Plant Competition along Soil Moisture Gradients: A Field Experiment with the Desert Annual Stipa Capensis

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Summary

1 The interaction between natural and experimental gradients of productivity on competition intensity was tested by neighbour removal experiments. Water is the main limiting factor in this system and experimental gradients of productivity were obtained using a series of watering treatments.

2 Competition was determined as the total effect of neighbours on per-capita seed production of *Stipa capensis*. Both absolute and relative competition intensity were calculated for three types of habitats, during two successive years, and under different watering treatments in each habitat–year combination.

3 Both measures were positively correlated with productivity, but absolute competition intensity was more sensitive to changes in productivity than relative competition intensity. Natural gradients of productivity appeared to have stronger effects on competition intensity than experimental gradients, but this was largely due to their wider range. In those cases where the ranges of the two types of gradients were similar, experimental gradients had a stronger effect on competition intensity than natural gradients.

4 Patterns of spatial variation in competition intensity were correlated with standing crop under all watering conditions. However, slopes of the regression equations obtained for the various watering treatments were not homogeneous. This indicates that per-gram effects of standing crop on competition intensity may fluctuate from year to year, depending on rainfall conditions. Regression models constructed to test the relationships between standing crop and competition intensity over different years, habitat types and watering treatments accounted for 88% of the variation in absolute competition intensity and 83% of the variation in relative competition intensity.

5 The overall results of this study are consistent with the hypothesis that plant competition increases along productivity gradients. The results also indicate that patterns of variation in competition intensity along productivity gradients may be influenced by the type of the gradient along which competition is measured (natural vs. experimental), its range, and the way competition intensity is defined.

Keywords: competition, desert annuals, habitat heterogeneity, Jordan Rift Valley, neighbour removal, *Stipa capensis*

Journal of Ecology (1995) **83**, 253–262

Introduction

Experimental studies suggest that the degree to which competitive interactions affect the attributes of individuals, populations and communities may vary considerably over both space and time (see reviews by Connell 1983; Schoener 1983; Sih *et al.* 1985; Underwood 1986; Fowler 1986; Keddy 1989; Grace & Tilman 1990; Goldberg & Barton 1992; Gurevitch *et al.* 1992). Although high estimates of the proportion of species or studies showing evidence of spatial variability in competition intensity (59%, Connell 1983) as well as temporal variability (31%, Connell 1983; 41%, Schoener 1983) have since been questioned (Underwood 1986; Goldberg & Barton 1992) they pointed to the importance of describing and explaining patterns of spatial and temporal variations in the intensity and relative importance of competitive interactions.

Studies of plant competition have emphasized the

role of productivity and standing crop as factors influencing the intensity of competitive interactions (Grime 1973; Newman 1973; Tilman 1987, 1988; Keddy 1989; Wilson & Shay 1990; Wilson & Keddy 1991; Wilson & Tilman 1991, 1993; Inchausti 1995). However, there is continuing controversy about the nature of the relationships between productivity, standing crop and competition intensity. Grime (1973), Huston (1979) and Keddy (1989) have proposed that the intensity of plant competition increases along productivity gradients because highly productive habitats support larger amounts of standing crop that therefore impose greater demands for resources. Unproductive habitats support less standing crop and were therefore expected to show lower intensities of competition. In contrast, Newman (1973), Grubb (1985) and Tilman (1988) proposed that the limited availability of soil resources in unproductive habitats may lead to intense competition there as well. Tilman (1987, 1988) suggested distinguishing between competition for light and competition for soil resources, and proposed that, while competition for light should increase, competition for soil resources should decrease with increasing productivity. According to this view, there may be no quantitative change in the intensity of competition along productivity gradients. Experimental tests of variation in competition intensity along productivity gradients have provided mixed results: some studies (e.g. Gurevitch 1986; Reader & Buck 1986; Wilson & Keddy 1986) were more consistent with Grime's (1973) hypothesis, while others (e.g. Wilson & Shay 1990; Wilson & Keddy 1991; Wilson & Tilman 1991, 1993; Campbell & Grime 1992) were more consistent with Newman's (1973) hypothesis. Recently, a number of explanations for these conflicting results have been suggested including the use of absolute versus relative measures of competition intensity (Turkington *et al.* 1993), differences in the range of the productivity gradients along which competition was studied (Wilson & Shay 1990), and differences in the type of the gradient (natural versus experimental) used for the study (Goldberg & Barton 1992).

In this paper I analyse the relationships among productivity, standing crop and competition intensity in the desert annual *Stipa capensis*. Previous results indicated that relative competition intensity in this system was positively correlated with both spatial and temporal changes in productivity (Kadmon & Shmida 1989) and I therefore tested the following questions:

1 Do experimental gradients of productivity differ from natural gradients in their effects on competition intensity?

2 Are there any differences between the absolute and relative effects of competition in their responses to natural and experimental changes in habitat productivity?

3 What are the relationships between standing crop and competition intensity? In particular, what is the value of standing crop as a predictor of spatial and temporal variations in competition intensity?

Materials and methods

DESCRIPTION OF THE STUDIED SYSTEM

The study was conducted at the Jericho research site, about 20 km east of Jerusalem, Israel (35°27′N, 31°45′E). The area has an extremely dry Mediterranean climate with rainfall being limited to the winter season. Average annual rainfall is 100 mm, but yearly amounts vary considerably (Rosenan 1970). Differences in microtopography produce three distinct types of habitats in the study area: gentle slopes, small wadis (drainage channels that are usually dry), and shallow depressions that are scattered over the slope areas. Height differences between the wadi beds and the surrounding slope areas are 1–2 m. The depressions are 1–10 cm deep and 2–4 m wide. The differences in microtopography lead to spatial gradients of water availability with slopes representing the driest and wadis representing the wettest conditions (Kadmon & Shmida 1990b). Yet, in all habitat types, water is the main limiting factor (Kadmon & Shmida 1990b). The vegetation consists of winter annuals with *Stipa capensis* being the most abundant species (see Kadmon & Shmida 1989a,b; Kadmon 1993 for details about the demography of *S. capensis* in the study area).

EXPERIMENTAL DESIGN

A representative area of about 100 m × 100 m was selected for the study. This area consisted of very gentle slopes in which shallow depressions and wadis occurred as distinct units. Differences in water availability among the three habitat types provided natural gradients of productivity within the study area. Experimental gradients of productivity were obtained by supplementary watering of experimental plots in each of the three habitat types. The general design of these experiments is shown in Fig. 1. Before the beginning of the study, 18 plots were selected and marked in each type of habitat. Plots were spread over the entire area and distances between neighbouring plots were 3 m or more. Plot diameter varied between 2 and 3 m, depending on the expected density of *S. capensis* and the structure of the habitat. The 18 plots of each habitat were then divided randomly into three rainfall manipulation treatments (Fig. 1): six plots were left as a control and received only natural rainfall, another six plots were exposed to two simulated rainstorms equivalent to 13 mm precipitation on 2 December 1985 and 17 mm on 4 December 1985; a total of 30 mm, and the remaining plots received six supplementary rainstorms (13 mm on 2 December 1985; 17 mm on 4 December 1985; 13 mm on 10 December
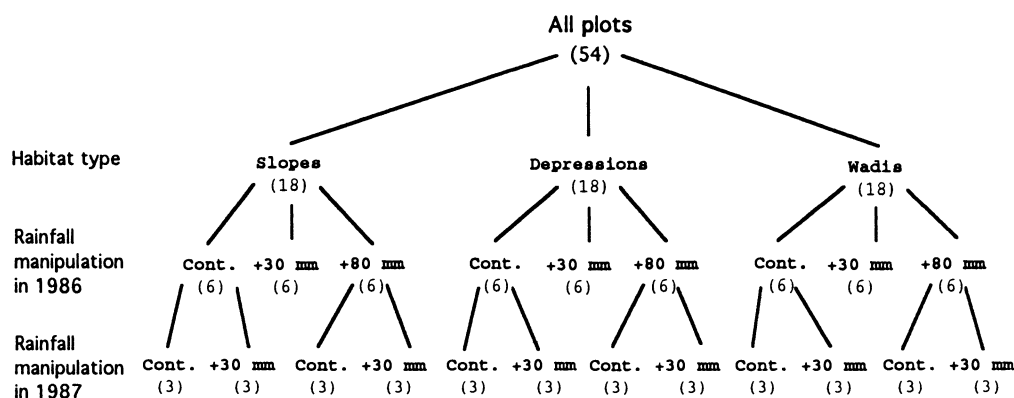
All plots
(54)

Fig. 1 Experimental design of the study. Values in parentheses denote number of plots in the relevant habitat–rainfall combination.

1985; 13 mm on 18 January 1986; 10 mm on 30 January 1986; and 14 mm on February 28th, 1986; a total of 80 mm). Water was supplied from overhead sprinklers. The duration (3–5 h) and intensity (4 mm h^{-1}) of the simulated rainstorms were typical of the rainstorms which occur naturally in the study area (Kutiel 1978).

Before the second year of the study, the control plots and the +80 mm plots of each habitat were further divided into two treatments (Fig. 1): half received only natural rainfall in this year and the remainder received a total of 30 mm in two simulated storms (13 mm on 9 January 1987 and 17 mm on 12 January 1987). Sprinkling intensities were the same as in the first year of the study. Plots that received 30 mm extra in 1986 were not monitored in the second year of the study.

Natural rainfall was 60 mm in 1986 and 85 mm in 1987. The 1986 treatments were therefore equivalent to 40% below, 10% below, and 40% above the annual mean, and those of 1987 were equivalent to 15% below and 15% above the annual mean. Such deviations from the mean are common in the study area (Rosenan 1970).

In each plot, 10–20 individuals of *S. capensis* were selected immediately after germination and were randomly divided into two treatment groups: one half of the seedlings was left as a control (i.e. at natural density conditions) and the other half was subject to a removal of all seedlings (of any species) from a radius of 50 cm. Preliminary observations of root distribution and shoot sizes indicated that such a distance is sufficient to prevent direct shoot or root interactions. Target plants were marked at the seedling stage by placing a ring of a very thin iron wire around their base. The ring was attached to a plastic label and was tied to a nail that was inserted into the ground 10 cm from the seedling. During the period of seed set, each marked plant was harvested and its seed number was determined. Biomass of above-ground standing crop was determined for each plot by harvesting three randomly placed 10-cm × 10-cm quadrats, drying the samples at 80°C for 48 h, and weighing them on an analytical balance.

DEFINITION OF COMPETITION INTENSITY

Two measures of competition intensity were calculated: absolute competition intensity (CI_A), and relative competition intensity (CI_R). For a given plot in a given year, absolute competition intensity was determined as:

$$CI_A = Y_E - Y_C$$

where Y_E denotes the mean per-capita seed production of experimentally isolated plants and Y_C is the mean per-capita seed production of control plants. Seedlings that did not survive to maturity were considered to have zero seed production and were included in the calculation of plant means. Relative competition intensity was determined as:

$$CI_R = (Y_E - Y_C)/Y_E.$$

The first measure (CI_A) expresses the absolute reduction in per-capita seed production due to competitive effects, while the second measure (CI_R) expresses the corresponding reduction standardized by per-capita seed production of plants growing in the absence of competitive effects.

The above measures were calculated for each plot in each combination of year, habitat type and rainfall treatment.

STATISTICAL ANALYSIS

Differences in standing crop among habitat types and rainfall treatments were tested using ANOVA models with average standing crop per plot as the dependent variable, habitat type and rainfall treatment as fixed effects, and among-plot variation as the error term. Plot means were log-transformed to reduce heteroscedasticity (Sokal & Rohlf 1981). Data from 1986 were analysed using two-way ANOVA with habitat type and rainfall treatment as the main effects. Data from 1987 were analysed using three-way ANOVA with habitat type, rainfall treatment in 1986, and rainfall treatment in 1987 as the main effects. In both models, sums of squares were decomposed with each effect being adjusted to all other effects. Between-year differences

in standing crop of the nine plots that were left as a control in both years were analysed using repeated-measures analysis of variance with habitat type as a between-subject effect and year as a within-subject effect (see Fig. 1).

Data on per-capita seed production from 1986 were analysed using a three-way ANOVA with neighbour removal, habitat type and rainfall manipulation as main effects. The corresponding data from 1987 were analysed using a four-way ANOVA with neighbour removal, habitat type, rainfall manipulation in 1986, and rainfall manipulation in 1987 as main effects. Both analyses were performed on log-transformed data because means and standard deviations were positively correlated (Sokal & Rohlf 1981).

Patterns of variation in competition intensity (both CI_A and CI_R) were analysed in two steps. First, each of the two measures of competition was analysed using the same procedure as described for the standing crop data. The purpose of this stage of the analysis was to test for possible interactions between natural and experimental changes in habitat productivity which could affect the magnitude of absolute and relative competition intensity.

In a second step, the same procedure was repeated, but with average standing crop per plot being introduced as a covariate in the analysis. Such a procedure allowed me control for differences in standing crop when testing the effects of natural and experimental changes in habitat productivity on the intensity of competition. A similar procedure was used to correct for among-habitat and among-treatment differences in population density of *Stipa capensis*. Statistical analyses of variation in competition intensity were performed on log-transformed values of CI_A and arcsine square root transformed values of CI_R to reduce heteroscedasticity and improve the linearity of the models (Sokal & Rohlf 1981). All assumptions of the ANOVA were met in the transformed variables.

The effect of standing crop on competition intensity was analysed using a regression approach. Two series of analyses were performed. In the first series, data from each rainfall treatment were analysed separately with each plot being treated as an independent sampling unit. In this series of analyses, average standing crop per plot was treated as the independent variable and the corresponding values of CI_A and CI_R were the dependent variables. The purpose of this part of the analysis was to test whether patterns of spatial variation in competition intensity can be related to differences in standing crop. Plots receiving different rainfall treatments were analysed separately in order not to confound effects of natural and experimental gradients of standing crop. The effect of rainfall conditions on the relationship between standing crop and competition intensity was tested using analysis of covariance with rainfall regime as a single main effect and standing crop as a covariate. A significant interaction between rainfall regime and standing crop indi-

cated that the relationship between standing crop and competition intensity depends on rainfall conditions.

In a second series of regression analyses, the average intensity of competition was calculated for each combination of year, habitat type and rainfall treatment, and the resulting values were regressed against the corresponding averages of standing crop. In order not to use data from the same plot more than once (i.e. to keep the sampling units independent), plots that were subject to the +30 mm treatment in 1987 were excluded from this analysis (see Fig. 1 for clarification). The purpose of this part of the analysis was to test the degree to which absolute and relative competition intensity correlate with standing crop across different habitat–rainfall combinations.

Results

STANDING CROP

Standing crop was lowest on the slopes, intermediate in the depressions, and highest in the wadis under all rainfall treatments (Fig. 2, Tables 1 and 2). Supplementary watering had a significant positive effect on standing crop in both 1986 and 1987, but the
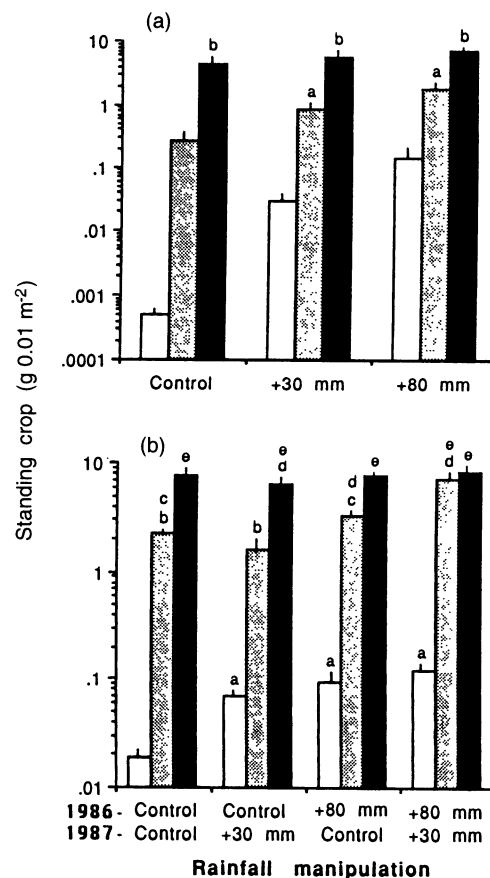
Fig. 2 Standing crop as a function of habitat type and rainfall manipulation treatment (mean and 1 SE) in (a) 1986 and (b) 1987: (☐) slopes; (▨) depressions; (■) wadis. Bars with common letters in a given year do not differ from each other ($P \geq 0.05$, Duncan range tests). Note the logarithmic scale.

Table 1 Analysis of variance for the effects of habitat type and rainfall manipulation on standing crop, absolute competition intensity, and relative competition intensity in 1986. Analyses of variation in competition intensity were performed with and without standing crop as a covariate

| Effect (d.f.) | Standing crop | | Absolute competition intensity | | | | Relative competition intensity | | | |
| | | | Without standing crop | | With standing crop | | Without standing crop | | With standing crop | |
	MS	F	MS	F	MS	F	MS	F	MS	F
Standing crop (1)	–	–	–	–	53.3	1354***	–	–	5.58	437.3***
Habitat (2)	37.5	348.0***	20.5	520.7***	1.1	28.3***	2.91	164.8***	0.41	21.9***
Rain (2)	6.7	61.2***	8.7	221.0***	1.9	48.3***	0.45	25.5***	0.22	17.0***
Habitat × rain (4)	2.3	21.7***	1.7	42.7***	0.9	21.8***	0.14	7.8***	0.19	15.0***
Error (45)	0.1		<0.1		<0.1		0.02		0.01	
Total (53)	1.9		1.3		1.3		0.16		0.16	
R^2	0.86		0.87		0.92		0.83		0.83	

$*P < 0.05; **P < 0.01; ***P < 0.001.$

magnitude of this effect varied among habitat types: it was highest on the slopes, intermediate in the depressions, and lowest in the wadis (Fig. 2). The interaction between the effects of habitat type and rainfall manipulation was highly significant in both 1986 and 1987 (Tables 1 and 2). Water supplementation in 1986 had a positive and statistically significant effect on standing crop in 1987 (Fig. 2), although the interaction of this effect with the effect of habitat type was also statistically significant (Table 2). The three-way interaction term (Habitat × Rain 86 × Rain 87) was also statistically significant, indicating that the degree to which habitat conditions were important in determining the effect of watering in 1987, was dependent upon the watering treatment of 1986 (Fig. 2, Table 2). Analysis of the standing crop data from plots that received only natural rainfall in both 1986 and 1987 revealed a statistically significant

increase in standing crop from 1986 to 1987 ($F = 115.7$, $P < 0.001$), although the interaction of this effect with the effect of habitat type was also statistically significant ($F = 23.9$, $P < 0.001$).

EFFECT OF NEIGHBOUR REMOVAL ON PER-CAPITA SEED PRODUCTION

In 1986, removal of neighbouring plants had a significant, positive effect on per-capita seed production of *Stipa capensis* (Tables 3 and 4). However, the interactions of this effect with both habitat type and rainfall manipulation were also highly significant (Table 4). In 1987, the effect of neighbour removal on per-capita seed production was highly significant, but its interactions with habitat type and the +80 mm treatment of 1986 were also statistically significant (Table 4). The interaction between the effects of neigh-

Table 2 Analysis of variance for the effects of habitat type and rainfall manipulation on standing crop, absolute competition intensity, and relative competition intensity in 1987. Analyses of variation in competition intensity were performed with and without standing crop as a covariate

| Effect (d.f.) | Standing crop | | Absolute competition intensity | | | | Relative competition intensity | | | |
| | | | Without standing crop | | With standing crop | | Without standing crop | | With standing crop | |
	MS	F	MS	F	MS	F	MS	F	MS	F
Standing crop (1)	–	–	–	–	11.9	428.3***	–	–	1.6	394.6***
Habitat (2)	14.8	490.4***	6.8	240.0***	0.9	30.8***	0.82	209.3***	0.07	17.3***
Rain86 (1)	0.8	25.9***	<0.1	0.6	<0.1	<0.1	0.07	18.1***	0.03	7.0*
Rain87 (1)	0.1	5.0*	0.3	9.7**	0.2	6.8*	0.03	6.6**	0.02	4.1
Habitat × Rain86 (2)	0.1	4.5*	<0.1	0.3	<0.1	0.3	0.05	12.8***	0.05	13.2***
Habitat × Rain87 (2)	0.1	4.5*	0.1	2.0	<0.1	1.1	0.01	2.7	0.01	3.5*
Rain86 × Rain87 (1)	<0.1	0.1	<0.1	0.4	<0.1	0.4	<0.01	0.3	<0.01	0.2
Habitat × Rain86 × Rain87 (2)	0.1	4.9*	<0.1	1.3	<0.1	1.7	<0.01	1.4	<0.01	0.6
Error (24)		<0.1		<0.1		<0.1		<0.01		<0.01
Total (35)		0.9		0.4		0.4		0.06		0.06
R^2		0.95		0.94		0.94		0.88		0.89

$*P < 0.05; **P < 0.01; ***P < 0.001.$

Table 3 Effects of habitat type and rainfall manipulation on per-capita seed production (mean + 1 SD) of experimentally isolated and control plants

	Neighbour removal	Control
1986		
Slope		
Control	1.4 ± 0.1	1.3 ± 0.1
+30 mm	30.0 ± 10.5	24.7 ± 13.2
+80 mm	130.2 ± 32.3	46.7 ± 24.5
Depressions		
Control	22.8 ± 6.8	8.5 ± 4.0
+30 mm	113.5 ± 37.7	13.7 ± 6.3
+80 mm	346.5 ± 146.3	25.0 ± 12.5
Wadis		
Control	466.8 ± 67.5	12.0 ± 8.8
+30 mm	975.2 ± 273.6	13.0 ± 3.3
+80 mm	1514.3 ± 648.3	17.5 ± 6.5
1987		
Slope		
Control, Control	35.7 ± 11.0	17.3 ± 4.1
Control, +30 mm	59.0 ± 25.2	24.3 ± 10.1
+80 mm, Control	27.7 ± 8.1	8.0 ± 0.1
+80 mm, +30 mm	56.7 ± 20.8	9.7 ± 4.6
Depressions		
Control, Control	160.3 ± 29.0	21.7 ± 5.5
Control, +30 mm	183.7 ± 40.8	16.3 ± 4.5
+80 mm, Control	175.3 ± 137.6	13.0 ± 4.0
+80 mm, +30 mm	185.0 ± 29.5	19.3 ± 7.5
Wadis		
Control, Control	582.0 ± 79.6	9.0 ± 1.7
Control, +30 mm	1088.7 ± 329.3	8.3 ± 0.6
+80 mm, Control	937.3 ± 23.1	8.7 ± 2.5
+80 mm, +30 mm	822.3 ± 27.0	9.7 ± 2.9

Table 4 Analysis of variance for the effects of habitat type, rainfall manipulation and neighbour removal on per-capita seed production of *Stipa capensis* in 1986 and 1987

Source of variation	d.f.	MS	F
1986			
Removal	1	24.9	780.0***
Habitat	2	7.1	222.4***
Rain	2	8.7	272.2***
Removal × Habitat	2	5.9	186.0***
Removal × Rain	2	0.5	15.5***
Habitat × Rain	4	1.7	51.7***
Removal × Habitat × Rain	4	0.1	1.7
Error	90	0.03	
Total	107	0.74	
1987			
Removal	1	24.1	1294.1***
Habitat	2	2.0	106.5***
Rain86	1	0.1	5.7*
Rain87	1	0.2	8.4**
Removal × Habitat	2	3.4	182.5***
Removal × Rain86	1	0.1	4.5*
Removal × Rain87	1	<0.1	2.6
Habitat × Rain86	2	0.1	5.1**
Habitat × Rain87	2	<0.1	1.6
Rain86 × Rain87	1	<0.1	0.1
Removal × Habitat × Rain86	2	<0.1	1.7
Removal × Habitat × Rain87	2	<0.1	0.2
Removal × Rain86 × Rain87	1	<0.1	1.4
Habitat × Rain86 × Rain87	2	<0.1	1.7
Removal × Habitat × Rain86 × Rain87	2	<0.1	1.7
Error	48	<0.1	
Total	71	0.5	

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

bour removal and the +30 mm treatment of 1987 was not significant (Table 4).

ABSOLUTE COMPETITION INTENSITY

In 1986, patterns of variation in absolute competition intensity (CI_A) were very similar to those obtained for the standing crop data: there was an increase in CI_A from the slope toward the wadi habitat under all rainfall treatments, water supplementation had a positive effect on CI_A in all habitat types, both effects were statistically significant, and their interaction was also statistically significant (Fig. 3, Table 1). Similar effects were obtained when density of *S. capensis* was introduced as a covariate to the analysis (habitat: $F = 127.7$, $P < 0.0001$; rainfall manipulation: $F = 211.7$, $P < 0.0001$, habitat × rainfall: $F = 41.4$, $P < 0.0001$). The effects of habitat type and 30 mm water supplementation were again statistically significant in 1987, but in contrast to 1986, their interaction was not significant (Fig. 3, Table 2). Both effects remained statistically significant after correcting for differences in population density (habitat: $F = 34.9$, $P < 0.0001$; +30 mm: $F = 9.5$, $P < 0.005$). Water supplementation in 1986 did not have any effect on the absolute intensity of competition in 1987 (Fig. 3, Table 2).

There was a significant increase in absolute competition intensity from 1986 to 1987 ($F = 185$, $P < 0.0001$). However, the interaction of this effect with the effect of habitat type was also highly significant ($F = 33$, $P < 0.001$).

Adding standing crop as a covariate to the ANOVA models had a small effect on the proportion of explained variation, but it reduced the sums of squares contributed by those main effects and interactions that were statistically significant (Tables 1 and 2). However, none of the terms which were statistically significant in the original analysis decreased to a non-significant level. Including standing crop as a covariate in the analysis of between-year differences decreased the effect of year to a nonsignificant level ($F = 2.16$, $P \geqslant 0.1$).

RELATIVE COMPETITION INTENSITY

The qualitative patterns of variation obtained for relative competition intensity (CI_R) were similar to those obtained for CI_A (compare Figs 3 and 4). However,
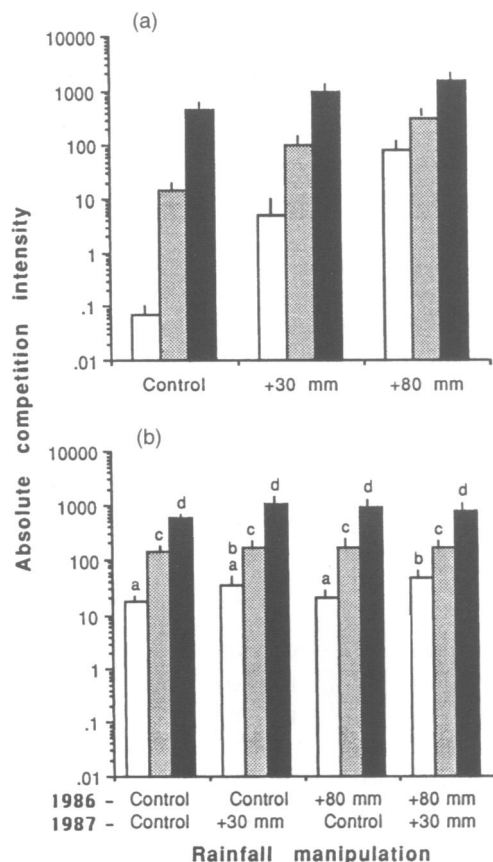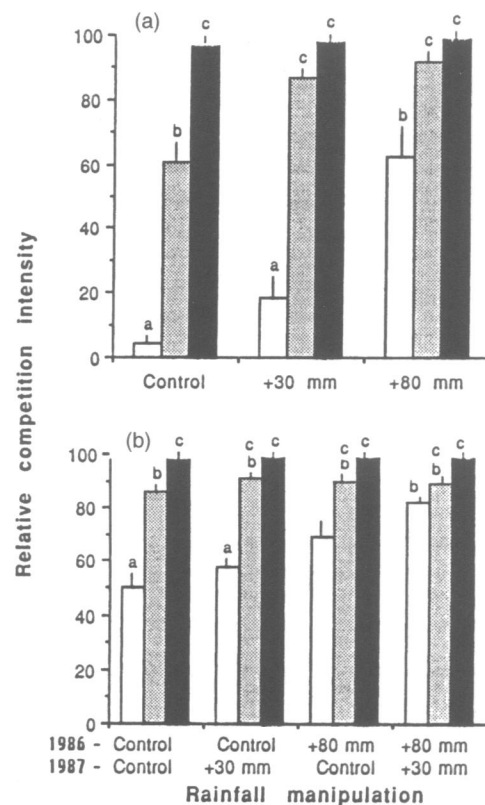
Fig. 3 Absolute competition intensity as a function of habitat type and rainfall manipulation treatment (mean and 1 SE) in (a) 1986 and (b) 1987: (□) slopes; (▨) depressions; (■) wadis. Bars with common letters in a given year do not differ from each other ($P \geq 0.05$, Duncan range tests). Note the logarithmic scale.

Fig. 4 Relative competition intensity as a function of habitat type and rainfall manipulation treatment (mean and 1 SE) in (a) 1986 and (b) 1987: (□) slopes; (▨) depressions; (■) wadis. Bars with common letters in a given year do not differ from each other ($P \geq 0.05$, Duncan range tests).

there were several differences between the two indices in the results of the statistical analyses. For example, in 1986, the overall effects of both habitat type and rainfall manipulation (as expressed by their F values) on CI_R were weaker than the corresponding effects on CI_A and 25% of the pairwise comparisons were not statistically significant (Fig. 4). The effect of water supplementation in 1986 on competition intensity in 1987, as well as the interaction of this effect with the effect of habitat type, were statistically significant in the case of CI_R, but not in the case of CI_A (Table 2).

Including density of *S. capensis* as a covariate in the analyses of CI_R had no effect on the results; all main effects and interactions that were statistically significant before correcting for differences in density remained significant also after such corrections were made (analysis of the 1986 data set: habitat, $F = 54.3$, $P < 0.0001$; rainfall manipulation, $F = 23.9$, $P < 0.0001$; habitat × rainfall manipulation, $F = 7.7$, $P < 0.0001$; analysis of the 1987 data set: habitat, $F = 46.9$, $P < 0.0001$; water supplementation in 1986, $F = 18.8$, $P < 0.0001$; water supplementation in 1987, $F = 6.3$, $P < 0.020$; habitat × water supplementation in 1986, $F = 11.3$, $P < 0.0001$).

The difference in relative competition intensity between the two years was statistically significant ($F = 9.5$, $P = 0.027$) and in contrast to the absolute effect, it was independent of habitat conditions (nonsignificant interaction between year and habitat type).

Adding standing crop as a covariate to the model constructed to analyse the data from 1987 reduced the effect of the +30 mm treatment to a nonsignificant level (Table 2). Interestingly, the interaction between the +30 mm treatment and habitat type, which was not statistically significant in the original analysis, became significant when standing crop was added as a covariate to the analysis (Table 2). When standing crop was introduced as a covariate to the analysis of the between-year differences, the effect of year decreased to a nonsignificant level ($F = 0.64$, $P \geq 0.1$).

RELATIONSHIPS BETWEEN COMPETITION INTENSITY AND STANDING CROP

Both measures of competition intensity were positively and significantly correlated with standing crop under all rainfall treatments (Table 5). However, slopes of the regression models obtained for the various rainfall treatments were not homogeneous (absolute competition intensity: $F = 3.6$, $P = 0.003$, relative competition intensity: $F = 3.6$, $P = 0.004$), indicating that per-gram effects of standing crop were influenced

Table 5 Results of linear regressions for the effect of standing crop on absolute and relative competition intensity. A separate analysis was performed for each rainfall treatment. Regression models are log(y) = a + b log (x) in the case of absolute competition and arcsine $\sqrt{(y)}$ = a + b log (x) in the case of relative competition intensity

	Absolute competition		Relative competition	
	Slope (1 SE)	R^2	Slope (1 SE)	R^2
1986				
Control	0.77 (0.06)	0.93***	0.24 (0.03)	0.81***
+30 mm	0.92 (0.08)	0.90***	0.40 (0.04)	0.88***
+80 mm	0.47 (0.09)	0.61***	0.18 (0.06)	0.38**
1987				
Control, Control	0.50 (0.07)	0.89***	0.23 (0.03)	0.90***
Control, +30 mm	0.72 (0.09)	0.90***	0.30 (0.02)	0.96***
+80 mm, Control	0.77 (0.12)	0.85***	0.23 (0.03)	0.86***
+80 mm, +30 mm	0.53 (0.12)	0.73**	0.12 (0.04)	0.49*

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

by rainfall conditions. Average values of R^2 obtained for absolute and relative competition intensity were 0.83 and 0.75, respectively. This difference was not statistically significant ($P \geq 0.1$, pairwise t-test). Models constructed to test the relationships between competition intensity and standing crop over different years, habitat types and rainfall treatments accounted for 88% of the variation in absolute competition intensity and 83% of the variation in relative competition intensity (Fig. 5).
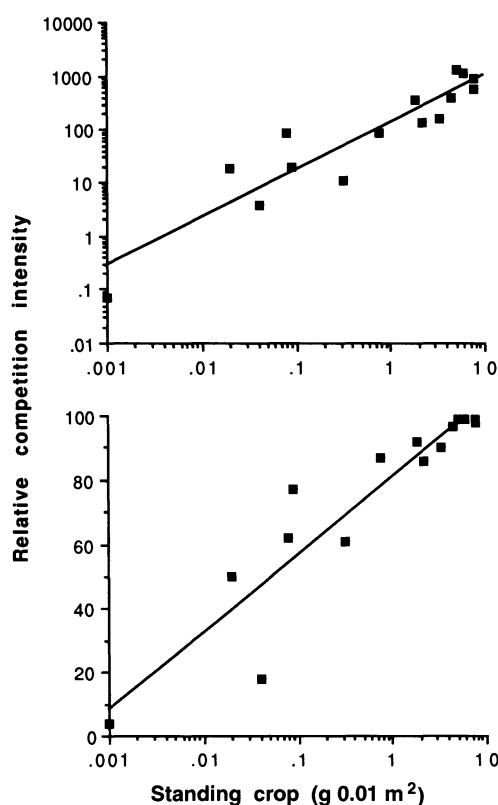
Fig. 5 Relationships between standing crop and competition intensity. Each point represents an average of a different habitat–rainfall combination (note the logarithmic scales). Absolute competition intensity: log y = 2.1 + 0.88log x, R^2 = 0.88, $P < 0.0001$; Relative competition intensity: y = 1.2 + 0.3 log x, R^2 = 0.87, $P < 0.0001$.

Discussion

CONSEQUENCES OF USING NATURAL VERSUS EXPERIMENTAL GRADIENTS OF PRODUCTIVITY

Goldberg & Barton (1992) have noted that results from studies in which competition intensity was measured along natural gradients of productivity (e.g. Friedman & Orshan 1974; Gurevitch 1986; Wilson & Keddy 1986; Reader & Best 1989) tend to support Grime's (1973) hypothesis that competition is more intense on relatively productive sites, while studies conducted along experimental gradients (e.g. Wilson & Shay 1990; Wilson & Tilman 1991) are more consistent with the hypothesis that competition does not change in intensity along productivity gradients (Newman 1973). Results from more recent studies (Wilson & Tilman 1993; Turkington *et al.* 1993) are in agreement with this distinction. In the study reported here, both natural gradients (differences among habitats under natural rainfall conditions) and experimental gradients (differences among watering treatments within the same habitat) were tested for their effect on competition intensity. The results are consistent with the distinction made by Goldberg & Barton (1992) and indicate that in both years, natural gradients had stronger effects on competition intensity than experimental gradients (Figs 3 and 4; Tables 1 and 2). However, this result is misleading because ranges of the natural gradients obtained in this study (as expressed by the magnitude of variation in standing crop) were greater than ranges of the experimental gradients (Fig. 2, Tables 1 and 2). It might be therefore that the stronger effects detected for natural gradients reflect differences in the range, rather than in the type, of the productivity gradients.

To test this hypothesis I selected two gradients representing a similar range of standing crop, one natural (slopes vs. depressions, both under natural rainfall conditions in 1986; see Fig. 2) and one experimental (control vs. a supplementation of 80 mm

water on the slopes in 1986), and compared the effects of these gradients on competition intensity. The results of this comparison indicated that absolute competition intensity was more sensitive to the experimental, rather than to the natural gradient (Fig. 3). The results of the corresponding ANOVA model (Table 1) were consistent with this finding and indicated that the effect of habitat type on absolute competition intensity was greater than the effect of rainfall manipulation when underlying differences in standing crop were ignored, but an opposite pattern, with a greater effect of rainfall manipulation, was detected when standing crop was added as a covariate to the model (Table 1). The two types of gradients did not differ from each other in their effect on relative competition intensity (Fig. 4). Whether these results can be extrapolated to other systems is unknown because no previous study has directly compared the consequences of using experimental vs. natural gradients of productivity in the same system. The argument proposed by Goldberg & Barton (1992) that natural gradients of productivity have a stronger effect on competition intensity because of a wider range of variation in initial standing crop cannot be applied to the system studied in this paper because initial aboveground biomass was zero in all cases.

ABSOLUTE VS. RELATIVE COMPETITION INTENSITY

Previous studies have used two types of indices for quantifying the intensity of plant competition; some studies have expressed the effect of competitive interactions as the absolute reduction in plant performance due to competitive effects (e.g. Friedman & Orshan 1974; Reader & Best 1989), while others have used 'relative' indices in which the absolute reduction is standardized by the performance of plants growing without competition (e.g. Wilson & Keddy 1986; Wilson & Shay 1990; Wilson & Tilman 1991, 1993). In the few cases where both types of indices were calculated in the same system (Campbell & Grime 1992; Turkington *et al.* 1993), absolute competition intensity was more sensitive to variations in productivity and standing crop than relative competition intensity. In the study reported here, the two measures of competition did not differ from each other in the main patterns of spatial and temporal variations (Figs 3 and 4). However, an examination of the ANOVA results (Tables 1 and 2) indicates that in both years, natural and experimental changes in productivity had a stronger effect on absolute competition intensity than on relative competition intensity. Furthermore, pairwise comparisons of the results obtained for relative competition intensity in 1986 were not statistically significant in 25% of the cases (Fig. 4). The corresponding comparisons of absolute competition intensity were statistically significant in all cases (Fig. 3). These results are consistent with the hypoth-

esis that absolute competition intensity is more sensitive to changes in productivity than relative competition intensity.

RELATIONSHIPS BETWEEN COMPETITION INTENSITY AND STANDING CROP

Both the absolute and relative effects of competition were positively and significantly correlated with standing crop. Such a result was obtained for spatial (among habitat), temporal (between year), experimental (between rainfall treatments), and combined gradients of standing crop. This result strongly supports Grime's (1973) proposal that the intensity of competition increases along productivity gradients.

A positive effect of standing crop on competition intensity has been documented in several previous studies (Wilson & Keddy 1986; Reader & Best 1986; Turkington *et al.* 1993). However, results from other studies have demonstrated that competition intensity may remain constant along standing crop gradients (Wilson & Shay 1990; Wilson & Tilman 1991, 1993). Two types of explanations have been provided for such results. Wilson & Shay (1990) suggested that the range of the standing crop gradient used in their study was too narrow to detect the effect of standing crop on competition intensity. To test whether the difference between my results and those obtained by Wilson & Shay (1990) can be related to differences in the range of the standing crop gradient along which competition was measured I reanalysed my data using the same competition index used by Wilson & Shay (relative competition intensity), but taking into account only those plots where standing crop fell within the range studied by Wilson & Shay (50–950 g m^{-2}). Analysis of the data obtained for natural gradients of standing crop (i.e. for plots receiving only natural rainfall conditions) revealed a statistically significant correlation between standing crop and competition intensity for both the 1986 and 1987 data sets (1986, $r = 0.83$, $P = 0.0219, n = 7$; 1987, $r = 0.95, P = 0.0024, n = 6$). Furthermore, an examination of the data presented in Figs 2 and 4 indicates that in several cases, experimental gradients of standing crop whose range was similar or even lower than the range used by Wilson & Shay (1990) resulted in statistically significant differences in the intensity of competition. These results suggest that the difference between my results and those obtained by Wilson & Shay (1990) cannot be related to differences in the range of the standing crop gradients.

An alternative explanation for the lack of correlation between standing crop and competition intensity was provided by Wilson & Tilman (1991, 1993). These authors have demonstrated that the intensities of above- and below-ground competition may be negatively correlated along productivity gradients, and that under such circumstances, total competition intensity is uncorrelated with standing

crop. The results obtained in the study reported here do not allow a distinction between above- and below-ground competition, but the hypothesis of no correlation between total competition and standing crop (or productivity) was rejected. In addition, total competition intensity decreased to nonsignificant levels toward the less productive parts of the gradients examined in this study (slopes receiving only natural rainfall conditions in both years). These results suggest that patterns of variation in above- and below-ground competition along productivity gradients may be more complicated than those suggested by Wilson & Tilman (1993).

Acknowledgments

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