

Density regulation in annual plant communities under variable resource levels

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Density regulation is assumed to be common, but is very rarely tested experimentally. Using annual plant communities, we tested the hypotheses that 1) regulation of abundance in plants occurs at the level of entire communities, not just within species, and 2) such regulation is strongest when resources are most limiting. We transplanted different amounts of seeds from two diverse source communities in Israel to an experimental garden and monitored plant densities and cover for two years under different irrigation regimes. Both total density and total plant cover showed strong evidence of community-level regulation; plots sown at higher than average natural density declined or stayed the same in total abundance over time, while plots sown at lower than average natural density increased in abundance over time. This convergence of community abundance was strongest with the lowest irrigation in both source communities, consistent with the hypothesis of stronger regulation when all resources are more limiting (light levels were high, regardless of irrigation level). The main mechanism of regulation was strong density dependent recruitment, while survival was either density independent or inversely density dependent. Thus, the results also emphasize the need for direct experimental studies of the population dynamic consequences of interactions, as well as of individual level consequences.

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The question of how population density is regulated has long been a controversial subject in ecology (Turchin 1999). While it is generally agreed that experimental perturbation of density and subsequent monitoring of population change is the most useful approach to test for the existence and underlying mechanisms of population regulation (Harrison and Cappuccino 1995, Turchin 1995), this is usually not possible because of the logistics of manipulating and monitoring population sizes of long-lived and/or large organisms. Nevertheless, an increasing number of studies use perturbations of natural populations to test for density dependence of a

subset of demographic parameters (animal studies reviewed by Harrison and Cappuccino 1995, plant studies reviewed by Fowler 1995). However, such experimental demonstrations of negative effects of increasing density on demographic parameters are not sufficient to demonstrate population regulation, let alone explain its mechanisms (Sinclair 1989). First is the problem of relating density dependence of separate demographic measures, such as mortality, growth or fecundity at particular age classes, to density dependence of net change in population size (McPeck and Peckarsky 1998). Second, while density dependence of net per

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capita population growth is a necessary condition for a population to be regulated, it is not sufficient (Turchin 1995); density dependence must also be of appropriate sign (i.e. generate a tendency for the population to return), it must be of sufficient magnitude to counteract "the disruptive effects of density independent factors", and any time lags must be sufficiently short to prevent diverging oscillations from being generated (Turchin 1995). Thus, an experimental demonstration of population regulation requires testing whether and how populations actually recover from perturbations of their densities to levels both above and below the original field density. Such field experiments are almost nonexistent (reviewed by Crawley 1990, Fowler 1995, Watkinson 1997 for plants; Sinclair 1989, Harrison and Cappuccino 1995 for animals).

For plants and other sessile organisms, most experimental studies of density dependence have an additional limitation that is less widely recognized: manipulation of only conspecific density. This may well be reasonable in many animal groups, but because all plants compete for similar resources, it is likely to strongly underestimate the magnitude of density dependence (Law and Watkinson 1989). This is because any reduction in density of one species is likely to be associated with increases in density (or biomass) of other neighboring species that are likely to be potential competitors. This notion of regulation by the total community is supported by the observation that removal of a single neighboring species or even entire growth forms from a community often has relatively little effect on the remaining individuals (Fowler 1981, Hils and Vankat 1982, Silander and Antonovics 1982, Miller 1994), while removal of all neighbouring species typically results in strong growth responses in plants (Gurevitch et al. 1992, Goldberg et al. 1999). Thus, studies of density dependent demography of a single species in a diverse plant community could give misleading results about the processes influencing both individual fitness and population dynamics of that species.

The argument that population growth of a single species of plant depends on density of the entire plant community leads further to the hypothesis that density of the entire plant community is itself regulated, that is, a community level carrying capacity can be defined. This hypothesis of regulation of total community density does not assume that all species in the community are equivalent competitors, merely that any increase in abundance in one species is compensated by a similar decrease in abundance of one or more other species. Such a "zero-sum" game of community density is assumed by a number of spatially based models of coexistence and community structure, including the lottery model of the storage effect (Chesson and Warner 1981, Chesson 2000) and Hubbell's (2001) unified neutral theory of biodiversity and biogeography. While

such models are actively debated and have received a number of supportive indirect tests, their very basic assumption of regulation of total community density has not been tested experimentally in any system.

Although it is important to demonstrate experimentally that regulation of community abundance can occur, generalizing beyond any particular community requires an understanding of how the intensity and mechanisms of regulation vary with environmental or organismal characteristics. Because one primary mechanism of density dependence is competition for limiting resources, a very general hypothesis is that density dependence and regulation of abundance should be strongest where all resources are most limiting (Davis et al. 1998).

In this study, we experimentally manipulated initial densities of entire, diverse communities of annual plants and monitored subsequent changes in total community abundance (density and cover) to test the following specific predictions:

- 1) Regulation of abundance occurs at the level of entire communities. Therefore, plots planted with diverse species assemblages at much lower and much higher total density than typically found in the field should increase or decrease, respectively, in density and cover over time, resulting in convergence of density and cover that is independent of initial conditions.
- 2) Regulation of total community abundance is stronger at greater resource limitation. Therefore, convergence of densities or cover should be faster when resources are more limiting.

To assess the mechanisms of regulation under different conditions, we also compared the density dependence of per capita performance among different life history stages and environmental conditions. Demographic studies have shown that competition may affect both survival, recruitment, and adult biomass (Harper 1977, Watkinson 1985, Symonides 1987, Kadmon and Shmida 1990). For example, is convergence detected primarily due to differential survival (i.e. lower survival of seedlings to adulthood at higher densities) and/or differential recruitment (i.e. lower fecundity of adults at higher densities or lower probability of germination the following season). Eventual understanding of general patterns of population or community regulation will require testing how the importance of different stages depends on life history and environment (Sinclair 1989).

We used two diverse annual plant communities in Israel to test these predictions. Initial density was modified by collecting naturally occurring assemblages as seed source and transplanting different amounts of these seeds to plots in an experimental garden (Goldberg et al. 1995). Resource levels were modified by adding different amounts of water throughout the growing

season. Therefore, resource limitation should have been greater at lower irrigation and, consequently, we predict convergence of community abundance should be more pronounced at lower irrigation.

In this paper, we focus on regulation of total community density and density dependence of survival and growth averaged over all species to address our hypotheses of community-level regulation. Effects on dynamics of individual species and functional groups within the experimental communities will be discussed in a subsequent paper (Turkington et al., unpubl.).

Material and methods

System and basic approach

We used annual plants occurring at two semistabilized sand dune sites (source communities) in Israel (Table 1). The less productive source community was a desert site at Holot Mashabim, a nature reserve in the Negev and the more productive community was a site near the Mediterranean coast at Caesarea. In both locations, annuals typically germinate with the start of the rainy season in November or December, grow rapidly as temperatures warm in March, and reproduce and dry up by mid to late April, as the rainy season ends. By using two source communities, we could ask how the tests of our predictions differed between communities with inherently different resource limitation.

Both communities are diverse, with 33 and 25 species found in the desert and Mediterranean communities, respectively, over the course of this experiment. Dominant species in the desert community included the grasses *Bromus fasciculatus*, *Aegilops kotschy* and *Vulpia brevis*, the legume *Trifolium tomentosum*, and other dicots, such as *Rumex pictus*, *Erodium lacianatum*, *Matthiola livida* and *Reboudia pinnata* (nomenclature follows Feinbrun-Dothan and Danin 1991). Dominant species in the Mediterranean community included the grasses *Aegilops sharonensis*, *Bromus rigidus* and *Cutandia philistaea*, the legumes *Medicago littoralis* and *Trifolium palaestina*, and other dicots, including *Rumex bucephalophorus*; the dynamics of these species will be

examined in a subsequent paper (Turkington et al., unpubl.).

The experimental garden

To eliminate confounding by factors other than resource availability, and to separate direct effects of the abiotic environment from effects of species assemblage, we transplanted seeds from the two source sites to an experimental garden at a site drier than either of the source sites (Table 1). An experimental "sandbox" garden was constructed at the Blaustein Institute for Desert Research at the Sde Boqer Campus of Ben-Gurion University, in the northern Negev Desert, about 25 km south of the desert source site of Holot Mashabim (Table 1). We used 12 "trenches" each having 8 large (1 × 1 m) and 8 small (0.5 × 0.5 m) plots. Each trench was 2 × 10 m and dug to 1 m depth. Corrugated plastic liners were placed in the excavated area to separate the individual plots in each trench from each other and from the surrounding loessal soil. The plots were then filled with sterile sand collected from at least 10 m below the surface from a commercial quarry located in the same dune system as the Holot Mashabim source site.

Density treatments: seedbank collection and preparation

At each of the two source sites, surface sand (0–2 cm depth) was collected in September 1994, after the dry summer and 1–2 months before the beginning of the next rainy season and subsequent germination. At both sites, we collected seeds from along transects laid out to include the complete range of topographies and species in the sites, with the constraint that samples were at least 30 cm from any shrubs and away from any ant nests or rodent burrows. The samples from within each source site were passed through a series of sieves to eliminate the sand (all particles < 500 µ). The samples were then combined and thoroughly mixed.

We established different initial densities by sowing different amounts of this homogenized, concentrated seedbank to the surface of the plots. Referring to

Table 1. Description of source and garden sites. Mean annual rainfall covers the period 1961–1990 for the desert and experimental garden sites and 1951–1980 for the coastal site. The seedbank for the experiment was collected from the two source sites in September 1994 and thus included seeds produced by plants from the 1993–4 growing season, as well as previous years; seed was sown on 22 Nov 1994. Precipitation data were provided by the Israel Meteorological Service. Annual amounts are given by season (Oct. 1 of the first year to Sept. 30 of the subsequent year).

Site	Name	Grid ref.	Precipitation (mm yr ⁻¹)			
			Mean annual	1993/4 (collect)	1994/5 (year 1)	1995/6 (year 2)
Desert	Holot Mashabim	31°00'N 34°44'E	110	85	134	27
Coastal	Caesarea	32°30'N 34°55'E	550	351	804	489
Experimental garden	Sde Boqer	30°48'N 34°48'E	98	66	142	52

“natural density” as the mean mass of seeds collected per m² in the source sites, we used three initial density treatments: 1/16 of natural (0.0625×), natural (1×), and 4 times natural density (4×). This approach allowed us to change the seed density while keeping the initial relative abundances of species constant, without having to count or identify individual seeds.

Irrigation treatments

The three irrigation treatments mimicked aspects of the precipitation regimes of the two source sites, and an intermediate regime, using a computer controlled pulsating sprinkler system (Netafim, Hazerim, Israel). Long term rainfall records indicate that, on average, the desert and coastal sites receive, respectively, 1.1 and 5.6 times the annual precipitation of the garden site at Sde Boqer (Table 1). After each naturally occurring rainfall event at Sde Boqer, water was supplied to the experimental plots to maintain these proportional differences, with the intermediate treatment receiving the midpoint of the extremes (3.45 times precipitation at Sde Boqer). Because natural rainfall at Sde Boqer (and the source sites) was higher than the long term average during the first growing season, but considerable less than the long term average during the second growing season (Table 1), this regime meant that the total amount of water added to the treatments was also greater during the first year.

In addition to less water, the desert source site and the garden site experience fewer rainfall events and longer inter-rain intervals than does the coastal source site (Israel Meteorological Service, unpubl.). However, it was logistically impossible to also mimic the frequency component of the natural rainfall regimes. Instead, if no rain fell at the garden site for a period of two weeks, each of the plots was irrigated with the equivalent of 1/12 of the mean annual precipitation of the desert site in the Low treatment, of the coastal site in the high treatment, or the midpoint in the Intermediate treatment.

Experimental design

The basic design was a factorial of three initial community densities (0.0625, 1, and 4 times natural density) × three irrigation treatments (low, intermediate and high) × two source communities (desert and coastal), all replicated in four blocks. Because irrigation treatments could only be assigned to entire trenches, we used a nested block design, with three trenches in each block. One trench of each block was assigned randomly to each irrigation regime and the combinations of source and density treatments were then assigned randomly to plots within each trench. Thus, source and density were nested within irrigation treatments.

The design was further complicated because it was necessary to have different plot sizes and numbers of replicates among densities. To produce enough of seedbank for the highest density (4×) in the large (1 m²) plots would have required enormous volumes of sand + seedbank collections from the field. Instead, the 4 × initial density treatment was planted into one small (0.5 × 0.5 m) plot per source per trench. However, such small plots would have resulted in so few plants in the lowest density plots (0.0625×) that no reasonable data could be obtained; instead, these were planted in the larger (1 m²) plots. To test for plot size effects, the intermediate density (1×) was planted in one small and one large plot per source in each trench. In addition, because we expected the lowest density (0.0625×) plots to have relatively few plants and hence to be quite variable in species composition, we replicated this treatment in three 1 m² plots per trench.

In summary, within each block, the six combinations of source and irrigation treatment were each replicated 3, 2, and 1 times for the 0.0625×, 1× and 4× density treatments, respectively, for a total of 36 plots in each of the 4 blocks and a grand total of 144 plots for the entire experiment.

Planting, monitoring and maintenance of experimental communities

The plots were planted by spreading the appropriate amount of seeds uniformly across the surface of the sand of each plot on 22 November 1994. The seeds were then covered by 1 cm of sterile sand and lightly sprinkled with an equivalent of 5 mm of rainfall to prevent loss of seeds by wind movement. Each plot had a 10 cm buffer zone in which we planted seeds but did not monitor. Therefore, effective plot sizes were 80 × 80 cm and 30 × 30 cm for large and small plots, respectively. The total number of seedlings was counted in all plots on 5–25 January 1995 by which time seedling emergence was largely completed but mortality had been minimal (Goldberg et al. 2001). The counts were repeated for adults surviving to the end of the growing season on 28 March to 3 April 1995. Percent plant cover was recorded in each plot on 19–20 April 1995.

In May 1995, the plots were covered by nylon screens to prevent dispersal and seed predation during the summer and to isolate local density and irrigation effects on community dynamics. In addition, throughout both years of the experiment, ant activity was largely eliminated by local applications of insecticide. Screens were removed in the beginning of November 1995 before initiation of the second rainy season. Major branches of the senesced plants were clipped, chopped, and returned to the plots to ensure that seeds remaining on the plants were part of the potentially emerging seedbank. The

litter layer was then covered by 1 cm of fresh sterile sand and watered as after the initial planting. Monitoring in the second year was similar to the first year, with seedling counts on 19–28 January 1996, adult counts on 5–8 April 1996, and cover estimates on 18–19 April 1996.

Statistical analyses

Analyses were conducted with SYSTAT 7.0 (SPSS 1997). All dependent variables except percent cover and light were natural ln transformed prior to analysis to meet the assumptions of parametric statistics; percent cover and percent of full sunlight were arcsine square root transformed.

Effects of plot size

Using only the $1 \times$ plots, we conducted three-way ANOVAs to test the effects of plot size (1 m^2 vs 0.25 m^2), irrigation, and source community and all possible interactions on the number of adults per m^2 in both years of the experiment.

Overall effects of resource addition

To test whether water could limit community density in these environments, we compared adult density and percent cover among the irrigation treatments in each year. These analyses used only the plots planted at the highest density ($4 \times$) so that the comparison would reflect effects of water availability on community carrying capacity rather than on individual performance. Combining both sources, we conducted nested ANOVAs, using the MS for trench (nested within irrigation treatments) as the error term for irrigation effects.

Dynamics of community density and cover

To analyze patterns of density and cover change over time, we used repeated measure ANOVAs, including irrigation, initial density, source community, time, and all possible interaction effects. We first analyzed numbers of plants over time including both seedling and adult density measures over the two years and then for each of the stages (seedlings, adults) and measures of abundance (percent cover) separately because population dynamics are more typically assessed by comparing abundances at annual intervals. To test statistically for complete convergence at each combination of source and irrigation regime, we used separate random block ANOVAs to assess effects of initial density on community abundance at each of the 6 stages (seedlings in each year, adults in each year, and cover in each year). Accordingly, when only a single irrigation treatment is considered, the design collapses to a standard block design, with each trench considered a block. Although

this involved a large number of separate tests of significance and therefore the exact probability level from each test is not very meaningful, these tests are still useful for interpreting degree of convergence over time and across treatments.

Per capita performance and change in abundance

To examine patterns of density dependent mortality and recruitment, we calculated in each plot the probability of survival (no. adults/no. seedlings) within each year, and the per capita recruitment rate between years (no. seedlings₉₆/no. adults₉₅). We also calculated the net per capita growth rate between the two years for seedling numbers (no. seedlings₉₆/no. seedlings₉₅), adult numbers (no. adults₉₆/no. adults₉₅) and plant cover (cover₉₆/cover₉₅). These data were compared among irrigation and initial density treatments, using a nested ANOVA for each source community since inspection and preliminary analyses showed strong differences in patterns between the source communities.

Results

Plot size effect

Using only the natural density ($1 \times$) plots, adult densities per m^2 were significantly higher on average in the smaller plots ($F_{1,35} = 9.27$, $p < 0.01$ in 1994/5 and $F_{1,36} = 4.21$, $p < 0.05$ in 1995/6; F values are for the main effects of plot size in three-way ANOVAs of plot size, source community, and irrigation). Across all irrigation treatments and source communities, in the first season, small plots had 42% (sd = 72%, $n = 23$) more adults per unit area than the larger plots on average, despite their equal planting density. In the second season, the mean difference was 65% (sd 89%, $n = 24$). The magnitude of this plot size effect on final density was independent of both source community and irrigation treatment (non-significant ($p > 0.10$) interactions in either year). Thus, there are unlikely to be any artifacts of plot size in the comparison of the magnitude of convergence in densities among irrigation or source communities. Further, our a priori prediction that density will decline over time at high initial planting density, is conservative (i.e. more difficult to achieve) given the methodological problem of higher densities in the smaller plots used for the high densities. Because only the $1 \times$ plots were replicated at both plot sizes, we used their average from each block/treatment combination in the analyses below to make them as comparable as possible to both the $0.0625 \times$ (only large plots) and $4 \times$ (only small plots) initial densities.

Degree of resource limitation

Restricting the analysis to the highest density plots, with the strongest potential for resource limitation, increasing water increased adult density by similar magnitudes in both years of the experiment (significantly so in the first season), but only increased cover in the second season (Table 2). Thus, results are mostly, but not entirely, consistent with the assumption that water limits community abundance in these environments. The lack of pattern for cover in the 1994/5 season may be because the higher than average natural rainfall (Table 1) led to higher individual growth and thus higher cover at low irrigation, relative to 1995/6. At intermeditate and high irrigation, cover was uniformly high in both years at around 90% plant cover. Although no data are available for the second season, adult density and percent cover in intermediate and high irrigation were quite similar to the first season (Table 2), suggesting that light levels would also be similar in those treatments. However, based on observations of the plots, it is unlikely that light levels were sufficiently lower at ground surface to be strongly limiting.

Based on these results, we suggest that the irrigation treatments do indeed represent resource supplementation treatments and therefore allow us to test the prediction that decreasing resource limitation should decrease the magnitude of density dependence.

Density dynamics and regulation

The communities changed drastically in density within and between years, especially in the desert source community (Fig. 1, significant main effects of time and time \times source interactions in Table 3). The apparently greater stability of the coastal community may reflect its initially much lower absolute seedling numbers for a given initial planting density (significant source effect for seedlings in Table 3), indicating either fewer seeds in the seedbank, greater dormancy of seeds, and/or lower viability of seeds (Fig. 1).

Not surprisingly, initial density had strongly significant effects on the number of plants over time (Fig. 1, significant main effect of density in Table 3); this result could simply reflect that when more seeds are planted, more germinate, survive, and reproduce. However, the effects of initial density tended to diminish over time, at least for some combinations of irrigation and source community (Fig. 1, significant time \times density interactions in Table 3), showing that community density regulation is occurring in some cases. At low irrigation in both source communities, the number of plants strongly converged, as initially low density plots increased and initially high density plots decreased over time. Consequently, by the adult stage in the year after planting (April 1996), the initial density treatments were statistically indistinguishable in the desert community and only weakly ($p < 0.05$) significantly different in the coastal community. Similar, but weaker trends towards convergence are also apparent in the desert community at higher irrigation levels, but not in the coastal community (Fig. 1). Thus, the results are also consistent with the prediction that density regulation should be stronger when resource limitation is greater, as at low irrigation. However, it should also be noted that the appropriate interaction terms in the repeated measure ANOVA's are not, or only weakly, significant (Table 3: time \times irrigation \times density and time \times irrigation \times source \times density interactions).

Results for percent plant cover were quite similar to those for number of plants, although in this case both the desert and coastal experimental communities tended strongly towards convergence in cover after two seasons. As with number of plants, this convergence was greatest at low irrigation, where cover at the end of the second season no longer differed significantly among the initial density treatments in either source community (Fig. 2). However, again, despite the clear patterns and differences in statistical results among irrigation treatments, the relevant interaction terms in the repeated measures ANOVAs of the entire data set were either not or only marginally significant (Table 3).

Table 2. Effect of resource supplementation (irrigation treatment) on mean \pm (sd), density ($n = 8$) and percent cover, measured at the end of the growing season. Also reported are results of nested ANOVAs. Density values were \ln transformed and % cover was arcsine square root transformed prior to analyses; untransformed means are shown. Only values for the highest density ($4 \times$) plots were included to test for degree of resource limitation near carrying capacity. Values were averaged over the two source communities because preliminary analyses showed no significant influence of source on patterns with respect to irrigation treatment (no source \times irrigation interactions) within the high density plots. 1994/5 was a wet year (ca 43% more than long term average precipitation at the garden site) and 1995/6 was a dry year (ca 50% less than long term average precipitation); see Table 1.

Year	Variable	Irrigation treatment means			ANOVA results		
		Low	Med	High	F _{irrig}	df	P
1994/5	adult density	2076 (630)	3889 (1309)	4630 (1274)	14.88	2,9	0.001
	% cover	87 (10)	92 (9)	86 (6)	1.14	2,9	0.361
1995/6	adult density	2491 (1010)	3622 (2155)	4160 (1865)	2.49	2,9	0.138
	% cover	68 (8)	87 (8)	88 (9)	6.51	2,9	0.018

Fig. 1. Changes in density (± 1 SE) over time in experimental communities started at different densities (0.0625, 1, and 4 times average natural seedbank densities), different irrigation levels (low, intermediate and high), and from a more xeric (desert) and more mesic (coastal) source community. Repeated measures ANOVA of these data, using ln-transformed data, are shown in Table 3. Symbols represent significance levels for comparisons of initial density treatments at each stage for each combination of source community and irrigation treatment. ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Means are of $n = 4$ for each value.

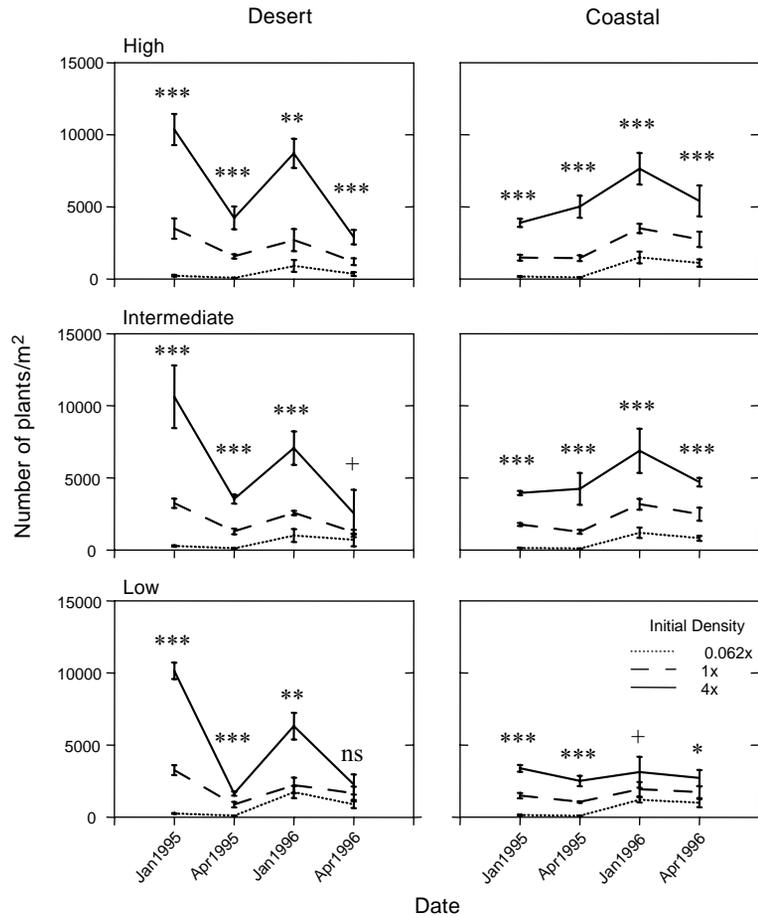


Table 3. Repeated measures ANOVA of the effects of source community, irrigation treatment, and initial planting density on the combined numbers of seedlings and adults, numbers of seedlings only, numbers of adults only, and percent cover of adults over two years. Numbers of seedlings and adults were ln-transformed and percent cover was arcsine square root-transformed before analysis. Bold values indicate statistically significant main or interaction effects ($p < 0.05$) and italicized values indicate marginally significant trends ($0.05 < p < 0.10$). Untransformed mean values for each treatment combination are shown over time in Fig. 1 (seedling and adult densities) and Fig. 2 (% cover).

Source	All stages			Seedlings only			Adults only			Percent cover		
	df	MS	P	df	MS	P	df	MS	P	df	MS	P
Between subjects												
Source	1	0.01	0.839	1	5.07	0.000	1	4.39	0.000	1	0.02	0.339
Irrig	2	0.92	0.048	2	0.28	0.198	2	0.72	0.036	2	<i>0.08</i>	<i>0.057</i>
Density	2	164.21	0.000	2	83.11	0.000	2	81.32	0.000	2	2.02	0.000
Source \times irrig	2	1.01	0.037	2	0.62	0.033	2	0.42	0.140	2	<i>0.07</i>	<i>0.074</i>
Irrig \times density	4	1.13	0.007	4	<i>0.41</i>	<i>0.058</i>	4	0.78	0.008	4	0.08	0.020
Source \times density	2	0.40	0.259	2	1.07	0.003	2	0.05	0.779	2	0.03	0.382
Source \times irrig \times density	4	0.27	0.450	4	0.08	0.774	4	0.23	0.358	4	0.00	0.954
Error	54	0.29		54	0.17		54	0.20		54	0.03	
Within subjects												
Time	3	20.27	0.000	1	12.66	0.000	1	20.60	0.000	1	0.02	0.205
Time \times source	3	5.56	0.000	1	5.38	0.000	1	1.87	0.000	1	0.05	0.038
Time \times irrig	6	0.23	0.043	2	0.14	0.243	2	0.46	0.031	2	0.37	0.000
Time \times density	6	8.88	0.000	2	11.59	0.000	2	14.83	0.000	2	0.25	0.000
Time \times source \times irrig	6	0.32	0.006	2	0.33	0.036	2	0.59	0.013	2	0.01	0.373
Time \times irrig \times density	12	0.12	0.287	4	0.28	0.026	4	0.02	0.971	4	<i>0.03</i>	<i>0.062</i>
Time \times source \times density	6	0.26	0.023	2	0.03	0.739	2	0.02	0.855	2	0.02	0.177
Time \times source \times irrig \times density	12	0.04	0.964	4	0.04	0.790	4	0.05	0.815	4	0.02	0.102
Error	162	0.10		54	0.09		54	0.13		54	0.01	

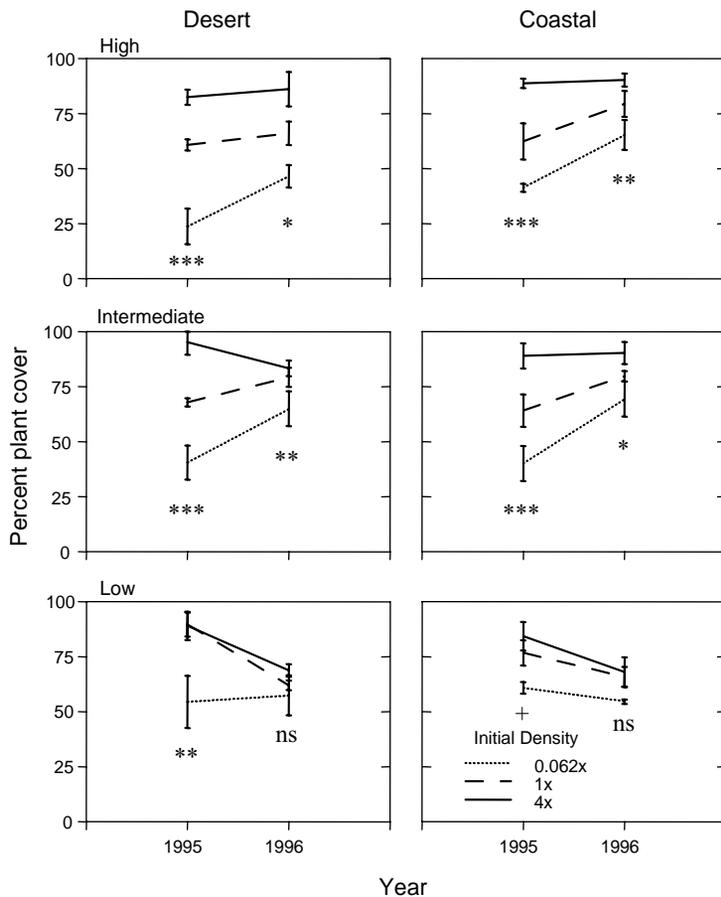


Fig. 2. Changes in percent cover of adult plants (± 1 SE) over time in experimental communities started at different densities (0.0625, 1, and 4 times average natural seedbank density), different irrigation levels (low, intermediate and high), and from a more xeric (desert) and more mesic (coastal) source community. Measurements were taken for adult plants at the end of the 1994/5 (95) and 1995/6 (96) growing seasons. Repeated measures ANOVA of these data, using arcsin square root-transformed data, are shown in Table 3. Symbols represent significance levels from comparisons of initial density treatments at each stage for each combination of source community and irrigation treatment. ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Means are of $n = 4$ for each value.

Per capita responses to density and irrigation: mechanisms of density regulation

The patterns in Fig. 1 and 2 reflect changes in total community abundance and so do not directly address the stages at which density dependence occurs. Thus, we also examined per capita survival, recruitment, and net change in total community density or cover between years. For the desert source community, increasing initial density significantly decreased almost all measures of per capita performance (Fig. 3) and net change in abundance at all irrigation levels (Fig. 4). Further, no interactions between initial density and irrigation were significant ($p > 0.05$), indicating that, for all life history stages, competitive effects were similar under all irrigation regimes (Fig. 3, 4).

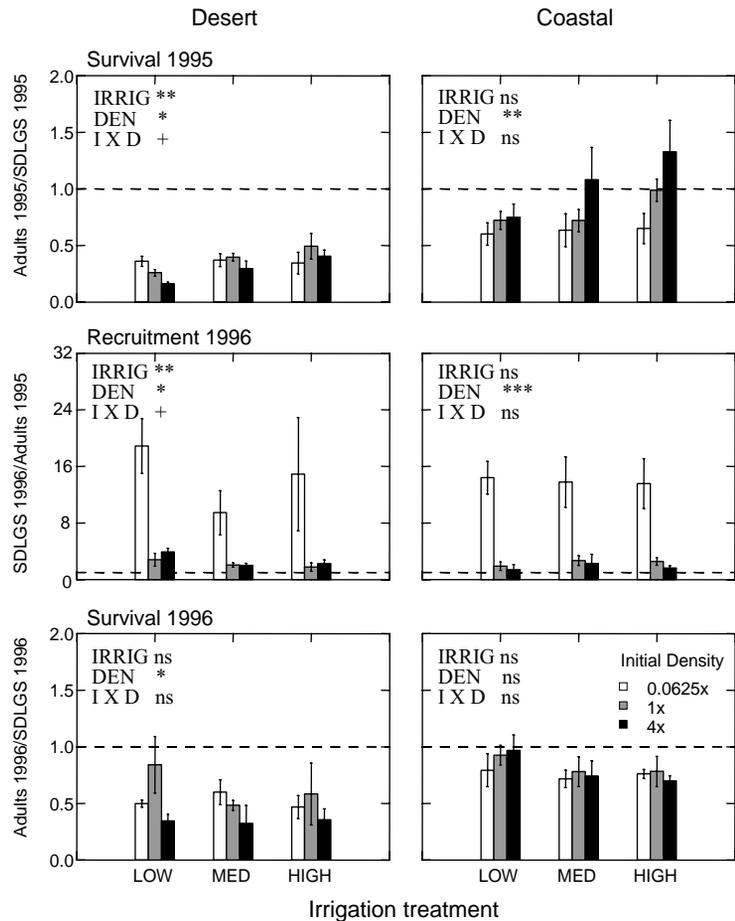
For the coastal source community, results are more complex. As in the desert source community, recruitment was similarly strongly negatively (directly) density dependent at all irrigation levels (Fig. 3, significant main effects of initial density and nonsignificant interaction with irrigation). However, survival was either independent of initial density (in 1995/6; Fig. 3) or, actually, positively (inversely) density dependent (1994/5; Fig. 3).

Nevertheless, the balance of survival and recruitment was clearly negative; as in the desert source community, net change in community abundance, whether in terms of seedling numbers, adult numbers, or adult cover, was strongly and significantly negatively density dependent (Fig. 4). Change in total cover in the coastal community was the only case in which irrigation significantly interacted with initial density ($p < 0.05$).

Effects of water addition on per capita survival and recruitment were relatively small and inconsistent (Fig. 3, 4). For the desert source community, survival in 1994/5 was significantly higher at high irrigation but, surprisingly, per capita recruitment declined at high irrigation (Fig. 3). The recruitment effect again outweighed the survival effect and net per capita change in adult numbers was also significantly lower when more water was available (Fig. 4). In the coastal source community, only net per capita change in seedling numbers was affected by irrigation, in this case, with the more intuitive pattern of higher performance when more water was available (Fig. 4).

For per capita performance in terms of change in cover per plant, effects of irrigation were much clearer and stronger: at a given initial density, increasing water

Fig. 3. Per capita survival and recruitment (± 1 SE) for experimental communities started at different densities (0.0625, 1, and 4 times average natural seedbank density), different irrigation levels (low, intermediate and high), and from a more xeric (desert) and more mesic (coastal) source community. The dashed lines are for a value of 1, throughout. For survival, values greater than 1 indicate that germination after the initial seedling census outweighed any mortality of earlier-germinated adults. For recruitment, values greater than 1 indicate greater than replacement recruitment, involving seed production, germination, and early survival (between germination and the seedling census in January of the second season). Statistical results for each parameter are from two-way nested ANOVAs of irrigation ($df = 2, 9$) and density ($df = 4, 18$) and their interaction ($df = 4, 18$), analyzed separately for each source community and using ln-transformed data. The error term for irrigation effects was the MS for trench (nested within irrigation) and for density and interaction effects was the MS for the density by trench (nested within irrigation) interaction. ns $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Means are of $n = 4$ for each value.



usually increased average increase in per-plant average cover growth (Fig. 4, significant irrigation effects in both source communities).

Discussion

Because of the great similarity in resource requirements among all plants, it could be difficult to detect regulation within single species in diverse natural assemblages. If low density of conspecifics is compensated by higher density of other species also using light, water, and the same mineral nutrients, variation in conspecific density is unlikely to have much impact on individual performance or per capita population growth. Instead, following Goldberg et al. (2001), we tested whether regulation of abundance could be detected at the level of entire communities. Although logistically difficult and rarely performed, the ideal approach for testing population regulation is to manipulate experimentally densities and subsequently monitor population dynamics (Sinclair 1989, Harrison and Cappuccino 1995, Turchin 1995). We used this approach that was originally developed to

study single populations to examine evidence of regulation at the level of entire communities at least under some conditions: communities starting at much higher than average natural density declined (or stayed close to constant) between years and communities starting at much lower than average natural densities increased between years. The premise of the present study is that only studies of density regulation at the level of entire communities can correctly account for the competitive regulation experiences by its members.

The relation between regulation of community abundance and resource availability

Results for both numbers of plants and cover were consistent with our prediction that density dependent regulation should be stronger when resources are more limiting. The test of this prediction depended on the assumption that increasing water availability would alleviate the degree of water limitation but not increase the degree of limitation of any other resource— in particular, of light. Light levels at 7 cm above the surface

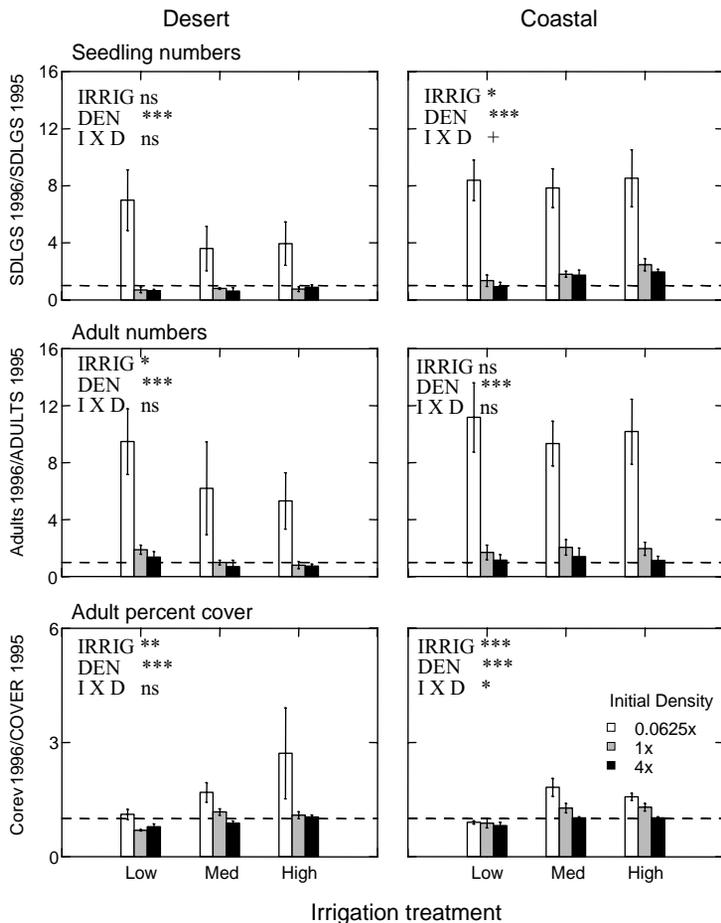


Fig. 4. Net population growth rate (± 1 SE) between the 1994–5 and 1995–6 growing seasons for experimental communities started at different densities (0.0625, 1, and 4 times average natural seedbank density), different irrigation levels (low, intermediate and high), and from a more xeric (desert) and more mesic (coastal) source community. Population growth rate was calculated as: change in numbers from seedling to seedling stage (a), change in numbers of plants from adult to adult stage (b), and change in cover from adult to adult stage (c). The dashed lines are for a value of 1; values greater than 1 indicate an increase in population size from the first to second season and values less than 1 indicate declining population size. Statistical results for each parameter are from two-way nested ANOVAs of irrigation ($df = 2, 9$) and density ($df = 2, 18$) and their interaction ($df = 4, 18$), analyzed separately for each source community and using ln-transformed data. The error term for irrigation effects was the MS for trench (nested within irrigation) and for density and interaction effects was the MS for the density by trench (nested within irrigation) interaction. NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Means are of $n = 4$ for each value.

were above 80% of full sunlight even at the highest density and irrigation levels (H. Shilo-Volin, unpubl.). Our data thus appear to be contrary to the predictions of both of the usual hypotheses pertaining to patterns of competition intensity along productivity gradients in plants: the Grime (1973, 1977) prediction that the intensity of competition should increase with increasing productivity and the Newman (1973)–Tilman (1988) prediction that competition intensity should not vary consistently between low and high productivity plant communities. However, we argue that these hypotheses should not be viewed as alternatives, but rather as applicable under distinct sets of circumstances.

Both the Grime and the Newman–Tilman hypotheses could be viewed as subcases of the general hypothesis that, rather than overall productivity, competition intensity depends on the level of resource limitation as described by Davis et al. (1998). Accordingly, competition should increase as the degree of resource limitation increases. Thus Grime predicted that competition should be least intense in the least productive (“favorable”) environments, Wiens (1977) predicted that it would be most intense in the least productive environments, and

Newman–Tilman that competition intensity would not vary with productivity. For plants, which of these three general predictions is appropriate will depend on the balance between limitation by nutrients or water and by light and, therefore, on the balance between root and shoot competition.

Our finding of decreasing competition with increasing productivity is consistent with results of a related study to the one reported here using the same experimental system but in different years and with comparisons of density dependence within years only (Goldberg et al. 2001), as well as with a study of competition between trees and perennial herbs in Minnesota (Davis et al. 1998). More generally, the results are also consistent with some of the results of a meta-analysis (296 cases in 14 studies) of the effects of competition on individual performance from published field experiments in plants (Goldberg et al. 1999). Thus, a decline in resource limitation and competition with increasing productivity, due to declining nutrient or water limitation without a completely compensating increase in light limitation may be a more general phenomenon than previously recognized.

At what life history stages are communities regulated?

Although both source communities appeared to show similar overall trends for density dependence of the dynamics of density and cover, they achieved this through quite different mechanisms. The desert source community showed strong negative density dependence at both the survival and recruitment stages and thus converged in densities both within and between years. In contrast, the coastal source community showed negative density dependence only at the recruitment stage, thus convergence only occurred between, but not within, years. In fact, in the coastal community, density dependence of survival was slightly positive (Goldberg et al. 2001). Although the reason for this difference between source communities is not clear, the important point in the context of a study of density regulation is that any positively density dependent effects on survival were always outweighed by the strong negative density dependence prevailing at the recruitment phase. Such compensation for facilitation at one stage by competition at another stage provides a caution in evaluating the accumulating body of evidence about facilitative interactions in plants (Callaway 1995, Callaway and Walker 1997, Choler et al. 2001). Although it is certainly becoming increasingly clear that facilitative interactions can be quite common in plant communities and that, in at least some cases, they can influence distribution and abundance (Bertness and Leonard 1997), it is necessary to evaluate the sign and magnitude of density dependence (whether intra- or interspecific) at all life history stages before concluding that dynamics may be driven by such positive interactions (McPeck and Peckarsky 1998).

Conclusions

Evidence of density dependence of measures of individual fitness abounds for many types of organisms in many types of environments. For plants, this evidence comes from studies of both intraspecific and interspecific interactions (Crawley 1990, Goldberg and Barton 1992, Gurevitch et al. 1992, Watkinson 1997). Thus, population regulation is usually assumed to be common in plants and it is not surprising that we found strong evidence of regulation of community abundance by manipulating initial density and monitoring dynamics over time. However, the logistics of manipulating density and monitoring total population or community abundance (rather than individual fitness components of selected plants) under field or even garden conditions is often daunting and therefore our study represents the first experimental test of community-level regulation of which we are aware. The test was made logistically feasible by using relative amounts of community seed-

bank to manipulate initial densities rather than counting individual seeds of all the component species. However, the cost of this approach is that we do not have data on initial densities of each species separately and so cannot directly compare density dependent dynamics at population vs community levels. This is the next important step in assessing the mechanisms of regulation of abundance in plants and is critical information for assessing how population and community dynamics should be modeled.

We also found strong evidence of greater density dependence and stronger regulation of abundance at lower irrigation levels, which were more resource limited. Because this result is inconsistent with both of the hypotheses typically brought to bear on questions of competition along productivity gradients (Grime 1973, 1977, Newman 1973, Tilman 1988), it suggests that the current theory and accompanying empirical studies are incomplete. Whether competition increases, stays constant, or declines with productivity depends critically on whether resource limitation increases, stays the same, or declines with productivity, and theory is needed that incorporates mechanisms to control variation in the net degree of resource limitation – what are the general processes that control the net balance of root and shoot competition? Empirically, understanding general patterns of the role of competition will require much more detailed information on resource limitation (and depletion) instead of just the net outcome of competitive interactions. Experiments that separate root and shoot competition are one critical component of this endeavor but also needed are experiments that assess the degree of limitation by different resources – this will depend on the particular natural history and physiology of each species.

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