3000
2500
2000
1500
1000
500
June
October
1996

Table 16. Two-level ANOVA of natural log transformed basal area difference from June to October 1996 (cm^2).

Source of variation	df	SS	MS	F	P
Tract	1	0.181	0.181	0.095	0.760 ns
Treatment	1	1.111	1.111	0.582	0.451 ns
Tract X Treatment	1	2.295	2.295	1.202	0.280 ns
Error	36	68.721	1.909		

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

Table 17. ANOVA of natural log transformed basal area (cm^2) effect of removal position bias.

Source of variation	df	SS	MS	F	P
Position	3	1.124	0.375	0.369	0.776 ns
Error	16	16.238	1.015		

ns = non-significant, + $P < 0.100$, * $P < 0.050$, ** $P < 0.010$, *** $P < 0.001$

FIG. 23. Effect of tract on basal area plant size for each one-half of an *S. nutans* plant (neighbor removal versus untreated side). See Table 18 for significant P values.

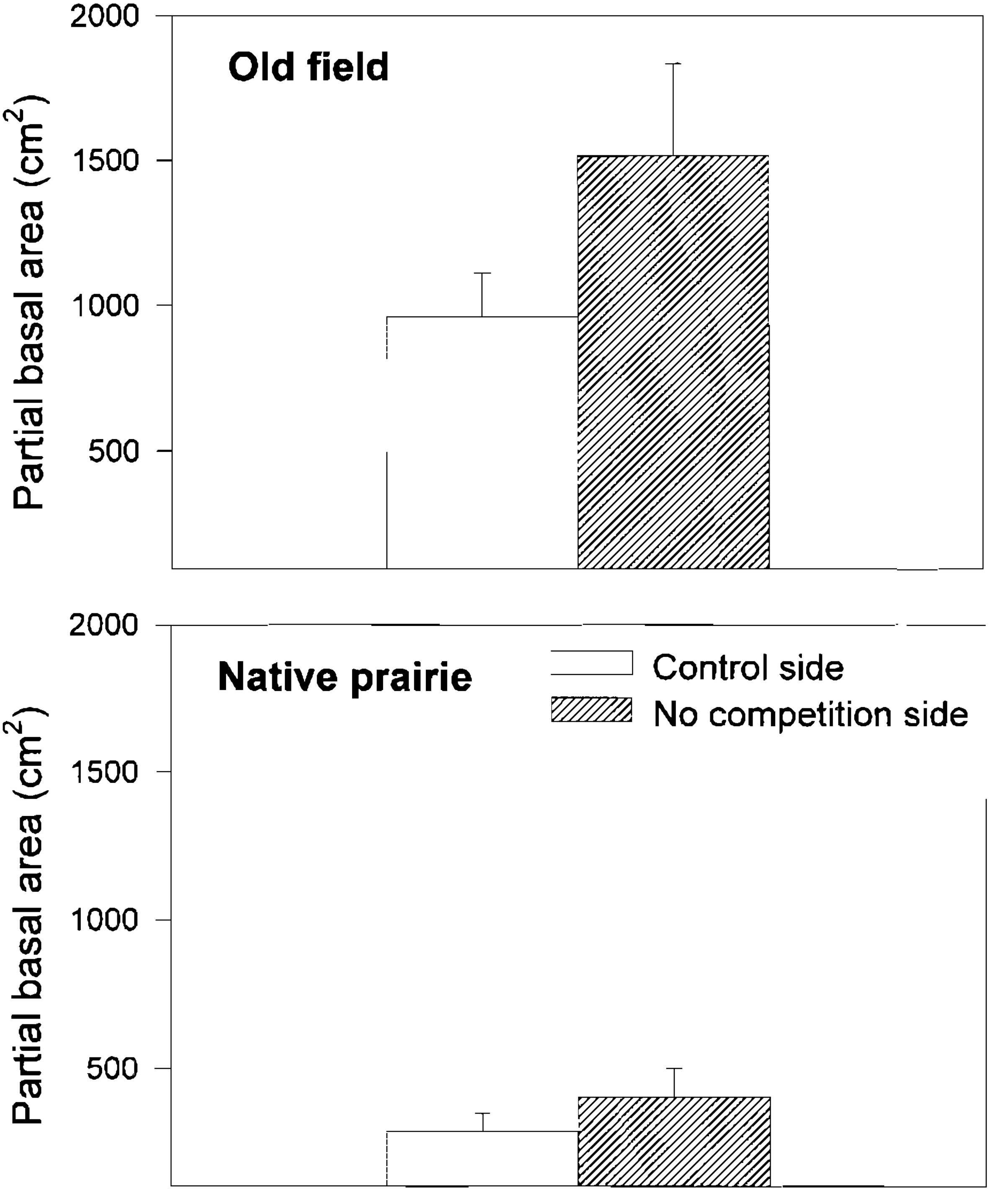

2000
1500
1000
500
Partial basal area (cm^2)
Old field
Native prairie
Control side
No competition side

Table 18. Paired t-test for natural log transformed basal area (cm^2) of control and potential competitor removal sides of individual plants.

Tract	Mean difference	df	T	P
Old field	-0.402	9	-3.659	0.005 **
Native prairie	-0.293	9	-1.136	0.285 ns

FIG. 24. Effect of tract on total aboveground biomass for each one-half of an *S. nutans* plant (neighbor removal versus untreated side). See Table 19 for significant P values.

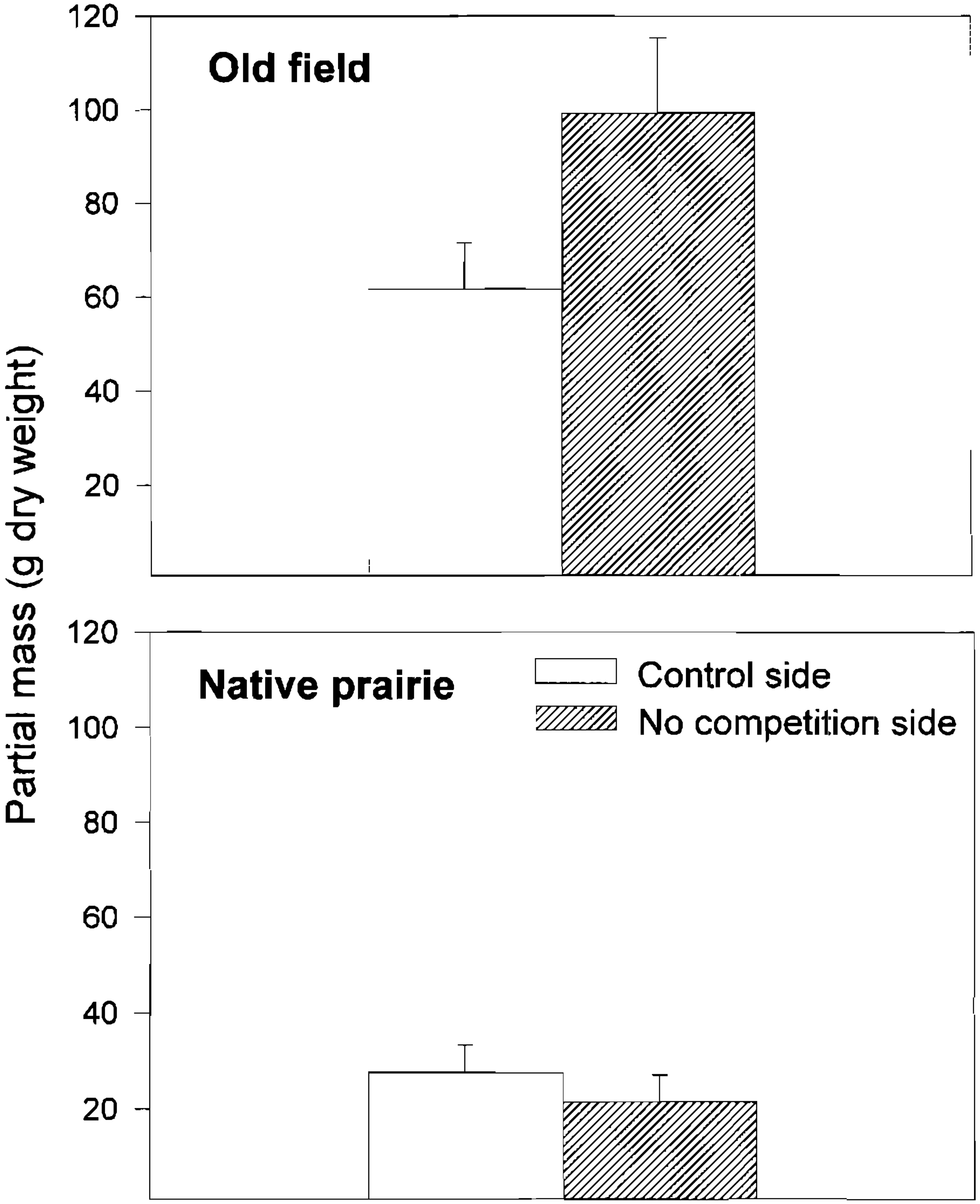

Old field
Native prairie
Control side
No competition side
Partial mass (g dry weight)
120
100
80
60
40
20

Table 19. Paired t-test for reproductive effort (g dry-weight of sexual reproductive structures / g dry-weight total) of control and potential competitor removal sides of individual plants.

Tract	Mean difference	df	T	P
Old field	0.002	9	0.355	0.731 ns
Native prairie	0.011	9	1.167	0.273 ns

There was little effect of removal of competitors on reproductive effort in experimental plants in either tract (Fig. 25). Reproductive effort was lower on the treatment side in native-prairie plants, but the difference was not significant (Table 20).

DISCUSSION

S. nutans plants in both old field and native prairie responded to neighbor removal by vegetative expansion in the competitor-free zone. The lack of significant growth difference between control and experimental plants suggests competition was not acting differentially in either tract or between the tracts, but that individual plants shifted their growth toward areas free from competitors.

Partial basal area plant size increased in response to competitive release only for old-field plants. Aboveground biomass also increased to a greater extent on the neighbor-removal side for old-field plants, but there was no difference for native-prairie plants. One season, is perhaps, not enough time to test fully the response of these plants to the elimination of competitors. However, in a four year study, Hartnett (1993) found similar yearly increases in radial expansion and tiller density in response to neighbor removal for the prairie grass, *P. virgatum*.

Sexual reproductive allocation in relation to aboveground biomass produced was not significantly different between treated and untreated sides of a plant. Reproductive effort may be less responsive to competitive pressure than tiller growth. Root damage from the herbicide also may have slightly reduced the sexual reproduction capabilities of the plant.

The non-significant response of native-prairie plants to competitive release is inconsistent with the theory of plant strategy (Grime 1977, 1979) which predicts competition will be greater in highly productive habitats. A late-successional prairie is highly productive because nutrient levels are higher and plants are able to exploit them, in terms of increased abundance. Earlier stage species have been removed from the

FIG. 25. Effect of tract on reproductive effort (RE = sexual biomass / total biomass) for each one-half of an *S. nutans* plant (neighbor removal versus untreated side).

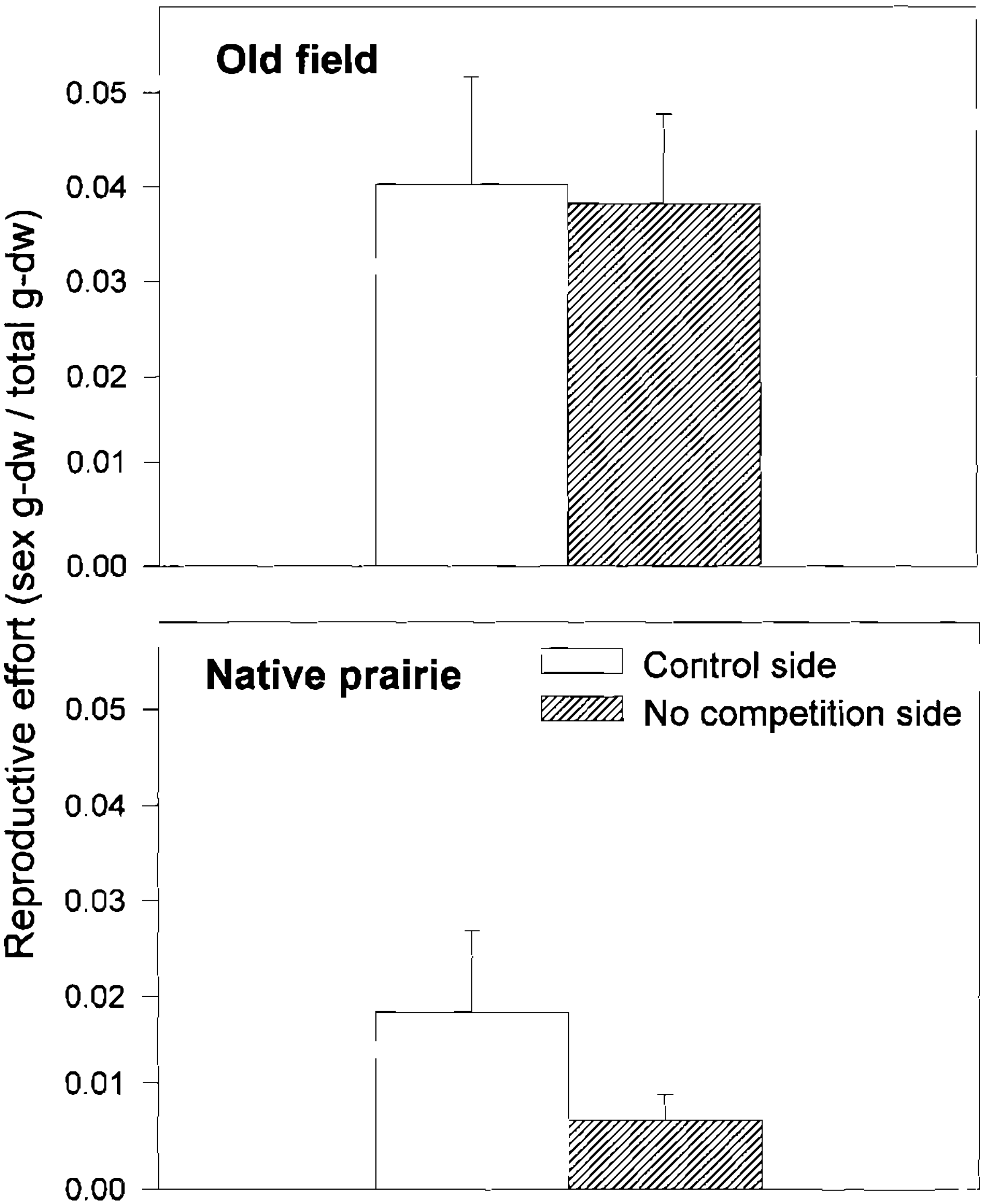

Old field
Native prairie
Control side
No competition side
Reproductive effort (sex g-dw / total g-dw)
0.00
0.01
0.02
0.03
0.04
0.05

Table 20. Paired t-test for natural log transformed mass (g dry weight) of control and potential competitor removal sides of individual plants.

Tract	Mean difference	df	T	P
Old field	-0.460	9	-8.012	< 0.001 ***
Native prairie	0.377	9	1.519	0.163 ns

community and replaced by more successful competitors. Successful competitors increase in abundance and tiller density over time. High productivity results in low light conditions within the canopy in a tallgrass prairie (Knapp 1984). Native-prairie plants may be competing, but light may be the limiting resource, and the plants grow faster and taller in an effort to capture it.

In contrast, significantly greater response by the old-field plants to a competitor-free environment supports the resource-ratio hypothesis of Tilman (1980, 1985, 1986), which suggests that competition drives the system along a gradient of changing amounts of limiting resources and the plant's ability to obtain resources determines its place in a succession. The old-field has experienced more recent disturbance than the native prairie. It is a more depauperate environment because years of farming have removed nitrogen from the soil and replacing it is a slow process. Plants that colonize and persist in the old field experience competitive intensity that is equally great or greater than their native-prairie complements.

S. nutans is a super-competitor grass that is, presumably, able to reduce nutrient levels in its environment and still maintain a population (Tilman 1988, 1990; Tilman and Pacala 1993; Wedin and Tilman 1993). Tall stems effectively capture light and spreading root systems (Weaver 1958), enable *S. nutans* to impact adjacent neighbors as well. *S. nutans* plants in both the old field and the native prairie increased tiller growth to exploit newly vacated habitat, indicating that they are also restricted by the presence of neighbors. In both communities of competitors, these plants appeared to be holding their space and would increase in size if opportunity permitted.

Plants, at any successional stage, face trade-offs between colonizing ability and competitive ability (Tilman and Cowan 1989; Tilman 1990; Tilman and Pacala 1993) that are resource based (Mooney 1972; Tilman 1988). *S. nutans* is a slow colonizer, however, once established it has traits that Chapin III (1980) attributed to species in infertile habitats, e.g., high biomass allocated to roots, low growth rate, and low rate of reproduction. Grime (1979) suggested these are traits that enable a plant to better tolerate the stress of old-field conditions.

S. nutans is a strong competitor on nutrient-poor soils because dominant prairie grasses allocate more resources to belowground biomass (Gleeson and Tilman 1990) and fewer resources to reproductive effort. Eventually, these grasses become successional dominants because their large root systems can obtain and store sufficient resources for the plant and deplete resources available to neighbors. Patterns of species in a successional stage may be the result of the allocation trade-offs that make plants better competitors.

CONCLUSIONS

Prairie grasses have invaded fairly early in the old-field succession. As colonizers they are mainly limited by the low dispersal ability of wind-borne dispersion. Once established, they must compete in an environment of low nutrient and high light availability. Traits evolved under the variable conditions of a tallgrass prairie, e.g., conservative nitrogen uptake, resistance to drought, and large root storage capacity, enable grasses to exploit newly opened habitats, locally adapt, and successfully persist over time.

At mid-succession the prairie grasses were strong competitors in a species rich and diverse community. My results showed that all three study species were correlated with decreased species richness and species diversity in their immediate neighborhoods. The impact of these species upon the neighbors suggests they were able to compete successfully at more than one successional stage.

Competitive ability derived from locally adapted life-history traits that differed from the traits of their putative population source in the native prairie may be due to phenotypic plasticity. In the common environment, trait differences observed in field plants tended to disappear. In the old-field population, plants maintained space and expanded annually by vegetative tillering. They were shorter, had greater basal area plant size, and grew at a slower rate than native-prairie plants.

The clumped distribution of *A. scoparius* and *S. nutans* in the old field (J.M. Mayo and A. Mayo unpublished data) suggests these species are advancing slowly across the tract, possibly propagated by occasionally successful seedlings. The distribution of *A. gerardii*, while not tested, probably has a similar pattern. *A. scoparius* may be increasing because of higher reproductive effort, a greater proportion of flowering plants, and better dispersal ability than the other two species. *A. gerardii* and *S. nutans* may have had lower reproductive effort in the old field because they invested more resources in roots and tillers or were beginning to spread by rhizomes. They also may have been constrained to allocate further resources due to nutrient-poor soil.

Competitive effects of neighbors on *S. nutans* caused the experimental plants to increase tillering substantially when potential competitors were removed. My results suggest that the old-field plants are slowly expanding, however, they do so at the resistance of their neighbors. Resource-allocation trade-offs from aboveground to belowground biomass have enabled these plants to make the most of their abiotic and biotic environment. The prairie grasses, *A. gerardii* and *S. nutans*, and to a lesser extent, *A. scoparius*, have flexible life history strategies and super-competitive abilities that lead eventually to successional dominance.

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APPENDIX

List of plant species recorded in species-area relationship and paired samples quadrats.

Herbaceous forbs:

Achillea millefolium L.

Ambrosia artemisiifolia L.

Amorpha canescens Pursh

Annual forb spp.

Apocynum cannabinum L.

Arenaria serpyllifolia L.

Artemisia campestris L.

Aster drummondii Lindl.

Cirsium altissimum (L.) Spreng.

Convolvulus arvensis L.

Croton texensis (Kl.) Muell. Arg.

Dalea purpurea Vent.

Desmanthus illinoensis (Michx.) MacM.

Erigeron strigosus Muhl. ex Willd.

Eupatorium altissimum L.

Euphorbia corollata L.

Gaura longiflora Spach

Gutierrezia dracunculoides (DC.) Blake

Helianthus maximilianii Schrad.

Mirabilis nyctaginea (Michx.) MacM.

Physalis heterophylla Nees.

Plantago major L.

Rosa arkansana var. *suffulta* (Greene) Cockll.

Ruellia humilis Nutt.

Rumex altissimus

Salvia azurea Lam.

Solanum carolinense L.

Solanum rostratum Dun.

Solidago canadensis L

Solidago missouriensis Nutt.

Sonchus oleraceus L.

Vernonia baldwinii Torr.

Woody shrubs:

Rhus glabra L.

Symphoricarpos orbiculatus Moench

Ulmus americana L.

Grasses and sedges:

Andropogon gerardii Vitman

Andropogon saccharoides Sw. var. *torreyanus* (Steud.) Hack.

Andropogon scoparius Michx.

Aristida oligantha Michx.

Bouteloua curtipendula (Michx.) Torr.

Bromus inermis Leyss.

Carex spp.

Chloris verticillata Nutt.

Dichanthelium oligosanthes (Schult.) Gould var. scribnerianum (Nash) Gould

Elymus virginicus L.

Eragrostis spectabilis (Pursh) Steud.

Koleria pyramidata (Lam.) Beauv.

Panicum capillare L.

Panicum virgatum L.

Sorghastrum nutans (L.) Nash

Sporobolus asper (Michx.) Kunth

Sporobolus neglectus Nash

Tridens flavus (L.) Hitch.

Jean H. Schulenberg
Signature of Graduate Student

James M. Mayo
Signature of Major Advisor

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