

Differentiation in populations of *Hordeum spontaneum* Koch along a gradient of environmental productivity and predictability: Intra- and interspecific competitive responses

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ABSTRACT

We compared intra- and interspecific competitive responses of wild barley, *Hordeum spontaneum*, from four populations originating in distinct environments in Israel. The environments ranged along two parallel gradients of rainfall amount and predictability, from low (desert) to moderate (semi-steppe batha) to high (Mediterranean grassland and mountain, the latter also experiencing frost stress). The target barley plants grew under one of five densities (0, 4, 8, 16, and 32 surrounding plants per bucket) of either barley from the same population or oats (*Avena sterilis*) from a neutral population. The traits examined included estimates of fitness, reproductive traits, and resource allocation.

The effect of intraspecific competition was stronger than interspecific competition at a high increment of neighbor density (from 4 to 32 neighbors). There was no difference in interspecific competitive responses of plants originating in the four environments at any neighbor density increments, but intraspecific competitive responses of the four ecotypes consistently differed at low competitive intensity (4 neighbors). The superior competitors were the plants originating from Mediterranean grassland, the most favorable with respect to rainfall and abiotic stress (i.e., drought or frost) environment. The plants from the mountain environment, which is highly productive and predictable with respect to rainfall but experiences severe frost stress, were the poorest competitors. Our results are inconsistent with the hypothesis that there is no relationship between competitive ability and environmental favorability. High competitive ability appears to be a distinct property of plants living in favorable environments (i.e., productive, predictable, and without abiotic stress) corresponding to the “competitive” strategy of the C-S-R model. However, in less productive and/or predictable environments, or under conditions of severe abiotic stress, plant features other than ability to tolerate low water or nutrient levels may be more important, with reduced competitive ability as a trade-off.

Keywords: abiotic stress, aridity gradient, comparative approach, competitive ability, plant strategy, wild barley

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INTRODUCTION

Competitive interactions between plants have been recognized as an important ecological force (see reviews by Connell, 1983; Schoener, 1983; Goldberg and Barton, 1992), and generalizations of how these interactions operate at community and ecosystem levels were made through the application of comparative approaches with several species evaluated under standardized conditions (Rorison et al., 1987; Grime et al., 1988; Keddy, 1992; Gaudet and Keddy, 1995; Wardle et al., 1998). However, relatively few studies have explored the importance of competition as an evolutionary force (Turkington and Harper, 1979; Martin and Harding, 1981; Aarssen and Turkington, 1985; Linhart, 1988; Platenkamp and Foin, 1990; Miller, 1995). Comparative approaches to competition were effectively used to analyze the relationship of competitive ability with habitat conditions (Van de Werf et al., 1993; Keddy et al., 1994; Gaudet and Keddy, 1995), but they did not provide evolutionary inferences because of their correlative (and not causal) nature. In order to investigate the evolutionary importance of competitive ability, we undertook a “comparative population approach”, which uses populations of the same species distributed along clear environmental gradients (e.g., amount and predictability of annual rainfall) after the populations were experimentally shown to be locally adapted (Volis et al., 2002a,b,c,d, 2004). This approach is potentially a powerful tool for identifying environmentally-induced effects of natural selection and resulting plant strategies. In this study, we examined the role of competitive ability in a set of “coadapted traits designed by natural selection, to solve particular ecological problems” (Stearns, 1976) using four populations of wild barley, *Hordeum spontaneum* Koch, from distinct environments in Israel. These populations are distributed along two parallel gradients of annual rainfall amount and predictability that determine steep climatic and ecological clines (from xeric desert to mesic Mediterranean) across relatively short distances in Israel (Yom-Tov and

Tchernov, 1988; Bitan and Rubín, 1991; Aronson et al., 1992; Kadmon and Danin, 1997). Water is a main limiting and fluctuating resource that creates a steep north-south productivity gradient in Israel (Aronson et al., 1992).

Intra- and interspecific competition were tested under a regular and copious supply of water and nutrients to test whether barley genotypes originating in a less productive environment are poorer competitors than genotypes from a more productive environment (Grime, 1973, 1977). It was suggested by Goldberg and Novoplansky (1997) that Grime’s hypothesis should apply more to water than to nutrients as the main limiting resource, and that xeric vs. mesic environments are more likely to induce a difference in competitive intensity than fertile vs. infertile environments. Therefore the aridity gradient especially suits our purpose of testing competitiveness in the evolutionary context. If competitive ability and ability to tolerate stress caused by either an irregular or a chronically low supply of limiting resource are coupled, a genotype from a stressed environment should be a better or equal competitor under favorable conditions than a genotype from a productive environment. The opposite, i.e., superiority of a genotype from a productive environment, can be interpreted as an indication of independence of stress and productivity as evolutionary forces.

METHODS

Experimental set-up

Wild barley, *Hordeum spontaneum* Koch, is a winter annual, predominately selfing grass distributed throughout Israel as one of the major herbaceous components. The populations selected represent four environments in order of increasing amounts and predictability of precipitation: desert (SB), semi-steppe shrubby vegetation community called batha (BG), grassland (AM), and mountain (MH) (Table 1). We use the same designations for the populations as those in Volis et al.,

Table 1
Ecogeographical data for the four study populations

Population	Environment/ vegetation	Region	Soil	Altitude (m)	Annual rainfall (mm)	CV (%)	n
MH	Mountain	Mount Hermon	Terra Rossa	1500	1600	–	–
AM	Grassland	Upper Galilee	Terra Rossa	300	580	29	42
BG	Semi-steppe batha	Shefela Hills	Rendzina	270	408	32	49
SB	Desert	Negev Desert	Loess	470	90	43	49

Abbreviations: CV—coefficient of variation in annual rainfall, n—years of observation, – —no reliable data.

2002a,b,c for ease of reference. For a detailed description of the environments, map with population locations, their coordinates, and other environmental parameters see Volis et al. (2002a). As all precipitation in Israel takes place during winter, the annual rainfall is also the amount of rainfall received by wild barley plants during a growing season. In two environments, desert and mountain, plants are exposed to contrasting abiotic stresses (drought in the desert and winter frosts in the mountain).

Pooled seed collections (made in 1997) of the four target populations (SB, BG, AM, and MH, viz., desert, batha, grassland, and mountain) were used. We tried to avoid a potential sampling problem that may occur when a population does not represent a locally-adapted ecotype, but rather a random subset of genes created by genetic drift. Consequently, we used only large populations comprising thousands of individuals in protected natural environments such as Nature Reserves or National Parks. We are aware that a single individual population within an environment cannot be assumed to represent the environment at large (i.e., in the statistical sense, we have internal validity of interpopulation comparisons but lack external validity for interenvironmental comparisons). Nonetheless, we believe, from many years of experience with the various populations of *H. spontaneum* throughout its range in Israel, that these populations are representative of populations in each environment at large.

Seeds were germinated in Petri dishes, and 2–3-day-old seedlings were transplanted into 10-l buckets (height 27 cm, upper diameter 31 cm, bottom diameter 23 cm) filled with a potting mixture of equal parts peat and vermiculite. Artificial soil was used because we wanted to exclude in an experiment (i) the effect of nutrient stress and (ii) an effect that could arise because of a possible adaptation of ecotypes to indigenous soil types. Buckets were placed 1.0 m apart in a nethouse at the Institutes for Applied Research, Be'er Sheva, Israel that contained drip lines with 2-l/h drippers, with 1 dripper placed in each bucket. The target barley plant was placed in the center of the bucket and surrounded either by barley plants from the same population or oat plants (*Avena sterilis* L.) from a selected population (near Ginnaton, sandy loam soil, annual rainfall around 500 mm) located more than 50 km from each sampled barley location. *A. sterilis* is an excellent candidate species to test the interspecific competitive ability of wild barley because the two species usually occur together as main components of annual plant cover, and have similar stature, life histories, and phenology (Volis, personal observations). The growth of the neighbors (both barley and oat) paralleled that of the targets, i.e., all seeds of

targets and neighbors were germinated and plantlets were transplanted into the buckets at the same time. The target barley plants grew under one of five densities of surrounding plants (0, 4, 8, 16, and 32 plants), representative of a range of wild barley densities in natural stands in the field (range = 1–500 adult plants/m² at two sites, BG (batha) and SB (desert), Volis, unpublished data). A randomized complete block design was used with a total of 324 pots arranged into 9 blocks with one treatment per population in each block. Irrigation and fertilization (20:20:20 NPK) was provided 3 times a week. The amount of irrigation allowed for 20–25% of the irrigation water to drain out of holes in the bottoms of the buckets. All trait measurements were obtained after plant maturation. The traits examined included: (i) estimates of fitness (number of spikelets, reproductive biomass); (ii) reproductive traits (number of spikes, number of spikelets per spike, spikelet and caryopsis weight); and (iii) reproductive allocation. The mean number of spikelets per spike was calculated from all spikes produced by a target plant, mean spikelet weight from 100 randomly-selected spikelets, and mean caryopsis weight from 20 randomly selected and peeled spikelets.

Data analysis

To estimate the effect of neighbor density on the traits examined, the results were standardized as proportions of maximum population value and then regressed against density. At first, untransformed regressions were calculated to determine the form of the relationship between each trait and density. Yield (number of spikelets) and related traits (reproductive biomass, number of reproductive tillers) showed an asymptotic relationship with density and after square-root⁻¹ transformation formed two distinct linear slopes (from 0 to 4 neighbor plants and from 4 to 32) (Fig. 1). In such reproductive traits as number of spikelets per spike, spikelet weight, and caryopsis weight, this relationship was also detected but much less pronounced. In all transformed regressions, positive slopes indicate a negative (competitive) effect.

Reproductive allocation was not asymptotically-related to density and was not reciprocally transformed, but was square-root transformed to reduce variation that increases at higher neighbor densities. All traits were tested for normality of distribution and homogeneity of variance among groups.

The regression slopes among the four populations were compared by analysis of covariance. A significant population*density interaction indicated differences in population competitive responses. Competitive response is defined using Goldberg and Werner's (1983)

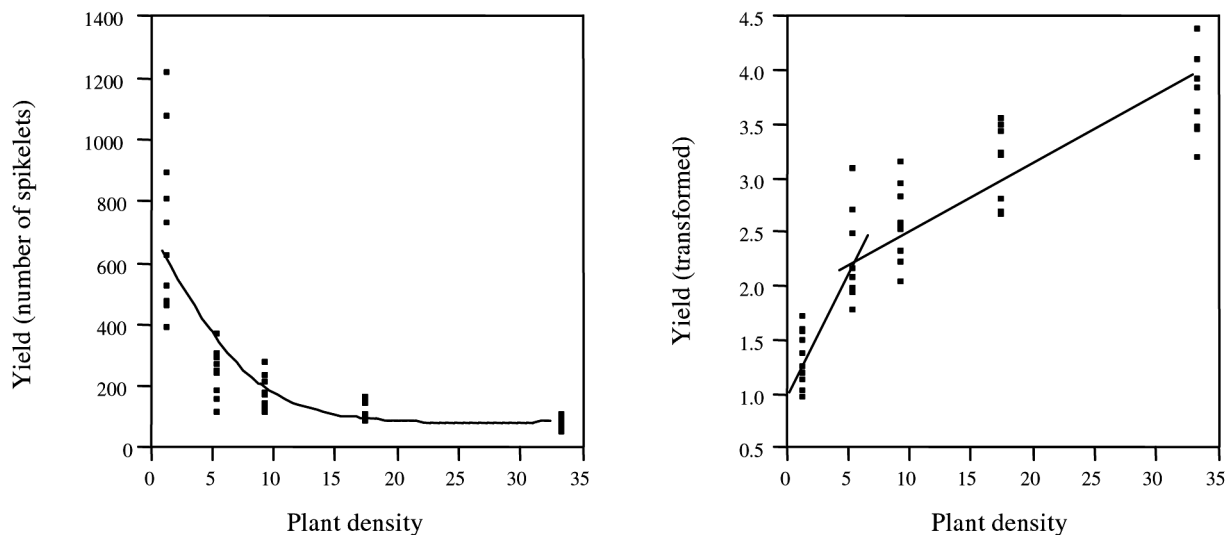


Fig. 1. An example of transformation applied to the traits showing asymptotic curve of decrease with increase in density of neighboring plants. Yield of MH (mountain) plants under increasing density of neighbor barley plants before (*left*) and after transformation (*right*). Values were standardized for each population into proportion of maximum population yield, then square-root transformed so that variance was homogeneous at different densities and then reciprocally transformed to linearize the slopes.

definition as “individual competitive ability to avoid being suppressed”, and is different from competitive effect or “ability to suppress other individuals”. In our study, we tested the competitive responses of 4 populations to (i) barley plants from the same population (intraspecific competitive response) and (ii) oat plants from a neutral population (interspecific competitive response).

Trait differences between the four populations in the absence of competition were analyzed using target plants without neighbors by one-way ANOVA followed by Fisher’s LSD test.

RESULTS

Reproductive traits in the absence of competition

In the absence of competition (i.e., no neighboring plants), all reproductive traits differed among the four populations (Figs. 2 and 3). These differences can be summarized as: (i) the desert (SB) population had the largest number of reproductive tillers, the highest yield and reproductive allocation, but the smallest seeds; (ii) the grassland (AM) population had the fewest reproductive tillers, the largest seeds, a low number of spikelets in a spike, and low yield and reproductive allocation; (iii) the batha (BG) population had intermediate values between desert and grassland populations in most traits; (iv) the mountain (MH) population had the fewest

spikelets per spike and lowest reproductive biomass among all 4 populations, a high number of spikes, but low reproductive allocation and small seeds (Figs. 2 and 3).

Intra- versus interspecific competition

The effects of intra- and interspecific competition at the low increment of neighbor density (from 0 to 4 neighbors) on fitness and related traits were either similar (yield, number of spikes, reproductive biomass) or the effect of intraspecific competition was stronger than that of interspecific competition (aboveground biomass). At the high increment of neighbor density (from 4 to 32 neighbors), the intraspecific competition effect was distinctly stronger than the interspecific one (Tables 2 and 3). The overall decrease in reproductive allocation was stronger under intra- than interspecific competition (Fig. 4).

Population competitive responses

The population*density interaction was not significant for yield at any density increment, but was marginally significant ($p < 0.05$) for reproductive biomass at low density increment and for number of spikes and number of spikelets/spike at high density increment. In contrast, the population*competition*density interaction was highly significant ($p < 0.01$) for all fitness and resource allocation traits at both density increments and in spikelet and seed weight at a high density increment (Table 2).

Population competitive responses under interspecific

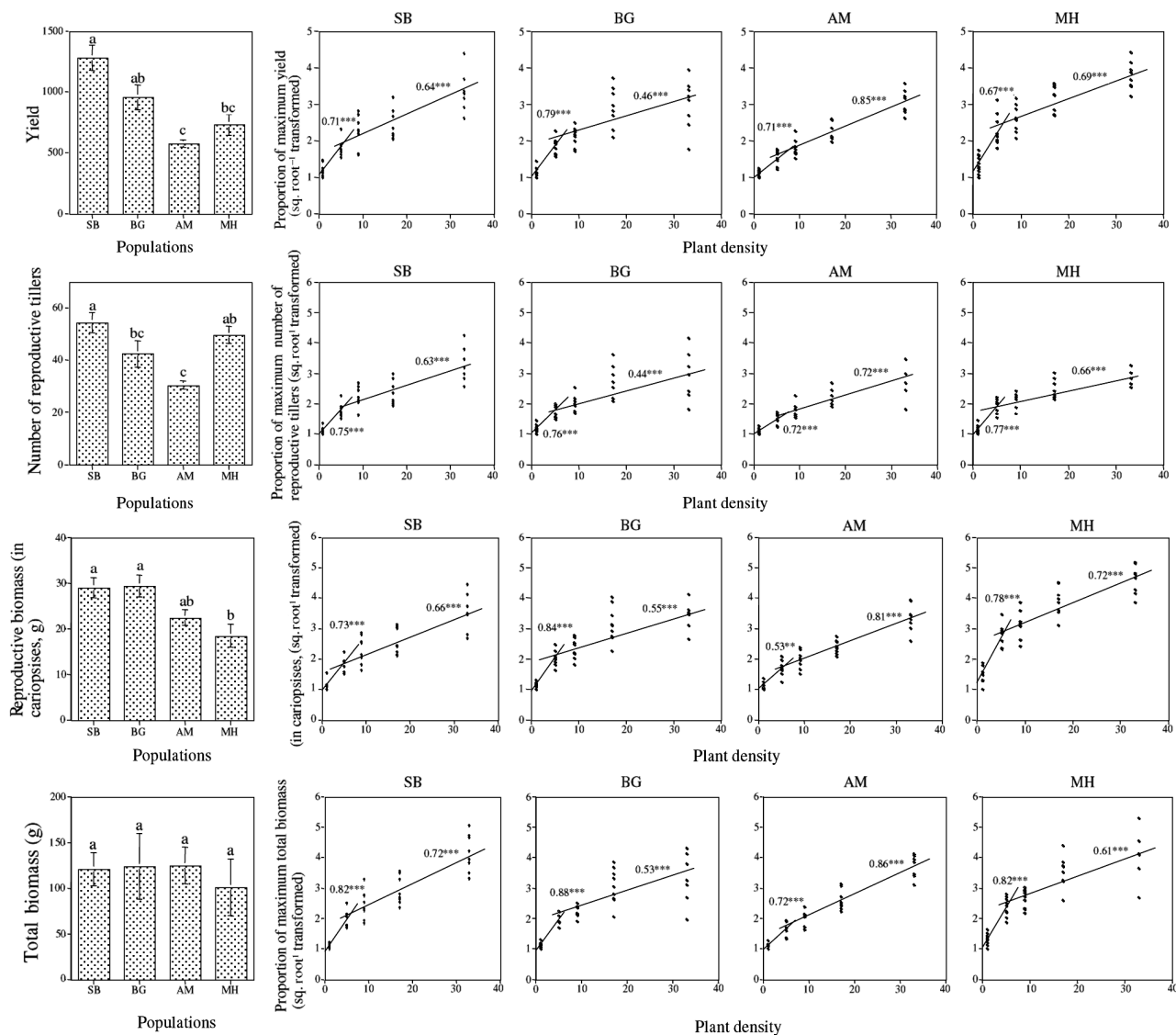


Fig. 2. Yield, number of reproductive tillers, and total and reproductive biomass of single plants (*left*) and under increasing neighbor density of barley (*right*). Population means are shown with corresponding SE and results of Fisher LSD test (denoted by letters). Regression slopes of each population for low density (from 0 to 4 neighbor plants) and for high density (from 4 to 32 neighbor plants) are provided with corresponding r^2 .

competition differed only for resource allocation ($F_{3,154} = 4.1$, $p < 0.01$, and 2.8 , $p < 0.05$ for spikelets and caryopses, respectively). In all other traits, the differences in population interspecific competitive responses were not significant.

Population competitive responses under intraspecific competition were different in both fitness estimates (yield and reproductive biomass) at a low density increment and in resource allocation ($F_{3,154} = 3.2$, $p < 0.05$, and 2.7 , $p < 0.05$ for spikelets and caryopses, respectively). In reproductive traits (number of spikelets per

spike, spikelet and caryopsis weights) the population responses did not differ. The proportion of variance in yield and related traits explained by neighbor density was high for reciprocally-transformed regressions at both density increments. For reproductive biomass, number of reproductive tillers and total number of seed differences in neighbor density explained, on average, 76% (low density) and 67% (high density) of the total variation (Fig. 2). All regression slopes for these traits were positive, indicating a strong competitive effect of neighbor plants on the target plant. However, neighbor

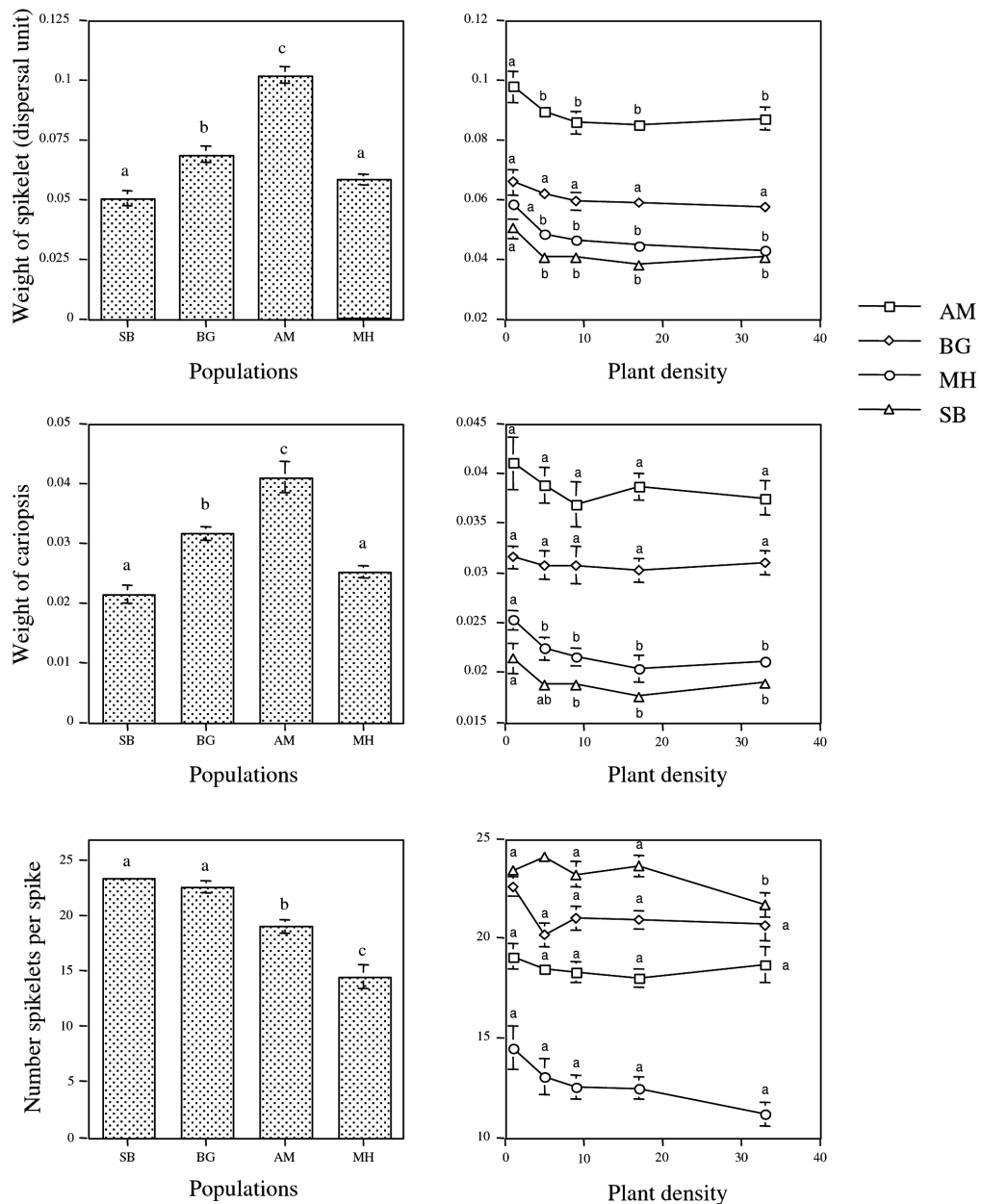


Fig. 3. Weights of spikelets and caryopses and number of spikelets per spike at different neighbor densities of barley plants. Population means at each density are shown with corresponding SE and results of Fisher LSD test (denoted by letters).

density explained only a small proportion of the total variance in the number of spikelets per spike, and the weights of caryopses and spikelets (on average, 19%, 1%, and 1% for low and high density). For reproductive allocation, neighbor density explained 23% of the total variation on average (for entire density range). The group of traits that was not influenced by neighbor density comprised morphological reproductive traits: number of spikelets per spike, spikelet and caryopsis weight (Fig. 3).

The competitive responses of the plants expressed as direct estimates of fitness (yield and reproductive biomass) consistently differed among the 4 populations, but only at relatively low competitive intensity (density of 4 neighbor plants). The overall order in fitness traits from worst to best competitive response was MH (mountain) < BG (batha) < SB (desert) < AM (grassland) (Tables 3 and 4). No significant difference in competitive response among populations was observed when neighbor density increased from 4 to 32 plants (Table 3).

Table 2

Interactive effect of increasing neighbor density (D) and (1) competition type (intra- vs. interspecific) (C); (2) population origin (P); and (3) C*P interaction on fitness, reproductive, and allocation traits of barley plants tested by analysis of covariance (neighbor density is covariate). For all traits except reproductive allocation two density increments were analyzed: 0–4 and 4–32 plants. F values are provided with corresponding significance level

Traits	Density increment	Interaction C*D	Interaction P*D	Interaction C*P*D
No. of spikelets	0–4	0.3 ns	2.0 ns	4.4**
	4–32	6.2*	1.3 ns	4.0**
No. of reproductive tillers	0–4	2.7 ns	1.6 ns	13.4***
	4–32	7.5**	3.6*	12.8***
Reproductive biomass (spikelets)	0–4	2.1 ns	3.2*	6.9***
	4–32	7.0**	0.7 ns	11.0***
Reproductive biomass (caryopses)	0–4	0.6 ns	3.6*	4.5**
	4–32	8.1**	0.7 ns	9.6***
Spikelet weight	0–4	1.0 ns	2.1 ns	0.6 ns
	4–32	2.0 ns	1.1 ns	4.3**
Caryopsis weight	0–4	0.3 ns	0.1 ns	2.2 ns
	4–32	0.1 ns	1.2 ns	7.0***
Reproductive allocation (spikelets)	0–32	6.7***	0.9 ns	15.9***
Reproductive allocation (caryopses)	0–32	4.9**	0.3 ns	38.4***

Level of significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns—not significant.

Table 3

Comparison of slopes of four populations' responses to intra- and interspecific competition in two neighbor density increments by analysis of covariance. Significant interaction population * density indicates difference in populations' competitive responses. All slopes are highly significant ($p < 0.001$)

Trait	Population	Slope			
		0–4 neighbor plants		4–32 neighbor plants	
		intraspecific	interspecific	intraspecific	interspecific
No. of spikelets	SB	0.148	0.186	0.055	0.047
	BG	0.168	0.121	0.041	0.038
	AM	0.113	0.128	0.053	0.040
	MH	0.233	0.162	0.051	0.031
	F 3.4*	1.0 ns	0.2 ns	1.0 ns	
No. of reproductive tillers	SB	0.152	0.181	0.048	0.045
	BG	0.143	0.099	0.050	0.034
	AM	0.106	0.135	0.052	0.029
	MH	0.176	0.120	0.034	0.023
	F 2.1 ns	2.4 ns	1.1 ns	2.5 ns	
Reproductive biomass (spikelets)	SB	0.189	0.187	0.060	0.057
	BG	0.206	0.132	0.052	0.046
	AM	0.132	0.166	0.053	0.048
	MH	0.291	0.204	0.068	0.031
	F 3.4*	1.0 ns	0.4 ns	1.6 ns	
Reproductive biomass (caryopses)	SB	0.168	0.171	0.060	0.048
	BG	0.209	0.139	0.042	0.043
	AM	0.119	0.170	0.060	0.043
	MH	0.296	0.208	0.067	0.029
	F 4.4**	0.8 ns	1.3 ns	1.1 ns	

Level of significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns—not significant.

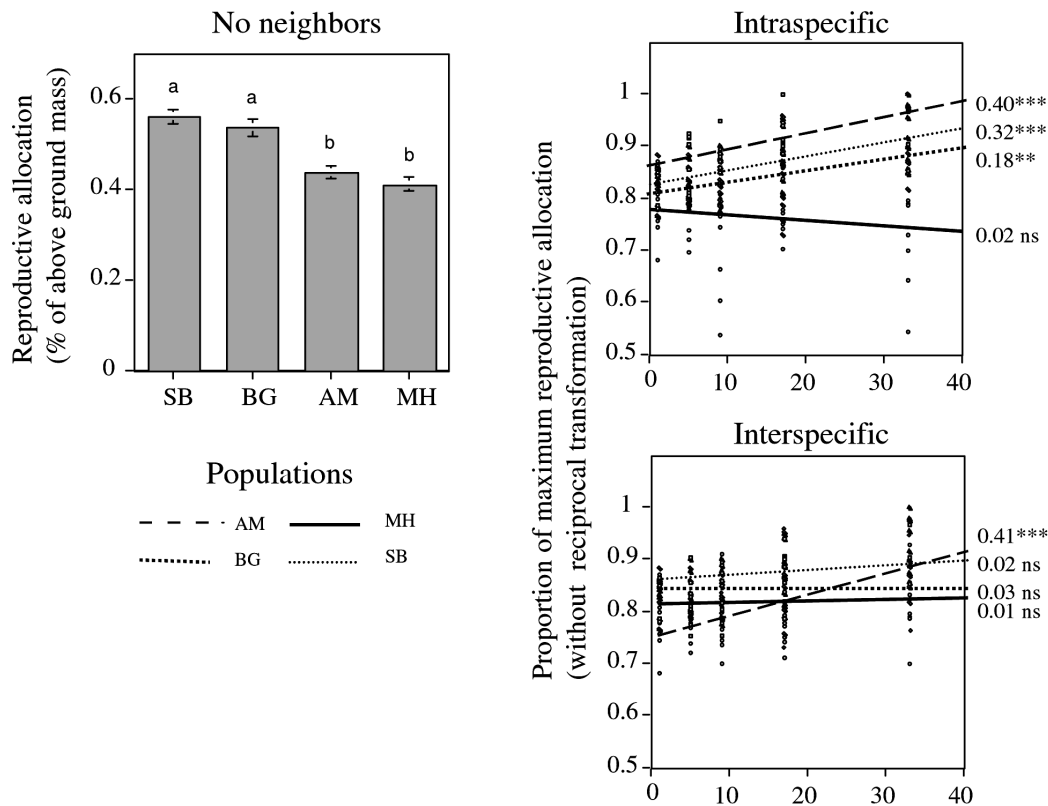


Fig. 4. Reproductive allocation (in spikelets) under intraspecific and interspecific competition.

Table 4

Comparison of regression slopes of the competitive responses of four populations to neighbor density of 4 plants tested by pairwise analyses of covariance: F values (above) and *p* values (below)

Traits	Pairs of populations					
	AM vs. BG	AM vs. MH	AM vs. SB	BG vs. MH	BG vs. SB	MH vs. SB
No. of spikelets	3.74 <0.07	7.45 <0.02	2.08 <0.20	1.90 <0.20	0.37 <0.60	3.19 <0.09
Reproductive biomass (spikelets)	4.32 <0.05	11.52 <0.002	3.31 <0.09	3.27 <0.09	0.01 <0.95	3.23 <0.09
Reproductive biomass (caryopses)	5.04 <0.04	12.48 <0.002	2.72 <0.10	3.08 <0.09	0.62 <0.50	5.48 <0.03

The population differences in competitive responses to a density of four neighboring plants were consistent and not related to population trait differences in the absence of competition.

The populations differed in resource allocation plasticity: in three populations (desert SB, batha BG, and mountain MH) a significant increase in reproductive allocation followed the entire range of increase in neigh-

bor density, while there was no change in reproductive allocation in the mountain MH population (Fig. 4).

There was no difference in intensity of intra- and interspecific competition as reflected in the slope of population response with a density of 4 neighbors. However, the intraspecific competition caused a stronger response in all populations and all fitness traits (except reproductive biomass of caryopses) under increment of

density from 4 to 32 plants (Wilcoxon signed-rank test for each trait separately, $Z = 1.82$, $p = 0.068$ for all traits except reproductive biomass of caryopses; for caryopses, $Z = 1.46$, $p = 0.144$; and Wilcoxon signed-rank test for all traits together, $Z = 3.88$, $p < 0.0001$).

DISCUSSION

We found that under relatively low intensity of competition (4 neighbor plants), the identity of a neighbor (i.e., barley or oat plant) had no effect on barley's competitive response. However, with an increase in neighbor density from 4 to 32 plants, intraspecific competition had a stronger effect than interspecific competition. This is predicted by classical competition theory (MacArthur and Levins, 1967) because individuals of the same species are more likely to have similar resource requirements. This received strong support in a study of competitive selection in *Brassica rapa* by Miller (1995). However, this phenomenon was not detected in two studies of competitive abilities of grasses in shortgrass steppe (Aguiar et al., 2001) and tallgrass prairie (Duralia and Reader, 1993). This may indicate that, despite the great similarity between wild barley and oats in growth habit, morphology, phenology, and ecophysiology, these two species either are dissimilar in root morphology, plasticity, or resource requirements and uptake—or that other important biotic interactions were not accounted for (e.g., mycorrhizal associations).

The population competitive response order found in this study demonstrates the superior competitive ability of plants originating from the most productive and predictable environment with respect to amount and inter/intra-annual variation in rainfall (grassland AM). Poorer competitive ability was found in plants originating from both less productive and less predictable environments (batha BG and desert SB). The population from a highly productive and predictable habitat with respect to rainfall but which experiences severe frost stress (mountain MH) was the poorest competitor. These results are more consistent with Grime's hypothesis of decreasing importance of competition in less productive and more stressed environments (Grime, 1977) than with Tilman's model of stress-competition interdependence (Tilman, 1982, 1987). However, the relatively small differences in productivity and predictability among population environments may explain why we found no significant difference in competitive responses of plants from batha BG and desert SB populations. With regard to the poor competitive ability of the mountain MH population, the effect of a strong environmental stress (low temperatures during a long winter with periodic frosts) may trivialize the effect of productivity if hard

selection reduces population density below the level of density dependence, or because adaptation to non-resource stress diverts energy away from adaptations contributing to resource capture and thus reduces the plants' ability to compete for all resources (Grace, 1990). A tradeoff between tolerance to a non-resource stress and the overall ability to compete, which is not a short-term phenomenon but rather a long-term evolutionary outcome, is well-documented (Wilson and Keddy, 1986a,b; Grace, 1987, 1988).

Differences in population competitive responses disappeared as neighbor density increased from 4 neighboring plants to 8 or more. This may suggest physiological constraints on plants from the same species to tolerate resource depletion (Weiner, 1988). Good competitive responses are either tolerance of depletion of resource levels by neighbors or the ability to avoid depleted resource levels because of preemption of the resource from neighbors. The latter mechanism is unlikely for intraspecific competition because plants have similar resource capture abilities. Thus, in the case of intraspecific competition, the former mechanism (viz. tolerance of resource depletion by neighbors) is highly plausible (Goldberg, 1990).

Plants originating in two environments with high intensities of stress (drought for desert SB and frost for mountain MH) but opposite extremes of stress predictability (very unpredictable in the desert and very predictable in the mountain) appear to have different strategies not only with respect to life history and resource allocation (Volis et al., 2002a,b,c), but also in competitive response to neighbor density. Plants from the mountain population were the poorest competitors and were non-plastic in resource allocation to reproductive organs. Plants from the desert population were also relatively poor competitors, but, in contrast to mountain plants, exhibited the same increase in reproductive allocation in response to increasing neighbor density as plants from batha BG and grassland AM populations. The latter may indicate stress-tolerance (mountain) versus stress-avoidance (desert) evolutionary strategies as evolved in: (1) stressed and predictable vs. (2) stressed and unpredictable environments. The first strategy was predicted to acquire such features as low total yield and reproductive effort, and reduced plasticity in resource allocation (Grime, 1977; Southwood, 1977; Greenslade, 1983; Grime et al., 1986). The predictions that fecundity and reproductive effort in adverse but predictable habitats will be relatively low due to metabolic costs of life in these environments were experimentally confirmed by Harper and Ogden (1970) and Abrahamson and Caswell (1982). The desert SB plants, in contrast, have such features as high fecundity and reproductive effort

and plastic reproductive allocation, as is predicted for temporally heterogeneous and unpredictable environments (Grime, 1977; Grime et al., 1986). The desert environment is one that periodically experiences ample rainfall and thus favorable conditions when plants produce a large amount of seeds, thereby creating a persistent seed bank and assuring population survival even after several years of drought. An escape or stress avoidance strategy is described in bet-hedging and similar concepts (Cohen, 1966; Stearns, 1976; Seger and Brockmann, 1987). Our results suggest that competition is more important in a desert environment, which receives its infrequent water supply in irregular pulses during rainy events, leading to short intense periods of competition, than in a mountain area where water is a nonlimiting factor, but where severe abiotic stress is unavoidable.

Our study provides indirect support for several predictions of the “two-phase resource dynamics” hypothesis of plant interactions along productivity gradients (Goldberg and Novoplansky, 1997) that incorporates temporal dynamics of soil resource availability. In these authors’ view, plants experience two distinct phases during their lifetimes that differ in duration across an environmental productivity gradient: relatively resource-rich pulses when resource uptake and growth take place, and interpulse periods when water availability drops below plant uptake level and most mortality occurs. These authors predict that inhabitants of more productive sites will be better competitors under varying resource availability only for short-term measurements during pulses of competition, and that competition will be relatively unimportant in unproductive environments if survival during interpulses is not strongly positively correlated (or even negatively correlated) with growth during resource pulses. Indeed, under conditions of almost permanent resource pulses, as in our study, plants from the most productive environment (grassland AM) were the best competitors. However, we also found that increasing aridity selects for a decrease in seed size in wild barley and that large seeds of grassland origin had the lowest survival among other ecotypes when introduced to the desert site (Volis et al., 2002a). This may indicate a situation where a positive correlation between plant growth and survival (which is expected in productive environments) may convert into a negative correlation under low water availability because smaller plants have lower water requirements and may survive better when water is very scarce (Goldberg and Novoplansky, 1997). However, the “two-phase resource dynamics” hypothesis cannot explain the poor competitive ability of the mountain ecotype. In mountains, frost is a factor that is not related to resource supply and for which pulse–interpulse dynamics are irrelevant. Intense com-

petition that may occur in both pulse and interpulse phases will not evolve as an evolutionary effect if frosts induce density-independent hard selection. Plants living under such conditions should rather evolve physiological adaptations or microhabitat selection to reduce the detrimental effects of cold stress rather than affecting their abilities to tolerate neighbors. This begs the question as to why plants that are already adapted to withstand cold stress have not subsequently undergone selection for competitive ability thereafter. It would appear that a trade-off between resistance to cold stress and competitive ability has evolved, although the mechanism is not known.

The superior competitive ability of plants from the most favorable environment and the variation in ecotype competitive responses is difficult to explain under the assumption that there is no relationship between competitive ability and environmental favorability (i.e., *contra* Newman, 1973; Tilman, 1982). High competitive ability appears to be a property of plants living in favorable environments (i.e., productive and predictable without severe abiotic stress), corresponding to a “competitive” strategy (Grime, 1974). However, in less productive and/or predictable environments, or under conditions of strong abiotic stress, plant features other than ability to tolerate low water or nutrient levels may be more important, with reduced competitive ability resulting as a trade-off.

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