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DENSITY-DEPENDENT DEMOGRAPHY IN TWO GRASSES: A FIVE-YEAR STUDY[1]

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Abstract. To determine the strength, frequency, and nature of density-dependent processes in natural plant populations, the densities of two perennial grass species, *Bouteloua rigidiseta* and *Aristida longiseta,* were perturbed in an otherwise undisturbed community. Both seed additions and adult removals, of each species separately, were used. Individual plant survival, growth, and reproduction were monitored, as well as recruitment to the population and the numbers in each size class of each species, for 5 yr.

The responses to the experimental perturbations were small relative to the magnitude of the perturbations, indicating that density dependence in demographic parameters in both populations was weak throughout the period. The results therefore do not support the suggestion of Fowler (1986) that the weak density dependence in the *Bouteloua rigidiseta* population in the 1st yr of the experiment was a temporary result of drought.

Significant responses to the density manipulations were scattered among annual intervals, characters, and replicates. This may be simply a result of testing responses at the limits of detectability, or it may reflect intermittent and scattered density dependence. Density effects were generally much smaller than other differences among quadrats and differences among plants within quadrats, indicating that other factors had much more effect on a plant's fate.

Key words: Aristida longiseta; Bouteloua rigidiseta; *competition; demography; density-dependent effects; grass; grassland; population regulation.*

INTRODUCTION

It is an axiom of ecology that there is some population size (or biomass, for a plant species) beyond which resources will be insufficient to provide all members of the population with all the resources they can use. A corollary of this axiom is that when a population exceeds this size, a shortage of resources will reduce survival and/or reproduction; the larger the population, the smaller the quantity of resources available to each individual and the greater the reduction in survival or reproduction. Before a population reaches this critical size, unequal division of resources will generally cause resource shortages to reduce the survival or reproduction of some individuals. Thus, unless a population is much smaller than its resource-determined potential size, one or more demographic parameters will exhibit negative density-dependent behavior, i.e., the rate of survival or reproduction will be a negative function of the number of conspecific individuals. Negative density dependence of demographic parameters can also be caused by specialist herbivores and pathogens.

Despite the centrality of these concepts in ecology, there are relatively few direct tests of negative density dependence in natural plant populations (Clay and Shaw 1981, Keddy 1981, Smith 1983*a, b, c,* Andrew 1986, Shaw and Antonovics 1986, Shaw 1987, Reed 1990), although there are a number of field studies that have measured one or more effects of manipulations of the density of conspecific neighbors (e.g., Platt and

Weis 1985, Nobel and Franco 1986, Goldberg 1987, Schmitt et al. 1987, Johnson and Mann 1988, Aguilera and Lauenroth 1993). There are also some descriptive studies that have measured the effects of different natural densities on demographic parameters (e.g., Watkinson and Harper 1978, Weiner 1984, Hubbell et al. 1990). There is also little evidence to indicate whether or not density dependence arising from specialist herbivores (Louda and Keeler 1990) or pathogens (Augspurger 1984, Burdon 1987) is common in natural populations. There are very few studies that address the questions, How strong is density dependence?, How frequently does density dependence occur? and What stages in the life cycle are most affected by density?

The experiment described here was initiated to determine whether or not negative density dependence of demographic parameters could be detected in a natural population of a small perennial bunchgrass, *Bouteloua rigidiseta,* hereafter *Bouteloua,* and if so, which demographic parameters were affected, the magnitude of the effect, and how frequently density dependence occurred. The effects of *Bouteloua* density on another small perennial bunchgrass in the same community, *Aristida longiseta,* hereafter *Aristida,* were also investigated, to compare intra- and interspecific interactions. Since purely descriptive studies confound the direct effects of density with the effects of other types of spatial variation in the environment (Fowler 1990), *Bouteloua* densities were manipulated experimentally by removing adults and by adding seeds. The results of the first census after the treatments were imposed

were reported in Fowler (1986). Positive but relatively weak responses to adult removals were detected in adult size and in the size of new recruits to the population. (Size is highly correlated with both survival and fecundity in these species.) Seed additions produced an increase in the number of new recruits to the population and a decrease in their size and in the size of new recruits to the *Aristida* population. In that paper I suggested that the relative weakness of negative density-dependent responses may have been due to a natural, drought-related reduction in size that the *Bouteloua* population apparently underwent just before the treatments were imposed.

This experiment was continued for another 3 yr (a total of five censuses, including the baseline census made before treatments were initiated). Two additional treatments were added to the design in the 2nd yr, the removal of *Aristida* adults and the addition of *Aristida* seeds, so that density dependence in *Aristida* demographic parameters, and the effects of *Aristida* on *Bouteloua*, could be investigated. The results from the final three censuses of the experiment are reported here, together with a reanalysis of the results of the first 2 yr.

METHODS

Species and site

The study site, in Pedernales Falls State Park, Blanco County, Texas, has been described elsewhere (Fowler 1984, 1986). Clumps of woody plants, primarily *Quercus fusiformis, Juniperus ashei, Berberis trifoliolata,* and *Prosopis glandulosa,* are scattered in a matrix of grassland vegetation. All of the experimental quadrats were located in open, grassy areas dominated by various perennial shortgrasses, including *Bouteloua rigidiseta* and *Aristida longiseta.*

Both *Aristida longiseta* and *Bouteloua rigidiseta* are small perennial bunchgrasses and superficially appear very similar when not reproductive. In central Texas, both set abundant seed in May or June each year. The seeds of *Bouteloua* are dispersed and germinate within a cluster of spikelets that form a branch of the infructescence. These units will be referred to as "spikelet clusters"; note that the same units have been called "infructescence branches" in some previous publications. These units, and individual seeds of *Aristida,* were collected each year at the field site (but not in the experimental quadrats) for later use in this experiment, and stored loosely so as not to damage the long awns (*Aristida*) or spikelet clusters (*Bouteloua*).

Experimental design

As described in Fowler (1986), six groups of quadrats, each containing four contiguous 45 × 90 cm quadrats, were permanently marked in 1982. In each group, one quadrat was randomly assigned to each of four treatments: control, addition of *Bouteloua* seed, partial removal of *Bouteloua* adults, or both seed addition and adult removal of *Bouteloua.* This design was expanded in 1983 when two additional treatments were added to the design and two additional quadrats were added to each group. One of these additional quadrats in each group was assigned to an *Aristida* seed addition treatment, the other to a partial removal of *Aristida* adults. While the two *Aristida* manipulations were randomly assigned to the two new quadrats in each group, the two added quadrats apparently differed systematically from the original four quadrats in at least some of the groups (see *Results*).

The seed addition treatments were conducted by adding either 1000 seeds of *Aristida* or 1000 spikelet clusters of *Bouteloua,* as appropriate, to each treated quadrat. The first addition of seeds of *Bouteloua* was made on 25 September 1982. Additions of seeds of both species were made on 15 October 1983, 6 September 1984, and 29 August 1985. Seeds were sown evenly over a quadrat, and then gently mixed into the vegetation to prevent wind dispersal.

In each year the seed sown had been collected the previous May or June and stored at room temperature until sown. Each year a sample of *Bouteloua* spikelet clusters from that year's collection was dissected and the seeds in each spikelet cluster counted. On average, a spikelet cluster had 1.81 seeds in 1982, 2.29 seeds in 1983, 1.54 seeds in 1984, 2.56 seeds in 1985, and 2.17 seeds in 1986.

Removals of *Bouteloua* were made from the six quadrats receiving this adult removal treatment and from the six quadrats receiving both adult removal and seed addition on 30 November or 7 December 1982 and again on 8 October 1985. Removals of *Aristida* were made from the six quadrats receiving this adult removal treatment on 6 November 1984. The quadrats were divided into strips, and every other plant larger than ≈10 tillers was removed. These plants were removed by cutting their bases from their roots, to minimize soil disturbance. When the 1982 removals were made, no record was kept of which plants were removed, but in 1984 and 1985 the census maps were taken out into the field and each plant was located and marked on the appropriate map as it was removed.

A census was made of all perennial plants in all 24 (1982 and 1983; years 1 and 2) or 36 (1984, 1985, and 1986; years 3, 4, and 5) experimental quadrats each year in May and June. A map of each quadrat containing the location, size, and fecundity of each plant was made each year. (See Fowler 1986 for details of mapping.) The maps were then superimposed and the records of each individual at each census matched together.

The matching process was straightforward for the larger plants (i.e., those with >7 tillers). As the numbers of very small plants increased in the seed addition quadrats, it was not always possible to determine whether a very small plant present one year was or was not the same individual as the very small plant present

in the same location the following year. To identify a set of plants definitely known to be new recruits and to obtain minimum recruitment rates, I adopted the conservative procedure of matching any two very small plants whose locations in two successive years were not more than 0.5 cm apart, unless the second year's plant was obviously a seedling (presence of a cotyledon and/or remnants of spikelet cluster). (This procedure had the added benefit of reducing the number of records of individuals of all species to ≈50 000.)

Statistical analyses

In all cases, each of the species was analyzed separately and each year or annual interval was analyzed separately. The numbers in the analyzed data sets vary because, for example, subsequently removed plants were included in the total number of plants in a quadrat before they were removed, but deleted from the analysis of growth during the subsequent interval. Or a plant on the edge of a quadrat would be included in the analysis of fecundity in a year in which it was recorded but might be absent from the analysis of growth during the subsequent interval if it was not present the following year.

Paired t tests.—Paired *t* tests were used to compare the numbers of plants in different treatments in year 5, at the end of the experiment. In these tests, the number of plants in one size class in one quadrat (e.g., the *Bouteloua* seed addition quadrat in quadrat group A) was paired with the number of plants in the same size class in another quadrat in the same quadrat group (e.g., the control quadrat in group A). Since there were six quadrat groups, $N = 6$ in each of these tests. Size classes (1–2 tillers, 3–4 tillers, 5–7 tillers, 8–15 tillers, 16 or more tillers) were the same for both species.

Analyses of covariance.—Analyses of covariance (ANCOVA) were performed on the subset of plants that had ≥8 tillers in two succeeding years. To analyze growth rate, the number of tillers per plant at the beginning of the interval was used as the covariate and the number of tillers at the end of the interval as the dependent variable. Both variables were log transformed before analysis; this transformation improved the normality of the residuals and the homogeneity of variances, and is more appropriate for a multiplicative process like plant growth. To analyze seed set, the number of tillers per plant in the given census was used as a covariate and the number of seeds (*Aristida*) or spikelet clusters (*Bouteloua*) as the dependent variable. Both variables were log transformed before analysis to improve normality and the homogeneity of variances, and to reflect the fact that the number of flowering culms is approximately proportional to the number of tillers in both species. Here again, log transformation converts a ratio to an additive relationship that better suits the linear ANCOVA model.

In these ANCOVAs, treatment was a fixed effect. Quadrat group was also a fixed effect, since the quadrat

groups were located so as to sample the range of spatial heterogeneity in the site. The interaction term, quadrat group × treatment, represents differences among quadrat groups in the ways in which the treatments affected the plants growing there, i.e., true interaction effects. This interaction term also includes the effects of random variation among quadrats within a quadrat group. Since there was only one quadrat per treatment per quadrat group, there is no way to separate random variation among quadrats within a quadrat group from true interaction effects. If *F* tests are conducted using the residual mean square, as was done in Fowler (1986), the random variation among quadrats within quadrat groups is assumed to be negligible; to the extent that it is not, the calculated *F* value will be too large, and a Type I error may result. Alternatively, the true interaction effect can be assumed to be negligible and the interaction term to represent only the random variation among quadrats within quadrat groups. Under this assumption *F* tests of group and treatment effects are conducted using the interaction mean square as the denominator mean square, as I have done in this paper. Type I errors are avoided, but at the expense of being extremely conservative in the testing of treatment as a main effect. However, this was usually a moot point, since a significant interaction term usually precluded the interpretation of any significant main effects.

Whenever a significant group × treatment interaction effect was found, a series of a priori, planned contrasts between the adjusted mean of each treatment quadrat and the adjusted mean of the control quadrat in the same group were done. The overall error rate remains 0.05 for all of the contrasts involving a single dependent variable (e.g., all 30 contrasts of *Bouteloua* tiller number in year 3). In one instance (*Bouteloua* seed set, year 5) a significant treatment effect was not accompanied by a significant interaction effect. In this case, contrasts were performed between each adjusted treatment mean and the adjusted control mean (five contrasts). Means were "adjusted" to correct for differences among quadrats in the distribution of covariate values: an adjusted mean is the height of the regression line fitted by the ANCOVA, at the point on the *x* axis where the covariate equals its grand mean.

The GLM procedure of SAS (SAS 1985) was used for these ANCOVAs. Type I (hierarchical) sums of squares are reported. The LSMEANS statement was used to calculate the adjusted means and the CONTRAST statement to do the contrasts. In the one instance when overall treatment means were compared, the CONTRAST statement specified the interaction term as the error term and ETYPE = 1 (i.e., the error mean square from the hierarchical sums of squares table). LSMEANS and CONTRASTs were calculated using a MODEL statement that did not include the covariate × group term if it was not significant, and never included the covariate × treatment or covariate × treatment × group terms (which were never significant).

Linear categorical models.—Linear categorical models ("GSK models"; Grizzle et al. 1969, Grizzle and Williams 1972, Kleinbaum and Kupper 1978) were used to analyze three sets of variables: the proportion of plants that reproduced, the proportion of plants that survived, and the size distribution of known new recruits to the population. The dependent variable for the analysis of the proportion of plants reproducing was "reproductive"/"nonreproductive" at the time of the specified census; for the analysis of survival, it was "survived"/"died" during the specified interval; for size distribution, the dependent variable was size class. Size classes were pooled as necessary for each analysis to increase cell size.

The CATMOD procedure of SAS (SAS 1985) was used for these analyses. The response vector (1 0) was specified for analyses with only two classes of the dependent variable (e.g., reproductive or not). The response matrix $(1 -1\ 0, 1\ 0 -1)$ was specified if there were three size classes.

RESULTS

Number of plants per quadrat

In the first census after the *Bouteloua* manipulations were initiated (i.e., year 2), the number of *Bouteloua* plants with one or two tillers was more than twice as great in the quadrats to which seeds of this species had been added as it was in the control quadrats (Fig. 1). This difference was greater in each successive year. By the end of the experiment there were >6 times as many plants with 1–2 tillers in the seed addition quadrats as in the controls. The numbers of plants with 3–4 tillers and with 5–7 tillers in the seed addition quadrats did not increase in all intervals, but the differences between these quadrats and the control quadrats did. By the end of the experiment the seed addition quadrats had 3.9 times as many 3–4 tillered plants and 2.4 times as many 5–7 tillered plants as the controls. The difference between the seed addition and control quadrats in numbers of 8–15 tillered plants increased in two steps, from year 1 (28% less than control) to year 2 (14% more than control) and from year 3 (13% more than control) to year 4 (52% more than control). Paired *t* tests comparing the seed addition quadrats and the control quadrats (paired by quadrat group) indicated that each of these differences was significant at the end of the experiment ($P < 0.01$ for the first three size classes; $P < 0.05$ for the 8–15 tiller size class).

The removal of *Bouteloua* adults in November/December during the first interval produced a 35% reduction in the number of *Bouteloua* plants with ≥16 tillers the following spring relative to the control quadrats, but had little effect on the number of plants with 8–15 tillers (Fig. 1). The direct effects of this treatment on plant numbers were less evident in successive years: the *Bouteloua* adult removal quadrats had only 20% fewer *Bouteloua* of 16+ tillers in year 3 and only 11%

fewer in year 4, than did the control quadrats. In the winter of the fourth interval the removal treatment was repeated, causing the *Bouteloua* adult removal quadrats to have 40% fewer *Bouteloua* plants of 16+ tillers and 21% fewer plants of 8–15 tillers than did the controls.

There was a tendency for the numbers of small *Bouteloua* plants to increase in the *Bouteloua* adult removal quadrats, although the differences were not significant (by paired *t* tests). By the end of the experiment these quadrats had 19% more 1–2 tillered plants, 16% more 3–4 tillered plants, and 30% more 5–7 tillered plants than did the control quadrats. The increase in 5–7 tillered plants was due primarily to the growth of plants that had germinated in preceding years, especially the new recruits of the census of year 4, when the adult removal quadrats had 46% more 1–2 tillered plants than did the control quadrats.

As planned, the quadrats that received both *Bouteloua* seed addition and *Bouteloua* adult removal had increases in the numbers of very small *Bouteloua* plants and reductions in the numbers of large *Bouteloua* plants quite similar to those observed in the quadrats that received only one of the two treatments (Fig. 1). There were no consistent effects of *Bouteloua* addition or removal on *Aristida* numbers.

Addition of *Aristida* seeds in the fall of intervals 2, 3, and 4 increased the number of small *Aristida* plants each year (Fig. 1). The seed addition quadrats had 2.1 times as many 1–2 tillered plants as did the control quadrats in year 3, 4.2 times as many in year 4, and 9.2 times as many in year 5. Comparable, though less dramatic, increases were observed in the numbers of 3–4 tillered and 5–7 tillered plants in these quadrats in years 4 and 5. Paired *t* tests comparing these seed addition quadrats and the control quadrats in year 5 found that the first two differences were significant (1–2 tillered plants: $P < 0.01$; 3–4 tillered plants, $P < 0.05$) and the third just missed significance (5–7 tillered plants, $P < 0.06$). A nonsignificant difference in the same direction also appears in the 8–15 tillered plants in year 5.

Because the *Aristida* manipulation treatments were added to the design during the third annual interval of the experiment, they were not randomly intermingled with the other four quadrats in each group, and on average differed from them in some ways. In particular, the *Aristida* manipulation quadrats had fewer medium and large *Aristida* plants in them in year 3, before the experimental removal of this species was done (Fig. 1): on average 37% fewer 8–15 tillered plants and 83% fewer 16+ tillered plants. Therefore a better comparison in some instances is between the two *Aristida* manipulations, which were randomly assigned to the two added quadrats in each group.

Following the removal of *Aristida* adults in November of the third interval, the removal quadrats had 77% fewer of the largest (16+ tillers) *Aristida* plants than did the seed additions, but this represented a total dif-

ference of only 10 plants. The *Aristida* removal treatment therefore had little effect on the environment of the remaining plants. This difference had decreased to only seven plants in year 5 (on average, just over one per quadrat), although it was still a 37% difference. The two *Aristida* manipulations did not differ in year 4 in the number of 8–15 tillered plants, although by year 5 the seed addition quadrats had significantly more *Aristida* plants in this size class (paired *t* test, *P* < 0.05), due to increased recruitment following seed addition.

There were no consistent effects of *Aristida* addition or removal on *Bouteloua* numbers.

The dramatic increases in the number of small plants in the seed addition quadrats were evidently due to annual increases in numbers of plants recruited to the population each year. The large numbers of small plants in the seed addition quadrats made a completely accurate determination of the fate of each individual plant impossible, but maximum estimates of survival rates were possible (see *Methods*). The percentage of *Bouteloua* plants in the smallest size class (1–2 tillers) that may have been >1 yr old was only 4 or 5% of the total number in this size class each year in the *Bouteloua* seed addition quadrats. The comparable figures for this size class of *Aristida* in the *Aristida* seed addition quadrats were also 4 or 5%.

Annual recruitment ("young of the year") was less important, however, in creating differences between the seed addition quadrats and the control quadrats in the numbers of plants in the larger size classes. In year 5 in the third size class (5–7 tillers), there was a 116 plant difference between the seed addition quadrats and the control quadrats. The seed addition quadrats had only 55 more known new recruits. Unrecognized new recruits may account for a few more, but about half of the difference must be ascribed to plants older than 1 yr, the result of seed additions before year 4. In the same size class, there was a 50-plant difference in the number of *Aristida* plants between the *Aristida* seed additions and the controls; there were 34 more known new recruits of this size in the seed addition quadrats.

The significant, 58-plant difference between the number of 8–15 tillered *Bouteloua* in the *Bouteloua* seed additions and the controls in year 5 was almost entirely due to the growth into this size class of plants that germinated in earlier intervals: the seed addition quadrats had only three more known new recruits than did the control quadrats in this size class.

Plant growth rate

In this species (as in most plant species), both survival and fecundity are highly correlated with plant size. (For example, note that plant size is a highly significant covariate in the analyses of seed set, below.) Treatments that affect plant size will therefore affect survival and fecundity. Where plant size can be measured as a continuous variable on each individual plant,

it is often the most sensitive measure of treatment effects.

Plant size was measured as the number of tillers per plant, a nondestructive, repeatable measurement. The single best predictor of plant size was that plant's size the previous year. For example, the regression of *Bouteloua* tiller number in year 4 on tiller number in year 3 accounted for 47% of the variation in year 4 tiller number; the comparable figure for *Aristida* was 30%. Since the plants in each quadrat had a different size distribution at the beginning of each annual interval, tiller number at the beginning of the interval was used as a covariate to prevent effects due to initial size from obscuring treatment effects. The effect of including initial tiller number in the analyses is that growth rate during an interval, rather than plant size at the end of the interval, is the parameter that is actually analyzed. Plant growth is usually multiplicative; this was accommodated in these linear models by the logarithmic transformation of both final and initial tiller number. Only plants having ≥8 tillers at both the beginning and the end of an interval were included in the analysis of growth during that interval, to be sure that no falsely matched new recruits were included (see *Methods*).

Effects on Bouteloua *growth.*—In no case did the slope of the regression of final size on initial size vary significantly among treatments (covariate × treatment term; Table 1) or among quadrats (covariate × treatment × group term). It is therefore appropriate to examine the effect of the interaction of quadrat group and treatment (group × treatment term). This term was significant in three of the four analyses of *Bouteloua* growth rate.

Interpretation of this term is complicated by the fact that it represents random variation among quadrats as well as any differences among quadrat groups in the ways that the experimental manipulations affected plants. Therefore a series of planned, a priori contrasts were done between each quadrat's adjusted mean and the adjusted mean of the control quadrat in the same quadrat group, for each of the four variables that had a significant group × treatment interaction effect (Fig. 2). In two instances (census of year 2, i.e., first annual interval, group E; year 4, group F), *Bouteloua* plants in quadrats from which *Bouteloua* adults had been removed grew significantly faster than did plants in the corresponding control quadrats. In five instances (year 2, group F; year 4, group C; year 5, groups C, D, and E), *Bouteloua* plants in quadrats to which *Bouteloua* seed had been added grew significantly more slowly than did plants in control quadrats. All of these significant differences were in the direction expected if density-dependent factors were operating. Significantly slower growth was also observed in two instances in quadrats that had received both treatments (year 2, group D; year 4, group E).

Ten instances of significant differences in *Bouteloua* growth rates involved the quadrats that had received
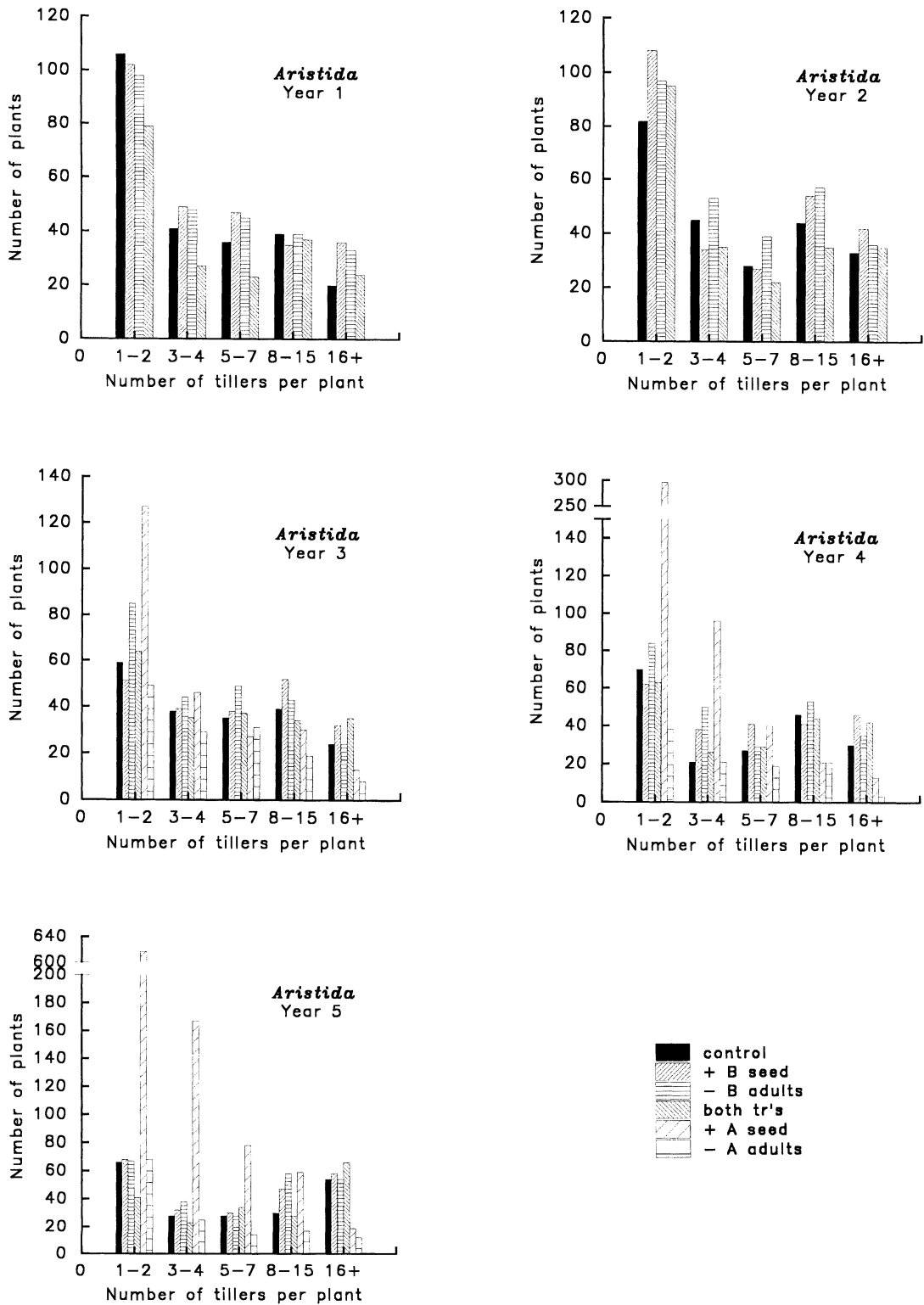
FIG. 1.   Numbers of individuals in each size class each year. The size classes are 1–2, 3–4, 5–7, 8–15, and ≥16 tillers. Treatments: control; + B seed, addition of *Bouteloua* seeds; − B adults, removal of *Bouteloua* adults; both tr's, addition of *Bouteloua* seed and removal of *Bouteloua* adults; + A seed, addition of *Aristida* seeds; − A adults, removal of *Aristida* adults.
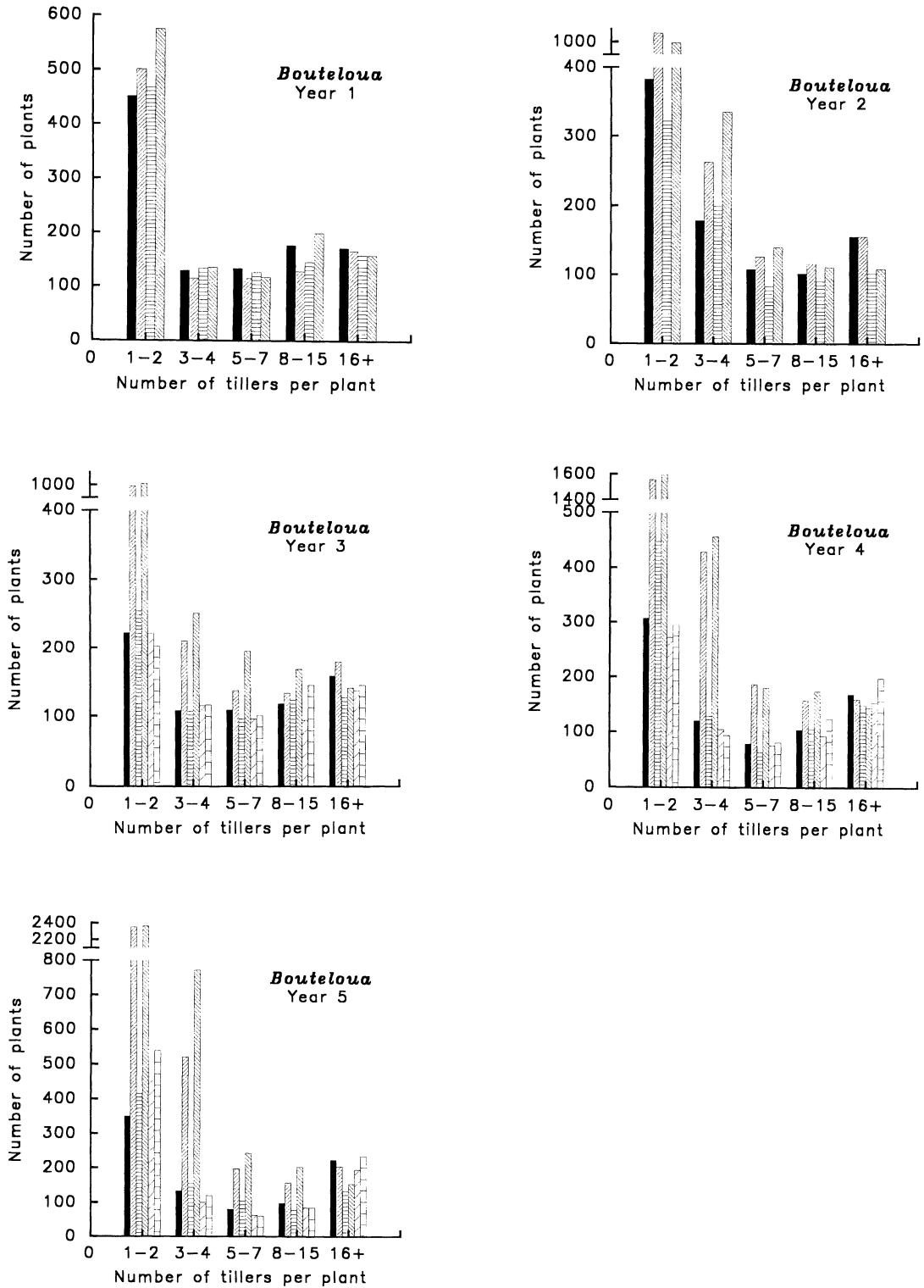
FIG. 1. Continued.

manipulations of *Aristida* density, but only five of these were in the expected direction. Further, note that where both the addition and the removal of *Aristida* had significant effects, the effects were in the same direction,

relative to the corresponding control quadrat. In year 5, for example, both treatments were associated with significantly lower *Bouteloua* growth rates in three different quadrat groups. Most likely, these differences

TABLE 1. Results of analyses of covariance testing the effects of treatment and quadrat group on plant size and reproduction. In the analyses of size, the dependent variable was log-transformed tiller number and the covariate was log-transformed tiller number at the previous census. In the analyses of reproduction, the dependent variable was log-transformed number of spikelet clusters (*Bouteloua*) or seeds (*Aristida*) and the covariate was log-transformed tiller number in the same census. Only plants with ≥8 or more tillers (at both censuses, for tiller number) were included in these analyses. The degrees of freedom differ among years due to the addition of the *Aristida* treatments.

	Construction of the ANCOVA		
	df, yrs 1 and 2	df, yrs 3 and 4	F
COVariate	1	1	MS_{COV}/MS_{RES}
Quadrat GROUP	5	5	$MS_{GROUP}/MS_{G\times T}$
TREATment	3	5	$MS_{TREAT}/MS_{G\times T}$
GROUP × TREAT	15	25	$MS_{G\times T}/MS_{RES}$
COV × GROUP	5	5	$MS_{COV\times G}/MS_{COV\times G\times T}$
COV × TREAT	3	5	$MS_{COV\times T}/MS_{COV\times G\times T}$
COV × GROUP × TREAT	15	25	$MS_{COV\times G\times T}/MS_{RES}$
RESidual			

	F values and significances			
	Year 2	Year 3	Year 4	Year 5
Bouteloua size				
COVariate	389.53****	1512.66****	1204.84****	1894.95****
Quadrat GROUP	7.63*	18.81****	9.61**	6.52 NS
TREATment	1.39 NS	1.73 NS	7.85*	7.69 NS
GROUP × TREAT	1.90*	1.09 NS	2.35***	2.98****
COV × GROUP	1.62 NS	1.50 NS	0.42 NS	1.15 NS
COV × TREAT	0.98 NS	0.65 NS	1.86 NS	0.85 NS
COV × GROUP × TREAT	1.26 NS	0.79 NS	1.30 NS	0.94 NS
Aristida size				
COVariate	112.72****	207.73****	111.75****	178.25****
Quadrat GROUP	7.07***	5.12 NS	3.24 NS	5.84*
TREATment	2.33 NS	2.40 NS	0.45 NS	4.41*
GROUP × TREAT	0.88 NS	2.05*	1.60 NS	1.68*
COV × GROUP	0.71 NS	3.61*	2.17 NS	1.96*
COV × TREAT	0.60 NS	0.63 NS	0.76 NS	0.40 NS
COV × GROUP × TREAT	0.58 NS	1.11 NS	1.22 NS	0.56 NS
Bouteloua seed set				
COVariate	305.18****	138.76****	193.09****	491.12****
Quadrat GROUP	12.15****	11.43****	17.86****	18.93****
TREATment	0.87 NS	2.36 NS	3.48 NS	2.64*
GROUP × TREAT	1.07 NS	1.08 NS	1.83**	0.78 NS
COV × GROUP	3.09**	2.08 NS	2.26 NS	3.49**
COV × TREAT	1.66 NS	0.33 NS	0.57 NS	1.08 NS
COV × GROUP × TREAT	0.53 NS	0.98 NS	1.27 NS	0.71 NS
Aristida seed set				
COVariate	189.65****	40.11****	21.83****	107.73****
Quadrat GROUP	6.67**	0.92 NS	1.36 NS	0.47 NS
TREATment	0.87 NS	0.57 NS	1.02 NS	1.37 NS
GROUP × TREAT	1.01 NS	1.28 NS	0.96 NS	1.09 NS
COV × GROUP	2.29 NS	1.56 NS	0.98 NS	2.21 NS
COV × TREAT	0.62 NS	1.66 NS	1.33 NS	1.13 NS
COV × GROUP × TREAT	1.24 NS	0.58 NS	1.46 NS	1.00 NS

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS nonsignificant.

were not the results of *Aristida* manipulations, but of underlying differences between the original four quadrats in each group, and the two *Aristida* treatment quadrats added later. The direction of the difference between the two *Aristida* treatments in each quadrat group was not consistent.

Neither the interaction between quadrat group and treatment, nor the main effect of treatment, had a significant effect upon *Bouteloua* growth rates during the second annual interval (i.e., census of year 3).

Effects on Aristida *growth.*—The analysis of *Aristida*

growth was exactly parallel to that of *Bouteloua* growth, whose results have just been described. Again, there were no significant differences in regression slopes among treatments or among quadrats (Table 1). There were no significant effects of treatment or of the interaction between treatment and quadrat group in two of the intervals (censuses of years 3 and 5). In the other two, the interaction effect was significant. A priori contrasts detected significantly lower *Aristida* growth rates in year 3 (i.e., second interval) in one quadrat to which *Bouteloua* seed had been added (group A) but also in

one quadrat from which *Bouteloua* adults had been re-moved (group D) (Fig. 2). One of the two significant differences involving an *Aristida* manipulation in year 5 (i.e., fourth interval) was also in the direction not expected. Again, there was no consistency in the di-rection of the difference between the two *Aristida* treat-ments in each quadrat group: in only two of the five was the difference in *Aristida* growth rates in the ex-pected direction (i.e., *Aristida* removal quadrat > *Ar-istida* seed addition quadrat).

Plant fecundity

The fecundity of *Aristida* was measured as the num-ber of seeds set per plant, that of *Bouteloua* as the number of spikelet clusters (i.e., infructescence branch-es) per plant. For both species, fecundity was highly correlated with plant size at the time of flowering. A simple analysis of fecundity would therefore be ex-pected to duplicate the analysis of plant size. I therefore chose to analyze size-adjusted fecundity. This was es-sentially equivalent to analyzing seed set per tiller. Rather than analyze the variable "seed set per tiller" directly, I included tiller number as a covariate in the analyses of fecundity.

Effects on Bouteloua *seed set.*—In no case did the slope of the regression of fecundity on tiller number vary significantly among treatments (covariate × treat-ment term; Table 1) or among quadrats (covariate × treatment × group term). It is therefore appropriate to examine the effect of the interaction of quadrat group and treatment (group × treatment term). This term was significant in one of the four analyses of *Bouteloua* fecundity.

The interpretation of this term presents the same problem as it does in the analyses of plant growth, that is, it represents random variation among quadrats as well as any differences among quadrat groups in the ways that the experimental manipulations affected plants. As before, a series of planned, a priori contrasts were done between each quadrat's adjusted mean and the adjusted mean of the control quadrat in the same quadrat group, for *Bouteloua* fecundity in year 4 (Fig. 3). In group E, *Bouteloua* plants produced significantly more spikelet clusters per tiller in the quadrats from which *Bouteloua* adults had been removed. There were also two instances in which plants in quadrats that had received both *Bouteloua* manipulations produced sig-nificantly more spikelets per tiller (groups B and E).

Four instances of significant differences in *Boute-loua* fecundity involved the quadrats that had received manipulations of *Aristida* density, but only two of these were in the expected direction, and there was no con-sistent direction in the difference between the two *Ar-istida* manipulations in the same quadrat group.

In year 5, the interaction of group and treatment was not significant and the main effect of treatment was significant (Table 1). We can therefore compare overall treatment means (adjusted for tiller number) from this census. Of the five a priori contrasts involving the con-trol treatment, only the difference between it and the *Bouteloua* seed addition treatment was significant: plants had on average fewer spikelet clusters per tiller in quadrats to which *Bouteloua* seed had been added.

Effects on Aristida *seed set.*—The analysis of *Aris-tida* seed set was parallel to that of *Bouteloua* seed set, but there were no significant effects of any term in-volving treatment at any census, so no contrasts were made.

Probability of reproducing

The probability that a plant having >8 tillers repro-duced was estimated for each census by the proportion of plants that set seed in each quadrat.

Effects on proportion of Bouteloua *setting seed.*—In the analysis of the data of year 3, the group × treatment term was not significant while the treatment term was (Table 2), and the proportion of plants setting seed in the seed addition quadrats was 8% less than it was in the control quadrats (Fig. 4). Since this treatment had not yet affected the size distribution of plants with ≥8 tillers, this appears to be a direct effect of density upon reproduction, in the expected direction. In years 4 and 5, the analyses detected a significant group × treatment interaction effect. The direction of the differences be-tween the seed addition quadrats and the control quad-rats was consistently in the direction expected: the pro-portion of plants setting seed was lower in the seed addition quadrats than in the controls (10% less than controls in year 4, 25% less in year 5; Fig. 4). However, the size distribution of plants in the seed addition quad-rats differed from the size distribution of the controls (Fig. 1), and the greater proportion of smaller plants in seed addition quadrats may have been responsible for the reduction in the proportion of plants reproduc-ing. These quadrats had 52 and 59% more plants of 8–15 tillers in years 4 and 5, respectively, and 5 and 9% fewer plants of >15 tillers, than did the control quad-rats. (The probability of a plant reproducing is highly dependent upon the size of that plant.) Unfortunately sample sizes were not large enough to use size class as a term in the analyses of the proportion of plants setting seed.

In year 3 the proportion of plants setting seed was also lower in the *Bouteloua* adult removal quadrats than in the controls, but this was most likely a result of the disproportionate removal of larger adults from these quadrats during the first interval. These quadrats had 20% fewer *Bouteloua* plants with ≥16 tillers, but 4% more with 8–15 tillers, than did the control quadrats. Differences in the size distribution of *Bouteloua* likely also account for the lower proportion of plants setting seed in the quadrats that received both *Bouteloua* adult removal and seed addition and in the *Aristida* removal quadrats in year 3.

Effects on proportion of Aristida *setting seed.*—Sam-ple sizes were too small to include quadrat group and
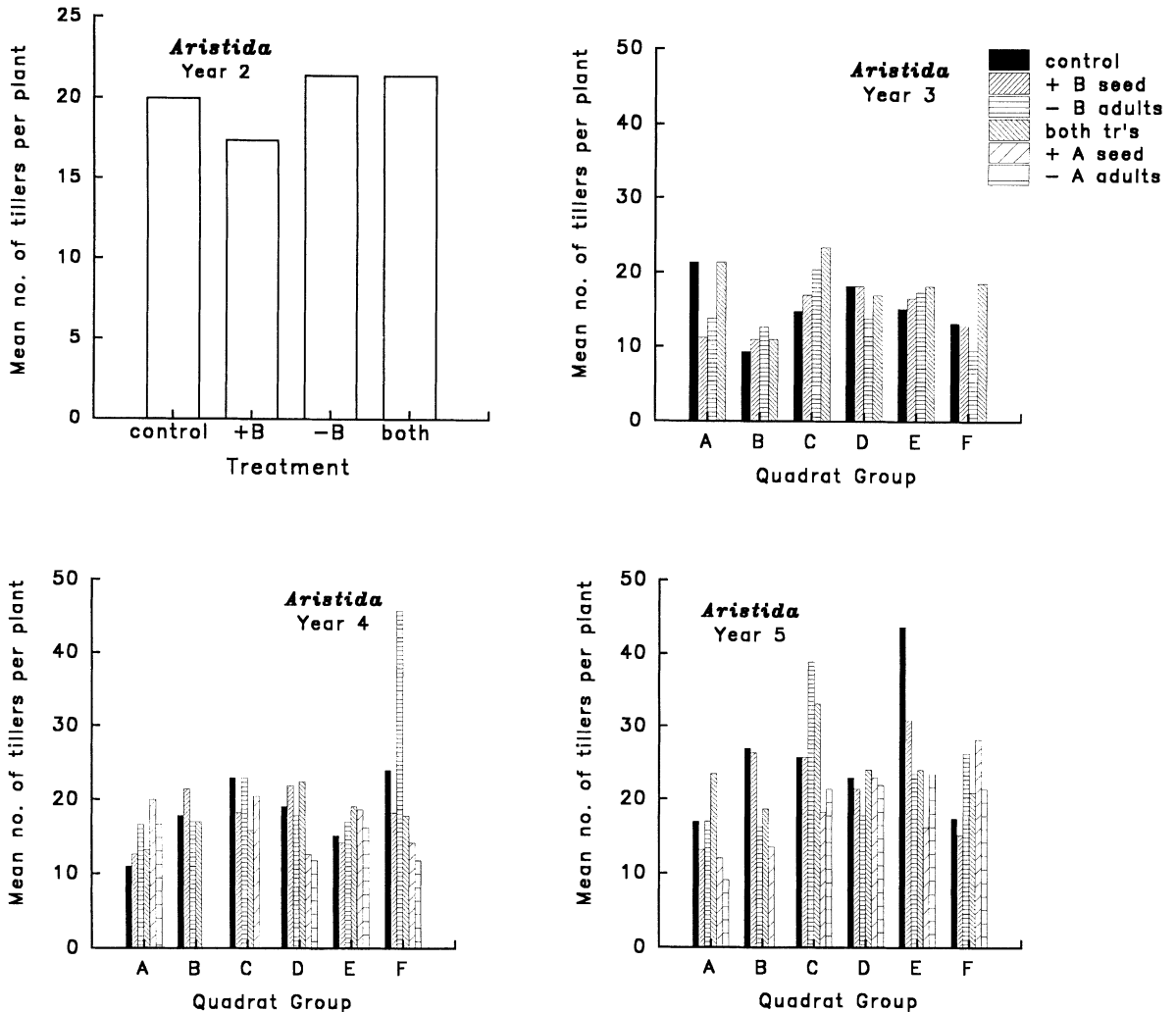
FIG. 2. Mean numbers of tillers per plant. These means have been adjusted for variation in individual plant size at the previous census, that is, they are the least square means (back-transformed). If there was a significant interaction between the effects of treatment and of quadrat group, the mean of each quadrat is shown; if not, the overall treatment mean is shown. Only plants with ≥8 tillers at both censuses were included in these calculations. Treatments as in Fig. 1.

hence a group × treatment term in most of the analyses of the proportion of *Aristida* plants that set seed; small sample sizes also prevented the inclusion of plant size (Table 2). The effect of treatment on the proportion of plants reproducing was significant in 3 of the 4 yr, but the differences between the control and treated quadrats were in the expected direction only slightly more than half the time (7 of 12) (Fig. 4). There is also evidence from the analyses of tiller number for the effects of quadrat-to-quadrat differences on this species. Therefore the possibility that these significant treatment effects are actually due to other sources of variation among quadrats, not causally related to the treatments and not included in the model, cannot be rejected.

Probability of surviving

It was not always possible to be sure that a small individual was a new recruit to the population, es-

pecially in quadrats where many seedlings had germinated in the previous year. Therefore no analyses of the apparent rates of survival of the smaller (1–4 tillers) plants were made. To obtain sufficient sample sizes for analysis, all size classes larger than this had to be pooled.

Survival of Bouteloua.—Only quadrat group significantly affected survival during the second interval, as it also did in the subsequent two intervals (Table 3). In these latter two intervals, the group × treatment term was highly significant, as was the treatment term. The effects of the treatments were inconsistent in the third interval, but in the fourth interval the survival rate was consistently lower in the quadrats to which seeds of this species had been added (*Bouteloua* seed addition < control in all but group D, in which the difference between these treatments was small) (Fig. 5). As discussed above, this may be partly or entirely the result
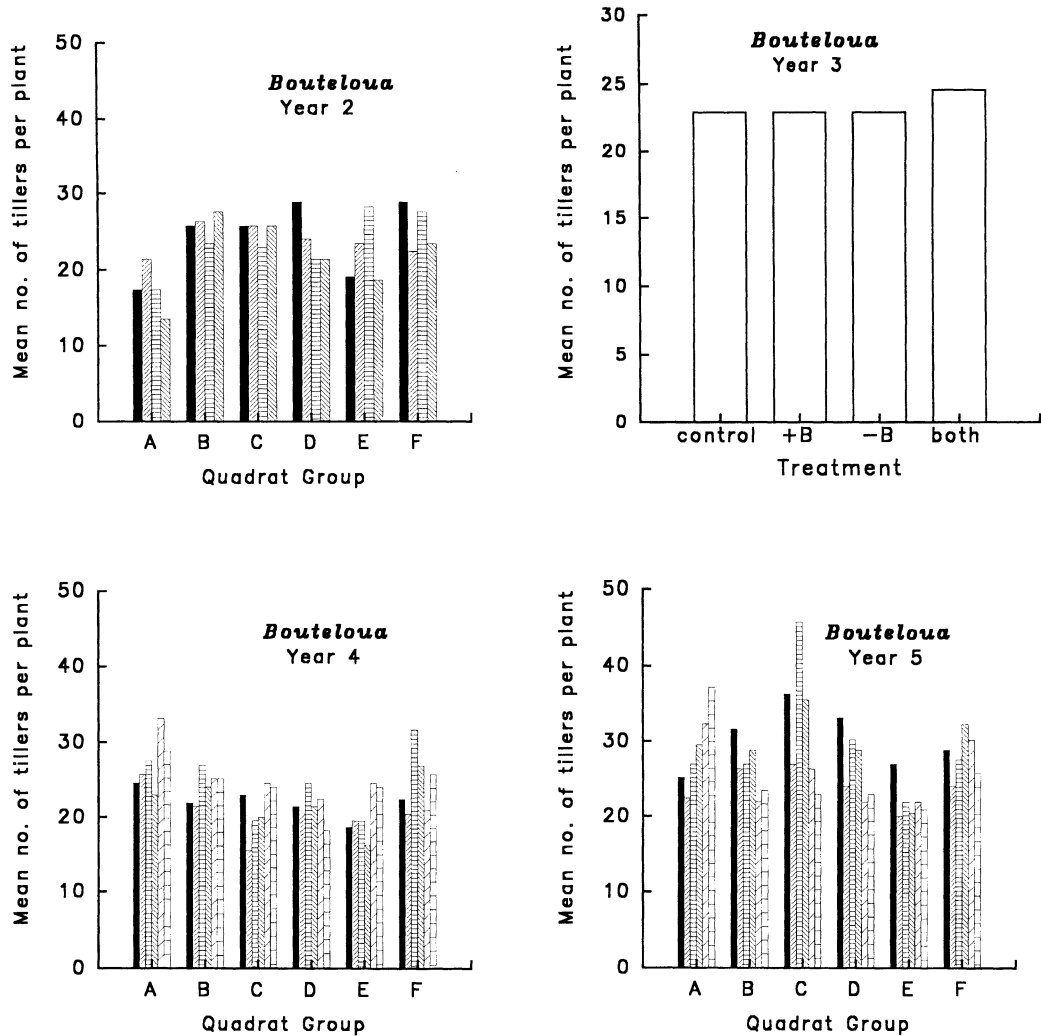
FIG. 2. Continued.

of the different size distribution in the seed addition quadrats. In several instances (groups A and D in both intervals, groups C, E, and F in one of the intervals) survival was higher in both of the *Aristida* treatment quadrats than in the control quadrat, another indication that the added quadrats were different from the original quadrats. The difference in survival rates between the two *Aristida* treatment quadrats was not consistent.

Survival of Aristida.—The treatments did not have a significant effect on the survival rate of *Aristida* (Table 3).

Recruit size

Only plants that were unambiguously less than 1 yr old at the specified census date (i.e., only unmatched plants) were included in these analyses. The proportion of plants in each size class in each quadrat was compared.

Size distribution of Bouteloua *recruits.*—In each year there was a significant interaction effect between quad-

rat group and treatment (Table 4). While some consistent differences among quadrat groups are evident, no consistent patterns of differences between treatments within quadrat groups emerge, nor are the larger differences in the expected directions (Fig. 6). Quadrat-to-quadrat differences, not density-dependent responses, seem to be the most likely cause of the variation in recruit size distribution.

Size distribution of Aristida *recruits.*—Sample sizes were too small to include group or group × treatment terms in these analyses (Table 4). A significant treatment effect was found in 2 of the 4 yr. However, in the 4th yr, when the effect was most significant, all three manipulations of *Bouteloua* density had a smaller proportion of very small plants that did the control, and both manipulations of *Aristida* density had a larger proportion of very small plants than did the control (Fig. 6). Following the same reasoning as above (see *Effects on proportion of* Aristida *setting seed*), these significant
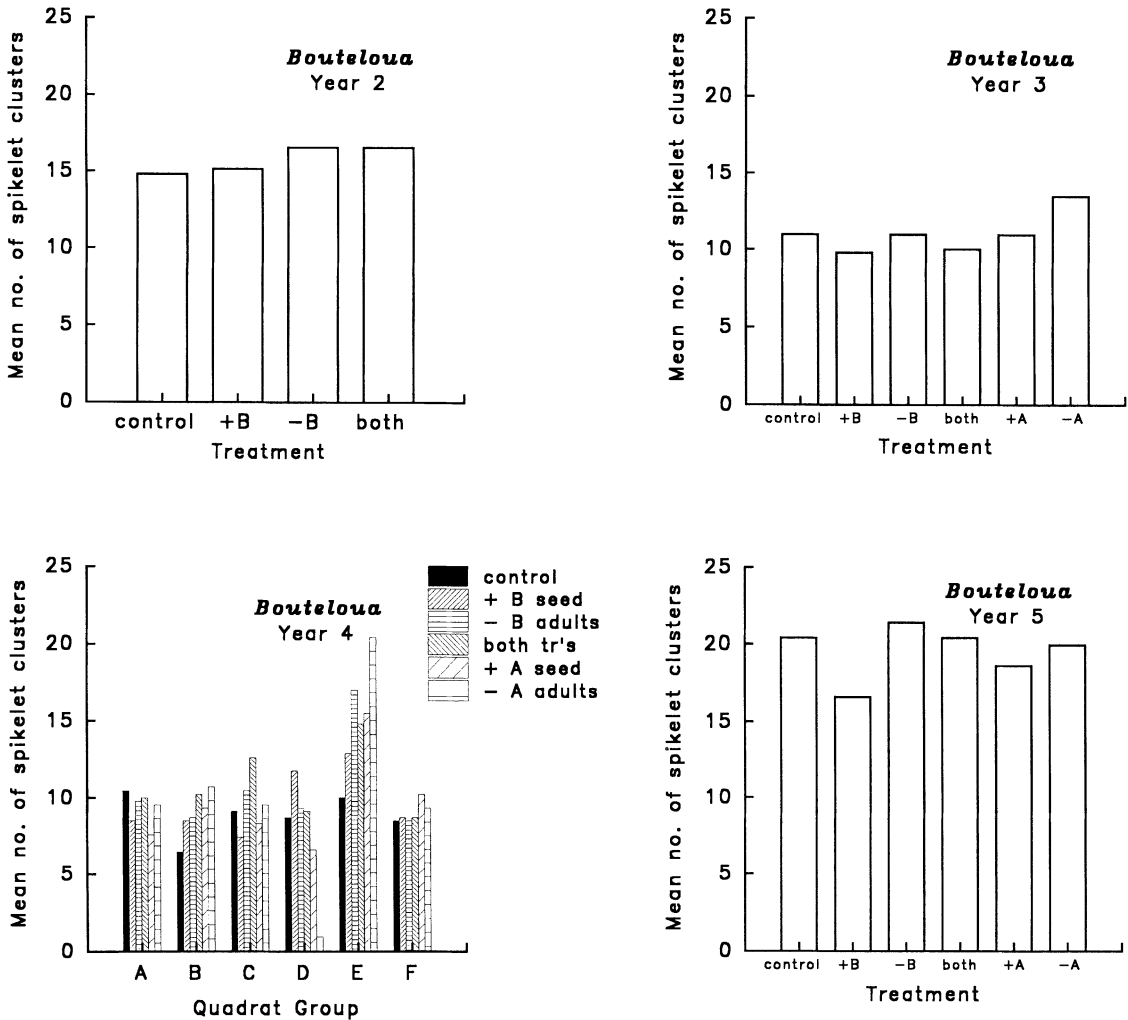
FIG. 3. Mean number of spikelet clusters of *Bouteloua*. These means have been adjusted for variation in individual plant size at the time of the census, that is, they are the least square means (back-transformed). If there was a significant interaction between the effects of treatment and of quadrat group, the mean of each quadrat is shown; if not, the overall treatment mean is shown. Treatments as in Fig. 1.

TABLE 2. Results of analyses using categorical models to test the effects of treatment and quadrat group on the proportion of plants reproducing. The dependent variable is the proportion of plants with ≥8 tillers in May–June that set seed that year.

	χ^2 values and significances			
	Year 2	Year 3	Year 4	Year 5
Bouteloua proportion setting seed				
Quadrat GROUP	31.34****	44.12****	122.39****	73.82****
TREATment	2.81 NS	11.88*	15.34**	103.10****
RESidual	19.45 NS	35.31 NS	58.32***	80.48****
Aristida proportion setting seed				
Quadrat GROUP	30.33 ****	not incl	not incl	not incl
TREATment	1.96 NS	14.45*	18.22**	15.43**
RESidual	16.66 NS	...	...	...

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS nonsignificant.
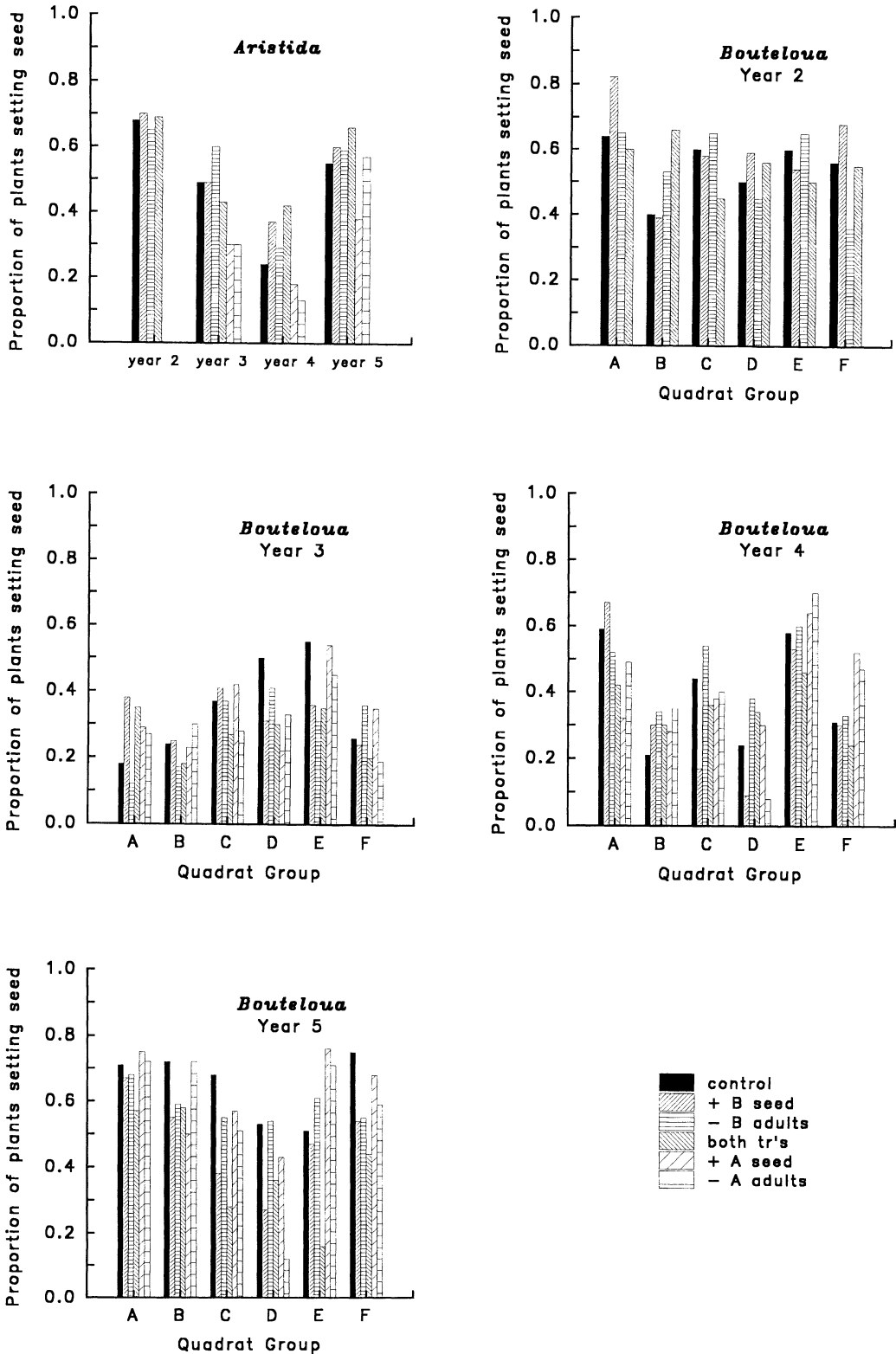
FIG. 4. Proportions of plants setting seed. Only overall treatment means of *Aristida* are shown, because sample sizes were small. The quadrat group × treatment interaction was significant in all analyses of *Bouteloua,* and therefore the proportion of plants setting seed in each quadrat is shown in this figure. Only plants with ≥8 tillers on the census date were included in these calculations. Treatments as in Fig. 1.

TABLE 3. Results of analyses using categorical models to test the effects of treatment and quadrat group on the proportion of plants surviving. The dependent variable is the proportion of plants with ≥5 tillers in May–June that survived the following annual interval. Quadrat group A was deleted from the analysis of *Bouteloua*, second interval, because it had too few deaths to analyze. Sample sizes were also too small to include quadrat group in the analyses of *Aristida* survival.

	χ^2 values and significances			
	Interval 1	Interval 2	Interval 3	Interval 4
Bouteloua survival				
Quadrat GROUP	···†	55.42****	71.59****	121.78****
TREATment	···	7.62 NS	78.24****	79.14****
RESidual	···	9.23 NS	64.17****	60.07****
Aristida survival				
TREATment	1.07 NS	6.79 NS	9.60 NS	8.15 NS

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS nonsignificant.
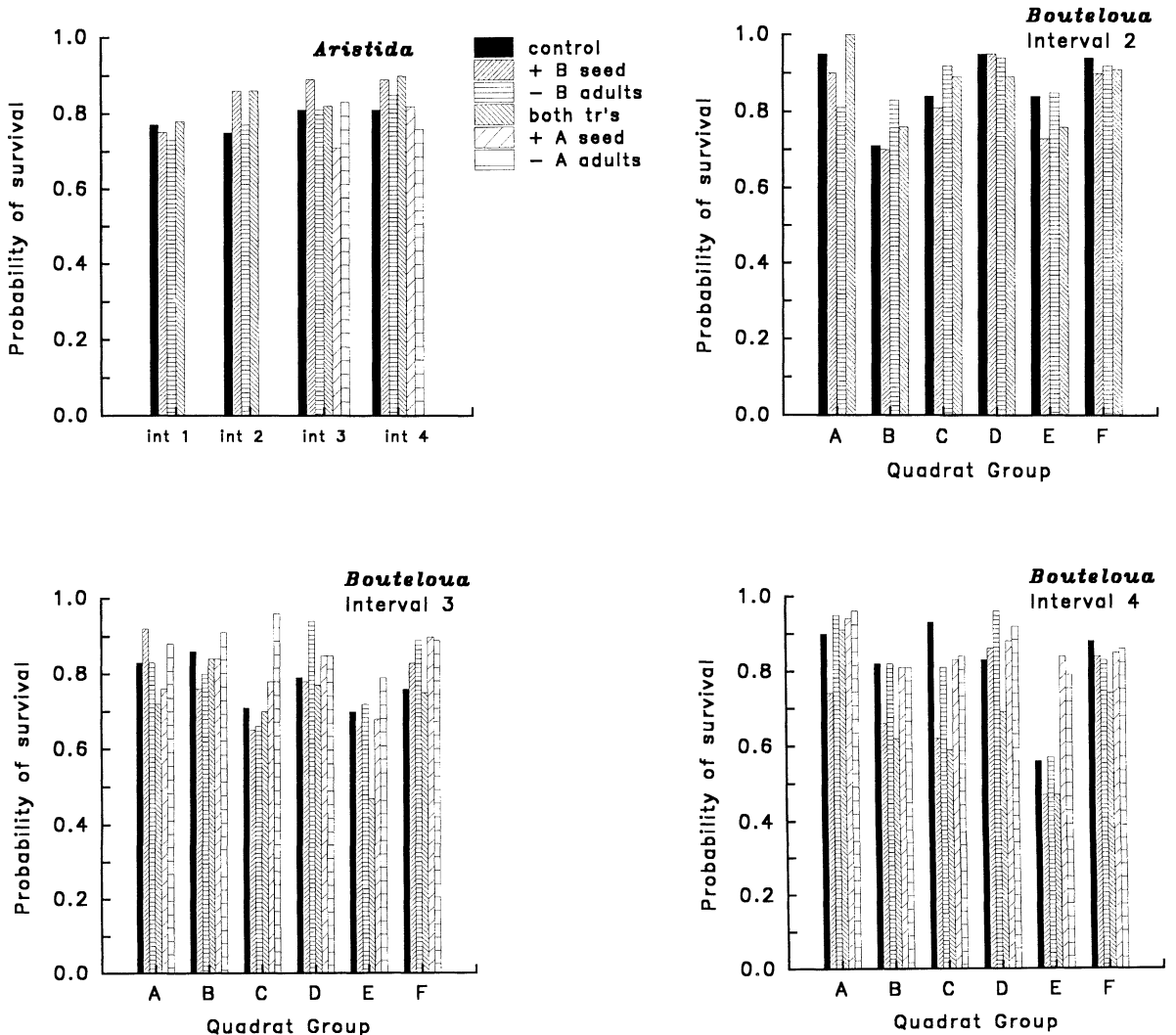† Natural mortality not distinguished from deliberate removals.

FIG. 5. Probabilities of survival (i.e., proportion surviving the following 12 mo) of plants with ≥5 tillers at the beginning of the interval. Only overall treatment means of *Aristida* are shown, because sample sizes were small. Treatments as in Fig. 1.

TABLE 4.   Results of analyses using categorical models to test the effects of treatment and quadrat group (*Bouteloua*) or treatment only (*Aristida*) on the size of new recruits to the population. The dependent variable is the proportion of recruits in each size class in May–June. Only unmatched plants were included in the data set. The size classes are 1–2 tillers, 3–4 tillers, and >4 tillers (*Bouteloua*, years 2 and 4; *Aristida*, all years) or 1–2 tillers and >2 tillers (*Bouteloua*, years 3 and 5).

	χ^2 values and significances			
	Year 2	Year 3	Year 4	Year 5
Bouteloua recruit size				
Quadrat GROUP	421.04****	56.87****	127.98****	962.16****
TREATment	42.83****	19.79***	36.66****	108.10****
RESidual	47.95*	44.06****	130.15****	167.47****
Aristida recruit size				
TREATment	9.28 NS	2.70 NS	19.81*	36.93***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS nonsignificant.

treatment effects probably do not reflect the effects of the treatments themselves.

DISCUSSION

The direct effects of the treatments

The detection of density dependence is dependent in part upon the strength of the perturbation, in this case the degree to which the treated quadrats differed from the control quadrats. The seed additions produced substantial increases in the numbers of plants per quadrat (Fig. 1, Table 5). Initially this effect appeared only in the smaller size classes; by the end of the experiment it had occurred in all but the largest size class of each species. The increased numbers in larger size classes reflected the growth of surviving plants from previous years: some of the "extra" seedlings of one year became "extra" 5-tillered plants the next year and "extra" 10-tillered plants the following year. Plants with <5 tillers were almost always <1 yr old. Seed carry-over, resulting in a larger and larger seed pool, best accounts for the larger and larger numbers in these size classes as the experiment continued. (Although buried seeds of these species do not survive, seeds can accumulate on the soil surface [N. L. Fowler, *unpublished data*].) These increases in the numbers of plants of each species following seed additions indicate that negative density-dependent processes affecting these species were too weak to counter completely the effects of seed addition. The relative constancy of plant numbers in the control quadrats argues for some sort of density-dependent regulation, however.

The adult removal treatments decreased the numbers of large plants (>7 tillers) by ≈50%. The differences between the treated and control quadrats in adult density tended to diminish in subsequent years until the treatment was repeated.

Negative density dependence was present but weak and sporadic

Responses to density: Bouteloua.—Throughout the experiment there were scattered instances of the large (>7 tillers) *Bouteloua* plants growing significantly more slowly in quadrats that had greater numbers of

small plants of this species (i.e., quadrats that had received seed additions). By the end of the experiment, this difference had become a consistent trend in all quadrat groups (i.e., growth was slower in the seed addition quadrats than in the control quadrat in each of the six quadrat groups). In the final census, size-adjusted fecundity was significantly lower in the seed addition quadrats than in the control quadrats. The proportion of plants surviving and the proportion of plants reproducing also were lower in the seed addition quadrats, differences that intensified throughout the course of the experiment, although the interpretation of these two parameters is clouded because they were not corrected for the effects of the change in size distribution that occurred in the seed addition quadrats. All of these are instances of negative density dependence of demographic parameters. However, the number of plants of intermediate (5–15 tillers) size in the seed addition quadrats increased as the experiment continued, and much of this increase was due to the continuing survival and growth of plants arising from earlier seed additions. Negative density-dependent growth and survival were not strong enough to prevent this increase in population size and the associated change in size distribution.

The effects of reducing the density of *Bouteloua* adults were very slight. This treatment had a significant negative effect on adult plant growth in one quadrat group in the second annual interval, and in another in the fourth annual interval. The effect on size-adjusted fecundity was limited to a significant increase over the corresponding control quadrat in one group in one year. Only in the first interval (second census) was the effect of the removals on the size of new recruits consistently in the direction of negative density dependence (larger recruits in removal quadrats), as reported in Fowler (1986); in subsequent years there was no consistent direction among quadrat groups. There was no effect on survival, and the effect on the proportion of plants reproducing was inconsistent. Although not significant (by paired *t* tests), the increase in the numbers of small plants in the quadrats from which adults had been removed (Fig. 1, Table 1) was the largest effect of this treatment.

Aristida

Bouteloua – interval 1

Bouteloua – interval 2

Bouteloua – interval 3

Bouteloua – interval 4

□ 8–15 tillers (top)
■ 5–7   tillers
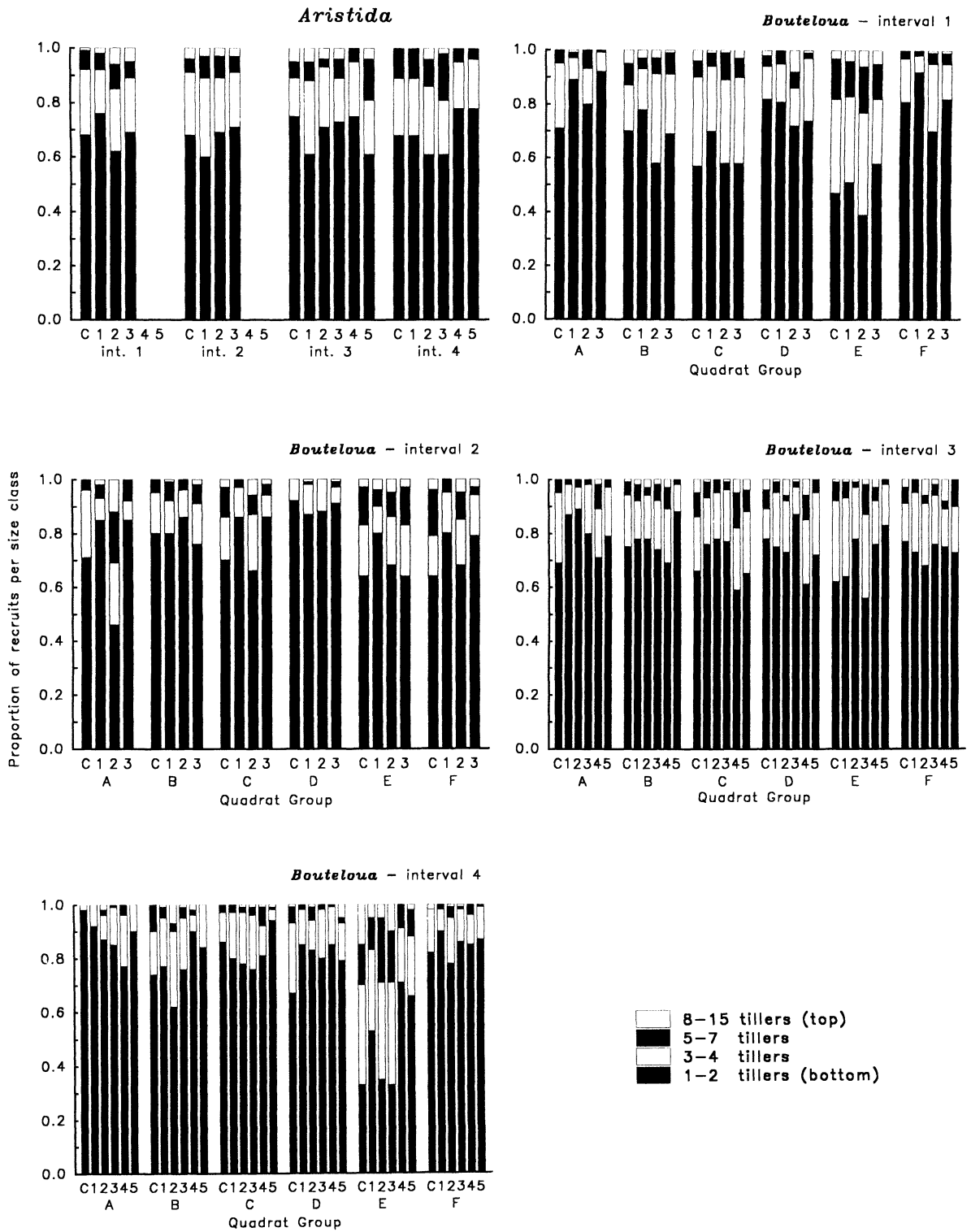□ 3–4   tillers
■ 1–2   tillers (bottom)

FIG. 6.   The size distributions of new recruits to the population. Only overall treatment values of *Aristida* are shown, because sample sizes were small. Treatments: C, control; 1, addition of *Bouteloua* seeds; 2, removal of *Bouteloua* adults; 3, addition of *Bouteloua* seed and removal of *Bouteloua* adults; 4, addition of *Aristida* seeds; 5, removal of *Aristida* adults. Quadrat groups are also indicated (A through F).

TABLE 5. Summary of the magnitudes of the alterations of density of *Bouteloua* and the responses of this species. Percentages calculated as (treatment − control)/control. Where the percentage was >100%, a ratio is reported, e.g., ×2.79 in place of 179%. Values were calculated from adjusted means (plant size, no. spikelet clusters) or actual proportions (surviving, setting seed) or numbers of plants. Each significant contrast between a treated quadrat and the control quadrat in the same quadrat group (from the ANCOVAS) is given separately; these quadrats were also included in the calculation of the overall differences.

	Differences between densities (treatments vs. controls)				
	Plant size classes				
	1–2 tillers	3–4 tillers	5–7 tillers	8–15 tillers	16+ tillers
	Adult removal				
Year 1	+4%	+3%	−5%	−18%	−8%
Year 2†	−16%	+11%	−23%	−6%	−35%
Year 3	+14%	−1%	−12%	+4%	−20%
Year 4	+46%	+7%	−20%	+1%	−11%
Year 5†	+19%	+16%	+30%	−21%	−40%
	Seed addition				
Year 1	+11%	−11%	−14%	−28%	−3%
Year 2‡	×2.79	+46%	+17%	+14%	0%
Year 3‡	×4.46	+94%	+26%	+13%	+13%
Year 4‡	×5.08	×3.55	×2.37	+52%	−5%
Year 5‡	×6.72	×3.88	×2.43	+59%	−9%

Plant responses (treatments vs. controls)

Plant growth rate (plants of ≥8 tillers only)

	adult removal	seed addition
Year 2	−1% group E: +13%	0% group F: −8%
Year 3	0%	0%
Year 4	+4% group F: +11%	−2% group C: −13%
Year 5	−1%	−7% group C: −8%; D: −9%; E: −9%

No. spikelet clusters, adjusted for plant size

Year 2	+4%	+1%
Year 3	0%	−5%
Year 4	+7% group E: +23%	+4%
Year 5	+2%	−7%

Proportion reproducing§ (plants of ≥8 tillers only)

Year 2	+4%	+2%
Year 3	−17%	−8%
Year 4	+15%	−10%
Year 5	−9%	−25%

Proportion surviving§ (plants of ≥5 tillers only)

Interval 1	⋯	+2%
Interval 2	+1%	−5%
Interval 3	+3%	−3%
Interval 4	0%	−15%

Size distribution of new recruits

  no consistent patterns attributable to treatments

† Adults were removed from treated quadrats during the preceding autumn

‡ Seeds were added to treated quadrats during the preceding summer.

§ These values are not adjusted for the effects of changes in plant size distribution.

Responses to density: Aristida.—There was no evidence at all of negative density dependence in any demographic parameter of this *Aristida* population. There were quite a few significant differences, but all of them are more plausibly ascribed to differences among quadrats not related in any consistent way to the treatments imposed. *Aristida* seems to have been affected by differences among quadrats even more than *Bouteloua*. The smaller sample sizes available for *Aristida* also reduced the sensitivity of the analyses to treatment effects.

Responses to density: general patterns.—Relative to the magnitudes of the experimental perturbations of density, the responses by conspecifics to these changes in density were small in magnitude (Table 5). Detectable (i.e., significant) density dependence in each demographic parameter occurred in only a few of the annual intervals of this experiment; in any year it was detectable in only a few parameters. Based on the results of the first interval, I concluded that density dependence of demographic parameters in this population of *Bouteloua rigidiseta* was quite weak (Fowler 1986). The results of subsequent years reinforce this conclusion. In the same paper, I suggested that the absence of strong density-dependent effects might have been due to a temporary reduction in population size caused by drought between the first two censuses. That hypothesis is not supported by the results of subsequent years. The numbers of plants in the control quadrats fluctuated from year to year, but there is no evidence that numbers were particularly low in year 2. Instead, a more general conclusion is supported by the cumulative evidence of this 5-yr experiment: density dependence in survival, growth, and reproduction in both populations is usually weak (density vague, sensu Strong 1983).

The results of this experiment are compatible with the conclusion that density dependence in this population occurred intermittently among years, life cycle stages, and patches. However, the scattering of significant density effects among years, quadrat groups, and characters could simply be an effect of the weakness of density dependence, as we expect a phenomenon at the limit of detectability to reach significance only sporadically. The apparent variation in the magnitudes of plant responses to density not correlated with changes in density (Table 5) could be due to real variation in the strength of density dependence, or to sampling error.

There is no reason to assume that weak density dependence is not a general property of these two grass species in central Texas. The vegetation of the study site is typical of flat sites in this region (Fowler and Dunlap 1986), the climate during the time period of this study was not unusual or atypical, and the climate of this region is not characterized by long-term cycles. The results of this experiment do not exclude the possibility that much stronger density dependence may

occur in infrequent, unusual years or in other sites, but neither do they provide any support for these hypotheses.

The results of this experiment may also be typical for other plant populations. Among comparable studies, Smith (1983*a, b, c*) found that a 16-fold decrease in density produced (approximately) twofold increases in survivorship and in seed set per plant and a decrease in seedling emergence. Shaw and Antonovics (1986) found that a twofold increase in seedling density (calculated from their Table 1) had no effect on seedling survival. Keddy (1981) found that a 10-fold increase in density decreased survival by approximately half (calculated from his Fig. 5) in one of three sites, the others showing no response, and increased fecundity approximately twofold in another of the three sites (calculated from his Fig. 6). Watkinson and Harper (1978) found no effect of density on survival over an eightfold range of densities, although seed set was density dependent at very high densities. Unfortunately many authors have not reported either actual treatment densities, or the magnitudes of the responses, or both, but only statistical significance.

Causes of weak and infrequent negative density dependence

This study did not address the mechanisms that determine survival, growth, and reproduction of these two grass species, including those that may act in a density-dependent fashion. Since plant responses to changes in soil moisture were obvious, shading was minimal, and there was very little visible evidence of disease or herbivory, competition for soil resources was probably the most important mechanism by which these plants interacted.

Why was density dependence so weak? *Bouteloua* was so abundant that individuals of this species were usually close neighbors of conspecifics, so we cannot ascribe weak density dependence to rarity within the community (Grubb 1986). This may, however, have been a factor weakening density dependence in the survival, growth, and reproduction of *Aristida*.

Several authors have suggested that negative (intra-specific) density dependence may be relatively weak or rare in plants because they believe that most plant species compete as ecological equivalents with little niche separation (e.g., Hubbell 1979, Hubbell and Foster 1986). In this situation, resource availability might set a strict limit on total plant biomass, productivity, and/or numbers, but not on the biomass or numbers of a particular plant species in the community. The rates of survival and reproduction of each plant species' population would be a negative function of the total number of individuals (or biomass) of all of the plant species present, and the relationship between the demographic parameters of a single species and its own density could be very weak. This hypothesis was not tested explicitly and cannot be rejected conclusively as an explanation for the weak density dependence found in the present study, but the results of this experiment do not support it. *Bouteloua* was such a large component of the vegetation of the experimental quadrats (Fowler 1986) that even if all plant species competed as ecological equivalents the alterations in *Bouteloua* density would have been expected to affect *Bouteloua*. In addition, the absence of responses of each species to alterations in the density of the other species does not support the hypothesis that these two species are ecological equivalents, i.e., compete as much with each other as with conspecifics.

It is possible that these two plant populations had densities too low, even in the seed addition quadrats, during all 4 yr of the experiment for strong density dependence to occur. An unusually low population size, relative to resources, was the explanation proposed for the weak density dependence found in the 1st yr of this experiment (Fowler 1986). However density dependence continued to be weak during the following 3 yr of the experiment. These are short-lived species (N. L. Fowler and R. E. Miller, *unpublished data*) whose demographic characteristics indicate that they can respond rather quickly to fluctuations in rainfall and other changes in resource levels, so this explanation seems unlikely. Nor was there any evidence of density-independent herbivory or disturbance keeping these populations so far below carrying capacity. Third, a population so far below carrying capacity that density-dependent regulation is essentially absent might be expected to exhibit wide swings in population size, but the control quadrats had remarkably constant numbers of plants.

I suggest that the explanation of the absence of strong, frequent density-dependent responses may be simply that the density of conspecific individuals has relatively little effect on an individual plant in comparison to all of the other factors affecting that plant. In other words, the effects of the differences in density caused by the experimental treatments were small compared to the effects of all of the other environmental and genetic factors affecting these plants.

The effects of some of the environmental heterogeneity present in the study site are reflected in the substantial, and significant, differences observed among quadrat groups and in the large group × treatment interaction terms. Although its effects were not separated out in the analyses (being pooled with other differences among plants within quadrats), a substantial amount of within-quadrat environmental heterogeneity was also present. Sources of environmental heterogeneity include microtopography, other plant species, and rocks above and below the soil surface. The effects of such environmental factors upon individual plant survival, growth, and reproduction of this species can be very large (Fowler 1988, Miller and Fowler 1994). Intraspecific density (the number of conspecific neighbors, and their size and distance away from an indi-

vidual) also varied among plants within a quadrat, so variations in effective density within treatments may have weakened the magnitude of treatment differences. Within-quadrat differences in intraspecific density are of course correlated with variation in other environmental factors within a quadrat.

Consequences for population regulation

Demonstrating that the magnitude of the effects of (conspecific) density on plant survival, growth, and reproduction is small is not equivalent to demonstrating that population regulation is ineffective. Consider the genetic analogy: population genetic models demonstrate that very weak responses to selection (whether arising from weak selective pressures or low heritabilities) may nevertheless cause relatively rapid changes in a population's genetic composition (Falconer 1989). It may be that small, almost undetectable levels of density dependence can be as effective at regulating populations as small, almost undetectable selective pressures are at changing or maintaining gene frequencies. The constancy of plant numbers in control quadrats and the increases in plant numbers in adult removal quadrats suggest that density-dependent regulation was in fact reasonably effective, although not strong enough to overcome the effects of seed addition.

The possibility that effective population regulation may occur despite density effects that are so small that they are barely detectable is not an encouraging one for plant population ecologists. It nevertheless is consistent with the results of this experiment. The alternative possibility, that weak density dependence led to weak population regulation, cannot be definitively excluded, however. Clearly, the question of "how much density dependence is enough?" is a critical one. One possible approach to answering it is the construction and analysis of demographic models (N. L. Fowler, *unpublished data*).

Despite 75 yr or more of attention, our understanding of the regulation of natural populations is by no means complete (Hassell and May 1990). Density-dependent regulation of plant populations has often been implicitly assumed, perhaps because of the apparent importance of competition in any closed stand or sward. Nevertheless, relatively little is actually known about the intensity, frequency, effectiveness, and nature of density dependent regulation of plant populations. The logistic challenges of conducting definitive experiments are undoubtedly responsible for some (most?) of our lack of information on this topic. Its importance, however, is incontrovertible: an understanding of plant population dynamics and regulation is critical to an understanding of abundance and rarity, of plant distributions, of metapopulation dynamics, and of plant community structure and plant–herbivore interactions. Practical applications range from the conservation of endangered species to the control of introduced species.

LITERATURE CITED

Aguilera, M. O., and W. K. Lauenroth. 1993. Seedling establishment in adult neighborhoods—intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis.* Journal of Ecology 81:253–261.

Andrew, M. H. 1986. Population dynamics of the tropical annual grass *Sorghum intrans* in relation to local patchiness in its abundance. Australian Journal of Ecology 11:209–217.

Augspurger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705–1712.

Burdon, J. J. 1987. Diseases and plant population biology. Cambridge University Press, Cambridge, UK.

Clay, K., and R. Shaw. 1981. An experimental demonstration of density-dependent reproduction in a natural population of *Diamorpha smallii,* a rare annual. Oecologia 51:1–6.

Falconer, D. S. 1989. Introduction to quantitative genetics. Third edition. Longman, London, England.

Fowler, N. L. 1984. Patchiness in patterns of growth and survival of two grasses. Oecologia (Berlin) 62:424–428.

———. 1986. Density-dependent population regulation in a Texas grassland. Ecology 67:545–554.

———. 1988. What is a safe site?: neighbor, litter, germination date, and patch effects. Ecology 69:947–961.

———. 1990. Disorderliness in plant communities: comparisons, causes, and consequences. Pages 291–306 *in* J. B. Grace and G. D. Tilman, editors. Perspectives on plant competition. Academic Press, New York, New York, USA.

Fowler, N. L., and D. W. Dunlap. 1986. Grassland vegetation of the eastern Edwards Plateau. American Midland Naturalist 115:131–145.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68:1211–1233.

Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. American Naturalist 139:771–801.

Grizzle, J. E., C. F. Starmer, and G. C. Koch. 1969. Analysis of categorical data by linear models. Biometrics 25:489–504.

Grizzle, J. E., and O. D. Williams. 1972. Loglinear models and tests of independence for contingency tables. Biometrics 28:137–156.

Grubb, P. J. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. Pages 207–225 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Hassell, M. P., and R. M. May, editors. 1990. Population regulation and dynamics: Proceedings of a Royal Society discussion meeting held on 23 and 24 May 1990. Royal Society, London, England.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical forest. Science 203:1299–1309.

Hubbell, S. P., R. Condit, and R. B. Foster. 1990. Presence and absence of density dependence in a neotropical tree community. Pages 147–281 *in* M. P. Hassell and R. M. May,

editors. Population regulation and dynamics: Proceedings of a Royal Society discussion meeting held on 23 and 24 May 1990. Royal Society, London, England.

Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314–329 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Johnson, C. R., and K. H. Mann. 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecological Monographs **58**:129–154.

Keddy, P. A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula,* growing along an environmental gradient in Nova Scotia. Journal of Ecology **69**: 615–630.

Kleinbaum, D. G., and L. L. Kupper. 1978. Applied regression analysis and other multivariable methods. Duxbury (Wadsworth), Belmont, California, USA.

Louda, S. M., and K. H. Keeler. 1990. Herbivore influences on plant performance and competitive interactions. Pages 413–444 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, San Diego, California, USA.

Miller, R. E., and N. L. Fowler. 1994. Life-history variation and local adaptation within two populations of *Bouteloua rigidiseta* (Texas grama). Journal of Ecology **82**:855–864.

Nobel, P. S., and A. C. Franco. 1986. Annual root growth and intraspecific competition for a desert bunchgrass. Journal of Ecology **74**:1119–1126.

Platt, W. J., and I. M. Weis. 1985. An experimental study of competition among fugitive prairie plants. Ecology **66**: 708–720.

Reed, D. C. 1990. An experimental evaluation of density dependence in a subtidal algal population. Ecology **71**: 2286–2296.

SAS. 1985. Sas user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

Schmitt, J., J. Eccleston, and D. W. Ehrhardt. 1987. Dominance and suppression, size-dependent growth and self-thinning in a natural *Impatiens capensis* population. Journal of Ecology **75**:651–665.

Shaw, R. G. 1987. Density-dependence in *Salvia lyrata*: experimental alteration of densities of established plants. Journal of Ecology **75**:1049–1063.

Shaw, R. G., and J. Antonovics. 1986. Density-dependence in *Salvia lyrata,* a herbaceous perennial: the effects of experimental alteration of seed densities. Journal of Ecology **74**:797–813.

Smith, B. H. 1983*a*. Demography of *Floerkea proserpinacoides,* a forest-floor annual. I. Density-dependent growth and mortality. Journal of Ecology **71**:391–404.

———. 1983*b*. Demography of *Floerkea proserpinacoides,* a forest-floor annual. II. Density-dependent reproduction. Journal of Ecology **71**:405–412.

———. 1983*c*. Demography of *Floerkea proserpinacoides,* a forest-floor annual. I. Dynamics of seed and seedling populations. Journal of Ecology **71**:413–425.

Strong, D. R. 1983. Natural variability and the manifold mechanisms of ecological communities. American Naturalist **122**:636–660.

Watkinson, A. R., and J. L. Harper. 1978. The demography of a sand dune annual: *Vulpia fasciculata.* I. The natural regulation of populations. Journal of Ecology **66**:15–33.

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Stable URL:
http://links.jstor.org/sici?sici=0006-341X%28196909%2925%3A3%3C489%3AAOCDBL%3E2.0.CO%3B2-N

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Stable URL:
http://links.jstor.org/sici?sici=0006-341X%28197203%2928%3A1%3C137%3ALLMATO%3E2.0.CO%3B2-D

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