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COMPETITIVE ABILITIES OF SPARSE GRASS SPECIES: MEANS OF PERSISTENCE OR CAUSE OF ABUNDANCE¹

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Abstract. Sparse species have chronically small local population sizes, even though they occur in several habitats over a wide geographic range. Greenhouse de Wit replacement series with seven species of sparse and common perennial grasses of tallgrass prairie were performed with seedlings and tiller fragments for 5, 10, and 15 mo. As younger and older seedlings, sparse grasses overyielded and were advantaged by the interaction with common grasses. The common grasses underyielded and were disadvantaged in mixture with sparse grasses. As tillers, the interaction was less antagonistic, and both common and sparse grasses either overyielded or were unaffected by the interaction. Seedlings of sparse species were largest when planted in low proportion, surrounded by individuals of a common grass. Because the sparse species are not disadvantaged by interactions with their common neighbors, their competitive abilities are not implicated as a cause of their local rarity. Rather, the good competitive abilities of these sparse grasses are best viewed as a mechanism that offsets the hazards of low density and makes local persistence more likely.

Key words: *Agrostis hiemalis*; *Andropogon gerardi*; *Andropogon scoparius*; *competition*; *de Wit replacement series*; *Festuca paradoxa*; *persistence*; *prairie grasses*; *rarity*; *Setaria geniculata*; *Sorghastrum nutans*; *Sphenopholis obtusata*.

INTRODUCTION

Although found in several habitats over large geographic ranges, sparse species have small local populations wherever they occur (Rabinowitz 1981). We are concerned with how competitive abilities of sparse plant species relate to abundance and persistence, and we contrast two ideas: first, species may be locally rare because they are disadvantaged in competition with their neighbors, and second, species that are locally rare (for whatever reason) may be more likely to persist if they are good competitors.

Citations from five decades show that two views predominate in the literature: interspecific competitive abilities are an explanation for local abundances, and whether a species is locally rare or common is dependent on its ability to garner limited resources also sought by neighbors (McNaughton and Wolf 1970, Grime 1979). Fisher (1930) explained, "... abundant species will, ceteris paribus, make the most rapid evolutionary progress, and will tend to supplant less abundant groups with which they come into competition." With specific reference to rare species, Griggs (1940) reasoned:

The difference between a rare species and a common one lies in the fact that the one fails or almost

fails to establish its progeny in the competition for its habitat where the other succeeds in doing so. The explanation of rarity must, therefore, lie in an evaluation of the competitive competency of species.

R. H. Whittaker (1965) stated that "competition is assumed to have a major role in determining species abundance of vascular plants." Grime (1979) argued that under productive undisturbed conditions, abundant species are those with high competitive abilities.

Of course, there are many explanations for local rarity other than competitive ability. Selective herbivory (Rausher 1980, Parker and Root 1981, Louda 1982, Landa and Rabinowitz 1983) and susceptibility to pathogens (Burdon and Shattock 1980) can keep abundances low. For example, Klamath weed, *Hypericum perforatum*, a once abundant western range pest, was made locally rare by a biological control agent, the leaf-eating beetle *Chrysolina quadrigemina* (Huffaker 1957). There is also a suite of ideas that locally rare organisms are specialists, have small niches, have restricted requirements for regeneration, or are physiologically narrow (Cain 1940, McNaughton and Wolf 1970, Drury 1974, Grubb 1977, Hubbell 1979). (Other explanations account for larger scale, nonlocal effects of rarity such as endemism; an example is climatic contraction of geographic range [Rabinowitz 1981].)

The second view on sparse-species' competitive abilities focuses on persistence, in contrast to population regulation. A species which persists does not become

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TABLE 1. Experimental design for three de Wit replacement series with sparse (S) and common (C) prairie grasses.

Experiment	Source of competitors	Date of planting	Date of harvest	Duration (mo)	Treatments	No. species	No. species pairs			No. replicates per pair per proportion
							C:C	S:C	S:S	
I	Seed	Apr 1978	Sept 1978	5	Greenhouse only	5 (3 S, 2 C)	1	4	3	4
II	Seed	Oct 1978	Aug 1979	10	Overwintered outdoors	5 (3 S, 2 C)	1	4	3	1-4
III	Tiller	Apr 1978	Aug 1979	15	Overwinter outdoors, burned in spring	7 (4 S, 3 C)	3	12	6	2 (4 for mono-cultures)

locally extinct. Persistence forms an implicit criterion of fitness in many population dynamic models (Mountford 1971, Slatkin 1978, Boyce and Daley 1980). Local rarity implies that an individual is likely to be surrounded by neighbors of other species (Rabinowitz et al. 1979). If a plant grows vigorously in this circumstance, competitive exclusion (and local extinction) will be less probable.

We have posed two contrasting ideas. If sparse species are poor competitors, their low abundance and eventual local extinction are insured in an environment tending toward equilibrium. Turning the problem around, vigorous interspecific competitive ability of sparse species will make their persistence more likely, despite the predicament of local low density.

These notions generate contrasting expectations. If competitive ability influences local abundance, sparse species should garner resources poorly. If related to persistence despite sparseness, the competitive ability of sparse species should be vigorous. This distinction is basically one of sufficiency vs. necessity. Competitive inferiority may be a sufficient explanation for abundance, but if abundance is regulated by another cause, competitive superiority may be a necessary condition for persistence (L. R. Ginzburg, *personal communication*).

These two views are not mutually exclusive. Rare species may persist and yet still be competitively inferior to dominants by two means. They may act as fugitives and colonize patches of open habitat created by physical or biotic disturbance (Levins and Culver 1971, Horn and Mac Arthur 1972, Slatkin 1974, Levin 1976, Rabinowitz 1978). Alternatively, if species are competitively advantaged when rare but disadvantaged when common, this frequency-dependent reversal of competitive ability would permit persistence of rare species (Haldane 1932, Harper and McNaughton 1962, Pimentel et al. 1965, Mac Arthur and Connell 1967, Kahn et al. 1975).

Whether locally sparse species are competitively advantaged or disadvantaged relative to related common species of the same habitat is unknown (but see Hart [1980] for competition between weedy congeners and serpentine endemics, which are common when found). This paper reports on experiments investigating com-

petition among seven species of native perennial prairie grasses on an abundance continuum (Rabinowitz and Rapp 1981a, b). Prairie plants are excellent objects for competition studies (Allen [1982] and Parrish and Bazzaz [1982] provide two recent examples), and the de Wit approach (de Wit 1960) has proved fruitful for two decades (Martin and Harding 1981, Fowler 1982).

METHODS

Sparse and common species

The common species are typical "dominants" of the tallgrass prairie *Andropogon scoparius*, *A. gerardi*, and *Sorghastrum nutans* (Weaver 1954). They have aboveground biomasses of 73, 58, and 19 g/m², respectively, or 52% of the total aboveground biomass (Rabinowitz et al. 1979) at Tucker Prairie, Callaway County, Missouri, the source of seed. They are members of the tribe Andropogoneae and are warm-season (C₄) perennial grasses (Gould 1968, Teeri and Stowe 1976).

The sparse species (*Festuca paradoxa*, *Sphenopholis obtusata*, *Agrostis hiemalis*, and *Setaria geniculata*) have large geographic ranges, occur in a variety of habitats, and are never very common. The first three are cool-season (C₃) festucoid grasses in the tribes Aveneae and Festuceae. *Setaria geniculata* is a C₄ member of the tribe Paniceae. In nature, all have generally small stature as adults (Rabinowitz and Rapp 1981a). Their aboveground biomasses constitute 7.8, 0.2, 1.3, and 0.8 g/m², respectively, summing to 3% of the total aboveground biomass at Tucker Prairie.

Although three of four of the sparse species are C₃ grasses in a C₄-dominated habitat, their local rarity is not caused simply by a disadvantageous photosynthetic apparatus. As one goes northward in prairie vegetation, dominance shifts from C₄ to C₃ grasses of taxa other than these. As climatic suitability presumably increases, the sparse species do not become increasingly common.

Experimental design and greenhouse procedures

In these greenhouse de Wit replacement series, species pairs interacted in mixtures at constant planting density but varying proportion of the components (de Wit 1960, 1971, Harper 1977, Mead 1979). At the Mat-

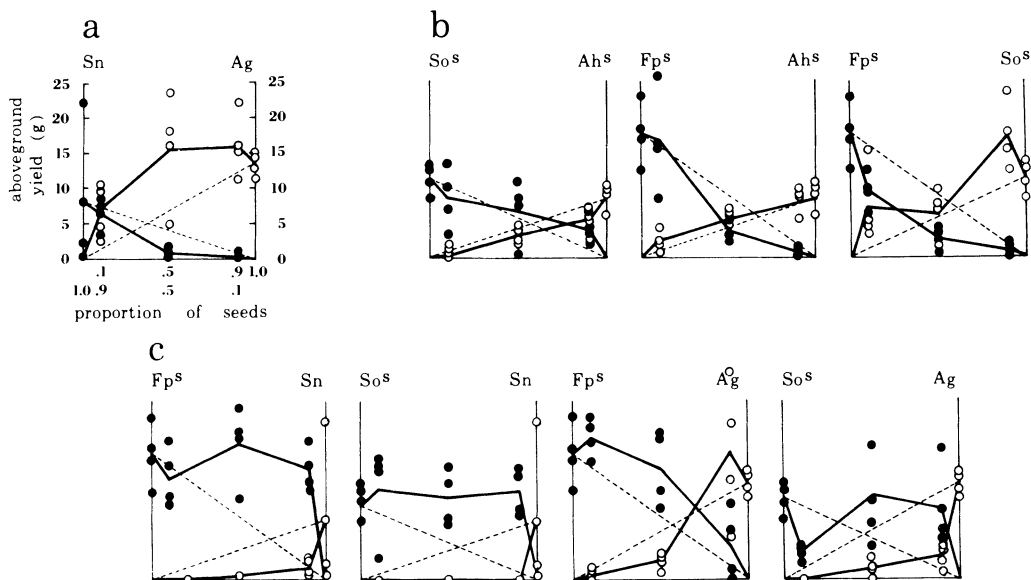


FIG. 1. de Wit diagrams for competition over 5 mo among seedlings of sparse and common grasses. The sparse species are marked with a superscript *s*. The *x* axis shows proportion of seeds in the mixture; the *y* axis shows total aboveground yield (g) of the species labeled at the top. ---- expected yield assuming equal competitive abilities. Ah = *Agrostis hiemalis*, Ag = *Andropogon gerardi*, Fp = *Festuca paradoxa*, Sn = *Sorghastrum nutans*, So = *Sphenopholis obtusata*. Each point is a replicate, and four replicates of each proportion are shown. a. The common : common pair. b. The three sparse : sparse pairs. c. The four sparse : common pairs. Modified from Rabinowitz (1981) and reprinted with permission.

thaei Botanical Gardens of the University of Michigan, Ann Arbor, Michigan, USA, competition was staged between pairs of sparse species, between pairs of common species, and between sparse and common species during 1978 and 1979 (Table 1 summarizes the design). In the greenhouse, each species within each pair was experimentally made both abundant and rare. Species consequently interacted both in natural abundance rank (sparse species were planted as rare, and common as abundant) and in the reverse rank (sparse species were planted as abundant, and common as rare). The experiments were begun from both seed and tillers (vegetative fragments) and were continued for three lengths of time: 5, 10, and 15 mo (Table 1). In the field, seeds germinate during a major period in the spring and a minor episode in autumn (Rabinowitz and Rapp 1981b); experiments with seedlings were initiated at both seasons.

Five planting proportions were employed: monocultures of each species and mixtures at 0.5:0.5, 0.9:0.1, and 0.1:0.9 ratios. The availability of seed and tiller stocks determined the number of species in each experiment. The number of replicates was generally four (lower for some combinations in experiments II and III [Table 1]). Planting densities were 4 seeds/cm² and 0.1 tiller fragments/cm². The former density was chosen because previous experiments demonstrated resource depletion at that planting rate (Rabinowitz 1979). The latter density was the closest spacing of tillers we could conveniently plant by hand. Tillers with roots

(rhizome fragments for *Setaria geniculata*) were planted in a 4 × 5 grid. For the 0.5:0.5 ratio, the tillers were arranged in a checkerboard. For the 0.9 to 0.1 combination, the minority component was placed so that each tiller fragment had eight neighbors of the majority species.

At Tucker Prairie, diaspores were collected from several hundred individuals of each species during summer 1977 and stored in kraft paper bags at room temperature. All species disperse both empty and full (i.e., containing a grain) diaspores, and the seed-set is greater for the sparse species than for the common; to compensate for empty diaspores the number of diaspores planted was corrected upward. The sparse species showed more rapid and more complete germination than the common species, so all statistical analyses for seedlings are performed on the masses of individuals, not total yields. We did not monitor mortality.

Soil was agricultural loam from Washtenaw County, Michigan, sterilized and mixed 4:1 with sand. Greenhouse flats (40 × 35 × 10 cm) were divided with wooden partitions into six sections (13 × 17 × 10 cm), and the plots were randomly assigned to a section. Seeds were covered with a thin layer of milled sphagnum to deter desiccation and damping off. Plants were mist-watered daily or when needed.

Space restrictions in the greenhouse dictated that plots were small to accommodate a larger number of species pairs and replicates. The entire plot was harvested. Although this procedure introduces the possi-

TABLE 2. Analyses of variance for species effects and competitive effects for experiment I: seedling competition lasting 5 months.

	df	SS	MS	F	Significance
Species effects					
Species	3	2.798	0.933	1.289	NS
Error	12	8.683	0.724		
Total	15	11.481			
Competitive effects					
Competitive effects	3	571.34	190.45	3.813	0.25 > P > .01
Species × competitive effects	3	345.70	115.23	2.352	NS
Ratio of densities	2	274.72	137.36	2.809	NS
Competitive effects × ratio	6	466.16	77.69	1.556	NS
Species × competitive effects × ratio	6	284.77	47.46	0.969	NS
Error	44	2155.34	48.98		
Total	64	4098.03			

bility of edge effects and may account to some degree for the variance among replicates, it is unlikely that the results were fundamentally altered by this protocol.

Individuals were clipped at soil level, counted, sorted by species, and oven-dried at 80°C. For each species, the mass of the total yield per plot was determined. For seedlings, mean mass per individual was calculated as the total yield per plot divided by the number of harvested individuals. Competitive interactions were visually evaluated using de Wit replacement diagrams. The outcome of each de Wit relative-yield diagram was assessed qualitatively and conservatively. If the data of an experiment were ambivalent (for instance, competition between tillers of *Festuca paradoxa* and *Andropogon gerardi*), we classified the result as uninterpretable. Only experiment III produced uninterpretable outcomes. We categorized each interpretable diagram as showing underyielding, overyielding, or yielding no different than expectation for each component. This procedure yields one of nine possible outcomes for each de Wit diagram (see Appendix).

Statistical analyses were performed on the mass per individual for seedlings and on total yield for tillers, and followed the analysis of variance procedure of McGilchrist (1965) and McGilchrist and Trenbath (1971). Our adaptation of their procedure has two parts. The first ANOVA, termed species effects, addresses the question of whether species differ in monocultural performances and is calculated on log-transformed masses for single-species plots only. The second ANOVA, termed competitive effects, tests whether the competitive abilities of the species differ and is performed as a measure of aggressivity:

$$A_{iju} = 0.5 (X_{iju}X_{ii} - X_{jiu}X_{jj}), \quad (1)$$

where X_{iju} is the mass of an individual of species i in a mixture with species j in replicate u , X_{iiu} is the mass of an individual in a monoculture of species i in replicate u , and X_{ii} is the average of the X_{iiu} over the replicates. $A_{iju} = -A_{jiu}$. Aggressivity measures whether individuals of each species gain or lose biomass as a

result of the interaction. Positive aggressivity indicates the superior competitor; negative aggressivity, the inferior competitor. If two species are competitively equivalent, the expectation for aggressivity is zero. (McGilchrist and Trenbath propose a third analysis of relative yield totals; we omit this ANOVA because competitive ability, not monocultural vs. polycultural yield differences, is our major focus.) We adapted the general linear models procedure in SAS to perform the calculations (Freund and Littell 1981).

RESULTS

Experimental I: seedling competition lasting 5 mo

De Wit diagrams show total aboveground yield (Fig. 1). When seedlings of common grasses were grown

TABLE 3. Mean aggressivities and contrasts for experiment I: seedling competition lasting 5 mo.

Species	Mean aggressivity
Common	
<i>Andropogon gerardi</i>	-2.176
<i>Sorghastrum nutans</i>	-1.021
Sparse	
<i>Festuca paradoxa</i>	2.309
<i>Sphenopholis obtusata</i>	0.689
Contrasts	
Sparse vs. common:	
$H_0: \mu_{AG+SN} = \mu_{FP+SO}$	$H_1: \mu_{AG+SN} \neq \mu_{FP+SO}$
Contrast = 6.19	SE = 2.48 SS = 310.95
F = 6.22	P < .02
<i>Andropogon gerardi</i> vs. <i>Sorghastrum nutans</i> (common vs. common):	
$H_0: \mu_{AG} = \mu_{SN}$	$H_1: \mu_{AG} \neq \mu_{SN}$
Contrast = 1.16	SE = 1.78 SS = 21.01
F = 0.42	NS
<i>Festuca paradoxa</i> vs. <i>Sphenopholis obtusata</i> (sparse vs. sparse):	
$H_0: \mu_{FP} = \mu_{SO}$	$H_1: \mu_{FP} \neq \mu_{SO}$
Contrast = 1.62	SE = 1.73 SS = 43.95
F = 0.880	NS

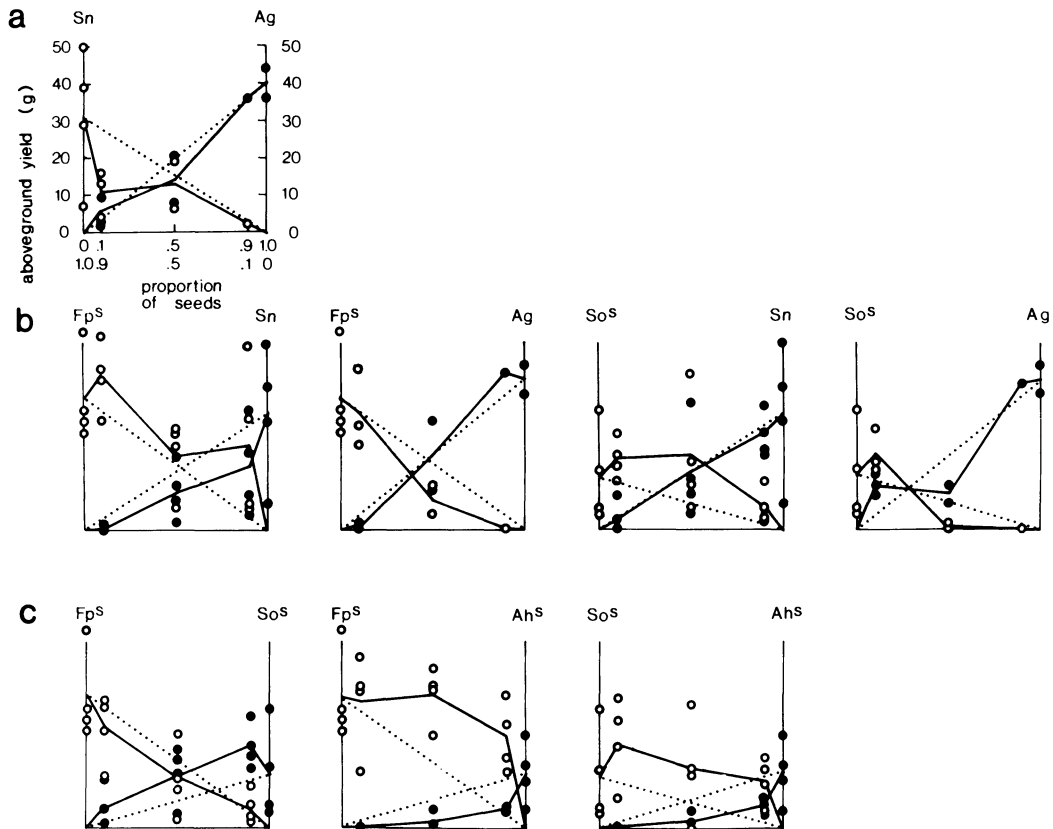


FIG. 2. de Wit diagrams for competition over 10 mo among seedlings of sparse and common grasses. The sparse species are marked with a superscript *s*. The *x* axis shows the proportion of seeds in the mixture; the *y* axis shows total aboveground yield (g) of the species labeled at the top. . . . expected yield assuming equal competitive abilities. Each point is a replicate. a. The common:common pairs. b. The sparse:common pairs. c. The sparse:sparse pairs. Ah = *Agrostis hiemalis*, Ag = *Andropogon gerardi*, Fp = *Festuca paradoxa*, Sn = *Sorghastrum nutans*, So = *Sphenopholis obtusata*.

together, one species was clearly advantaged; the other was disadvantaged (Fig. 1a). When sparse grasses interacted (Fig. 1b), they seemed in general more evenly matched. When a sparse grass was grown with a common grass (Fig. 1c), the sparse component was clearly advantaged and conspicuously overyielded. The common species underyielded in three of four cases.

The main competitive effect is significant in the analysis of variance on aggressivities calculated from individual masses. This result indicates that some species have better, and some worse, competitive abilities (Table 2). The mean aggressivities of the common grasses are negative, indicating their competitive disadvantage, and conversely, the mean aggressivities of the sparse species are positive, indicating their competitive superiority (Table 3). Contrasts show that this pattern is statistically significant. The sparse species do not differ among themselves in aggressivity, and neither do the common species. No other effects in the analysis of variance are significant. The species do not show different sizes of individuals in monoculture. Although species have greater or lesser aggressivities, the inter-

action term is not significant. This result shows that the competitive outcome depends on the abilities of the individual species, not the particular species pair under observation. Stated another way, particular pairs do not show unexpectedly strong or weak interactions. The ratio effect is not significant, showing that aggressivity does not vary greatly with relative planting density. The two-way interaction terms are not significant.

Experiment II: seedling competition lasting 10 mo

In terms of total yield, the de Wit diagrams demonstrate that seedlings of common grasses yielded at approximate expectation based on monoculture and were about evenly matched (Fig. 2a). When sparse and common grasses were grown together (Fig. 2b), the sparse species overyielded in two cases, were unaffected by the interaction in one case and underyielded in one case. The common species underyielded or yielded at expectation. Thus, relative to the common grasses, the sparse species were not markedly disadvantaged, but they were not as conspicuously advantaged as in the first experiment.

TABLE 4. Analyses of variance for species effects and competitive effects for experiment II; seedling competition lasting 10 months.

	df	SS	MS	F	Significance
Species effects					
Species	3	0.093	0.0310	0.31	NS
Error	10	0.989	0.0989		
Total	13	1.082			
Competitive effects					
Competitive effects	3	62.761	20.920	6.66	$P < .005$
Species \times competitive effects	3	7.499	2.499	0.91	NS
Ratio of densities	2	27.145	13.573	4.32	$P < .025$
Competitive effects \times ratio	6	40.492	6.749	1.92	NS
Species \times competitive effects \times ratio	6	5.1072	0.851	0.31	NS
Error	31	85.067	2.744		
Total	51	228.071			

However, in terms of individual plant masses, the statistical outcome of the second experiment was very similar to the first experiment (Tables 4 and 5). The ANOVA shows that aggressivity differs among species (Table 4), and the sparse species are superior competitors to the common species (Table 5). The first and second experiments differ in two ways. First, the absolute values of mean aggressivity vary from 0.13 to 0.95 in the second experiment, lowered from 0.69 to 2.31 in the first. Thus, the intensity of competition seems lessened as time passes. Second, the effect of ratio is significant: aggressivity differs at different planting proportion. Visual inspection of the de Wit plots (Fig. 2) shows no obvious way in which the effect of ratio is consistent, and the interaction of ratio with competitive effects is not significant. As with the first experiment, no interaction terms are significant, and monocultural yields do not differ.

Experiment III: tiller competition lasting 15 mo

The de Wit diagrams for experiment III (Fig. 3) are more difficult to interpret than those for the previous two experiments. Our interpretation is particularly conservative; we withdrew from consideration any cases where the coefficient of variation for any pair of replicates was > 1.5 (see Appendix). Four of 21 cases fell into this category and were sufficiently ambiguous that no clear result could be discerned.

Begun from tillers, the common grasses seemed equally balanced. The sparse species again had a hierarchy, with *Festuca paradoxa* overyielding. In mixture with common grasses, the sparse grasses overyielded in four of eight cases, and yielded at expectation in the remainder (see Appendix). In mixture with sparse species, the common species did not appear disadvantaged; they yielded at expectation in six of eight cases and overyielded in the other two. When grown together, none of the sparse:common pairs showed underyielding.

When populations are established from vegetative

fragments and the interaction has a duration of 15 mo, the competitive abilities of the species do not differ significantly (Table 6). Thus, species seem evenly matched when older, and the intensity of their interaction diminishes over the course of the three experiments. The only significant effect in the analysis of variance for aggressivity is ratio. As with the second experiment, aggressivities differ at different ratios, but the interaction with competitive effects is not significant. The species effect is significant. When the species have longer to grow and the common species escape the marked dominance of the sparse species, the differences in their stature, which are apparent in the field,

TABLE 5. Mean aggressivities and contrasts for experiment II: seedling competition lasting 10 mo.

Species	Mean aggressivity
Common	
<i>Andropogon gerardi</i>	-0.128
<i>Sorghastrum nutans</i>	-0.948
Sparse	
<i>Festuca paradoxa</i>	0.616
<i>Sphenopholis obtusata</i>	0.429
<i>Contrasts</i>	
Sparse vs. common:	
$H_0: \mu_{AG+SN} = \mu_{FP+SO} \quad H_1: \mu_{AG+SN} \neq \mu_{FP+SO}$	
Contrast = 2.12 SE = 0.719 SS = 27.28	
$F = 7.77 \quad P < .01$	
<i>Andropogon gerardi</i> vs. <i>Sorghastrum nutans</i> (common vs. common):	
$H_0: \mu_{AG} = \mu_{SN} \quad H_1: \mu_{AG} \neq \mu_{SN}$	
Contrast = 0.821 SE = 0.548 SS = 7.030	
$F = 2.00 \quad NS$	
<i>Festuca paradoxa</i> vs. <i>Sphenopholis obtusata</i> (sparse vs. common):	
$H_0 = \mu_{FP} = \mu_{SO} \quad H_1: \mu_{FP} \neq \mu_{SO}$	
Contrast = 0.187 SE = 0.466 SS = 0.508	
$F = 0.14 \quad NS$	

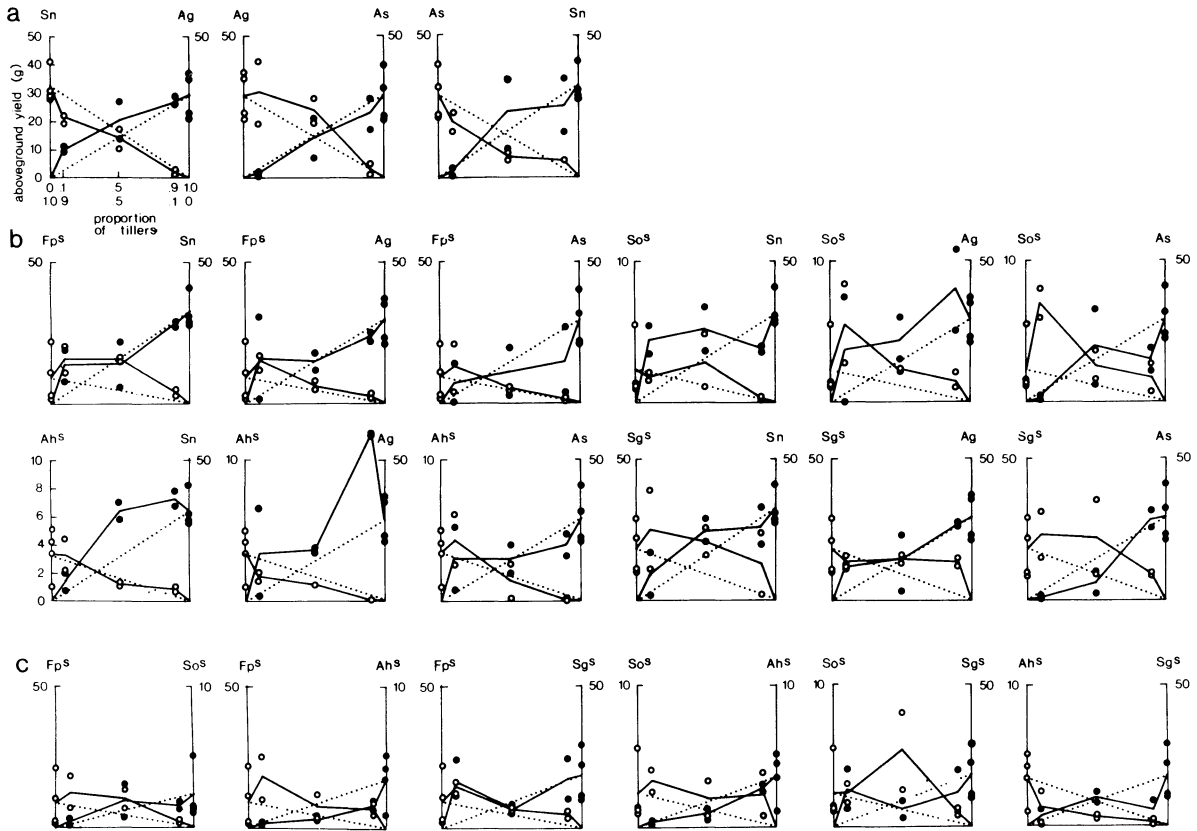


FIG. 3. de Wit diagrams for competition over 15 mo among tillers of sparse and common grasses. The sparse species are marked with a superscript *s*. The *x* axis is the proportion of tillers planted in the mixture; the *y* axis is the total aboveground yield (g) of the species labeled at the top. . . . expected yield assuming equal competitive abilities. Each point is a replicate. Two replicates of each proportion in mixture are shown, and four replicates for each monoculture. a. The common:common pairs. b. The sparse:common pairs. c. The sparse:sparse pairs. Ah = *Agrostis hiemalis*, Ag = *Andropogon gerardi*, As = *Andropogon scoparius*, Fp = *Festuca paradoxa*, Sg = *Setaria geniculata*, Sn = *Sorghastrum nutans*, So = *Sphenopholis obtusata*.

become expressed. Individuals of the common species are larger than those of the sparse species.

Summary

When planted in mixture with seedlings of sparse grasses, seedlings of common grasses were disadvantaged (Figs. 1 and 2, Tables 2–5). Sparse-species seedlings were competitively advantaged. For tiller fragments, the common grasses generally yielded at expectation or better (Fig. 3, Table 6). As tillers, the sparse grasses were either advantaged or unaffected by the presence of the common grasses. The interaction between common and sparse grasses was antagonistic at first, with the sparse species overyielding. The interaction became less antagonistic as plants matured, and interference was diminished.

Under what circumstances was the size of individual plants of each species largest? For seedling competition, an individual of a sparse species was largest when planted in low proportion (0.1) in mixture with a common species (Rabinowitz 1981). In mixtures with other

sparse species, the size of a sparse individual varied less with proportion. For the common species, in contrast, individuals were largest in monoculture or in combination with another common species. Because of the superior competitive abilities of the sparse species, the individuals grew largest in the proportion in which they are found in the wild. Sparse species thus grew best when sparse.

DISCUSSION

In greenhouse de Wit replacement series with seedlings and tillers, spanning 5–15 mo, sparse species of prairie grasses were generally advantaged and overyielded in competition with common grasses. In most cases where sparse species did not overyield, they yielded based on monocultural expectation and thus appeared unaffected by the presence of the common grass. In only 1 out of 16 cases, a sparse species underyielded in mixture with a common grass (see Appendix).

As seedlings, common grasses are generally disadvantaged in mixtures with sparse grasses. When the

TABLE 6. Analyses of variance for species effects and competitive effects for experiment III: competition among tillers lasting 15 mo.

	df	SS	MS	F	Significance
Species effects					
Species	6	33.837	5.640	14.71	$P < .0001$
Error	21	8.051	0.383		
Total	27	41.888			
Competitive effects					
Competitive effects	6	9.371	1.562	1.79	NS
Species \times competitive effects	15	3.637	0.242	0.28	NS
Ratio of densities	2	15.927	7.964	9.13	$P < .001$
Competitive effects \times ratio	12	1.768	0.147	0.17	NS
Species \times competitive effects \times ratio	30	5.397	0.180	0.21	NS
Error	57	12.072	0.212		
Total	122	43.957			

experiments run longer, tillers of common plants do not suffer yield depression from the interaction. The species appear to circumvent interference by some means (termed annidation [Kahn et al. 1975]). Either they were "keeping out of each other's way," or one species actually augmented the yield of the other.

There is no indication of frequency-dependent reversal of competitive ability when sparse species are artificially made common. The data show neither that sparse species are poor competitors nor that common species are superior ones.

Greenhouse experiments have conspicuous limitations for extrapolation, and they beg the question of what situations in nature, if any, they represent. These experiments are not intended as mimics of natural conditions, but rather as one realization of the dynamic behavior that these species may exhibit (Mertz and McCauley 1980). Slobodkin (1961) pointed out, ". . . the laboratory worker deals with all possible worlds and the fieldworker is confined to the real world." Under different conditions for growth, different results may occur, as is the case for any experiment. For instance, the advantage of barley over wheat can be eliminated by powdery mildew (Burdon and Chilvers 1977). Temperature (17°/14° and 34°/28°C day/night) reversed competitive advantage for *Amaranthus retroflexus*, a C4 forb, and *Chenopodium album*, a C3 forb (Percy et al. 1981). These experiments with prairie grasses also involved mixtures of C3 and C4 species. The C3 grasses usually overyielded, and the C4 grasses generally underyielded or were unaffected by the interaction. The sparse C4 grass *Setaria geniculata* overyielded in tiller mixtures with common C4 grasses. Although two cases are far too few to generalize, *Setaria geniculata* behaved in a manner similar to a sparse C3 rather than a common C4.

As a consequence of their good competitive abilities, individuals of sparse species grew largest when they were rare in combination with common species. Stated another way, although seedlings of sparse grasses were generally advantaged over common grasses at all por-

portions, they were most advantaged when surrounded by many common individuals. Sparse species grew most vigorously when planted in the proportion resembling nature. What might seem an initially paradoxical result (sparse species were good competitors) becomes a Panglossian one (Gould and Lewontin 1979).

These laboratory data are consonant with the idea that competitive abilities render persistence of rare species more likely, despite disadvantages of local small population size. Let us imagine that a species is rare because it is attacked by a lethal fungal pathogen, for example, American chestnut *Castanea dentata* and the blight *Endothia parasitica* (Anagnostakis 1982). If the pathogen is density dependent, individuals that are isolated (for whatever reason) will be more likely to escape infection (van der Plank 1975). Isolated individuals will be surrounded by individuals of other species, rather than by conspecifics. At Tucker Prairie, the flowering culms of the sparse grasses are separated by greater distances than are culms of common grasses (Rabinowitz et al. 1979). An organism in this situation will have enhanced probability of persistence if its growth is vigorous when in low proportion. Thus, competitive abilities of sparse species may reflect "preadaptation" to persistence in low density, or a life-history shift (Antonovics 1976).

If, in nature, the sparse grasses are good competitors, why are the common grasses not displaced? We suggest three possible reasons. Most simply, the low density of the sparse species may be caused by mechanisms distinct and independent from competitive ability, for instance, a specialized herbivore or pathogen. Sparse species may thus never become numerous enough to exclude common species. Alternatively, in grasslands, seedlings are likely to compete with one another on disturbances, such as badger mounds (Platt 1975, Platt and Weis 1977), molehills (Jalloq 1975), and ant mounds (King 1977). Disturbance may occur sufficiently frequently and set the interaction back to its beginning often enough to prevent exclusion of common species (Connell 1978, Huston 1979). Lastly, as

our data indicate, once past the seedling stage, the common species may simply be unaffected by the presence of the sparse species.

Why, in our experiments, did sparse grasses overyield? We tentatively propose two possible explanations. The smaller seeds of sparse species germinated before those of common species (beginning in 7 as opposed to 12 d [Rabinowitz 1978, Rabinowitz and Rapp 1981*b*]). Getting a head start may be crucial to interaction among seedlings (Ross and Harper 1972). Alternatively, the growth rates of the sparse species may simply be greater. From tillers, the cool-season sparse grasses grew most rapidly before the warm-season common grasses had their peak (Ode et al. 1980). The earlier sparse species may have overyielded, while the warm-season grasses were still small, but the warm-season grasses grew most actively after the sparse grasses had reached full size. This phenological separation may be responsible for the later competitive results.

Williams (1964) and May (1975, 1981) have pointed out that, if abundances are governed by numerous, largely independent factors with multiplicative interactions, then the lognormal species abundance distribution is implied by the central limit theorem. Field ecologists are not surprised that control of abundance cannot be attributed to a single process such as competition (Gleason 1926). The competitive abilities of sparse grasses are best viewed as a mechanism that offsets a hazard of low density, rather than a cause of rarity.

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APPENDIX

Summary of the outcomes of de Wit replacement series for sparse and common prairie grasses. Results were assessed visually from de Wit diagrams. "Over" indicates overyielding above expectation based on average monocultural yield; "under" indicates underyielding; "expect" indicates that yield was indistinguishable from monocultural expectation; — indicates that the data were uninterpretable.

Pairs	Origin of plants and duration of experiment		
	Seeds 5 mo	Seeds 10 mo	Tillers 15 mo
Common : common			
<i>Sorghastrum nutans</i> : <i>Andropogon gerardi</i>	under : over	expect : expect	expect : expect
<i>Andropogon gerardi</i> : <i>Andropogon scoparius</i>			expect : expect
<i>Andropogon scoparius</i> : <i>Sorghastrum nutans</i>			under : expect
Sparse : common (the sparse species is listed on the left)			
<i>Festuca paradoxa</i> : <i>Sorghastrum nutans</i>	over : under	over : under	over : expect
<i>Festuca paradoxa</i> : <i>Andropogon gerardi</i>	over : expect	under : expect	
<i>Festuca paradoxa</i> : <i>Andropogon scoparius</i>			expect : expect
<i>Sphenopholis obtusata</i> : <i>Sorghastrum nutans</i>	over : under	over : expect	expect : over
<i>Sphenopholis obtusata</i> : <i>Andropogon gerardi</i>	over : under	expect : expect	—
<i>Sphenopholis obtusata</i> : <i>Andropogon scoparius</i>			over : expect
<i>Agrostis hiemalis</i> : <i>Sorghastrum nutans</i>			expect : over
<i>Agrostis hiemalis</i> : <i>Andropogon gerardi</i>			—
<i>Agrostis hiemalis</i> : <i>Andropogon scoparius</i>			expect : expect
<i>Setaria geniculata</i> : <i>Sorghastrum nutans</i>			over : expect
<i>Setaria geniculata</i> : <i>Andropogon gerardi</i>			—
<i>Setaria geniculata</i> : <i>Andropogon scoparius</i>			over : expect
Sparse : sparse			
<i>Festuca paradoxa</i> : <i>Sphenopholis obtusata</i>	under : over	expect : over	over : expect
<i>Festuca paradoxa</i> : <i>Agrostis hiemalis</i>	under : expect	over : under	over : under
<i>Festuca paradoxa</i> : <i>Setaria geniculata</i>			over : expect
<i>Sphenopholis obtusata</i> : <i>Agrostis hiemalis</i>	expect : expect	over : under	over : under
<i>Sphenopholis obtusata</i> : <i>Setaria geniculata</i>			over : expect
<i>Agrostis hiemalis</i> : <i>Setaria geniculata</i>			under : expect

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