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Author(s): T. E. Miller

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EVOLUTION OF *BRASSICA RAPA* L. (CRUCIFERAE) POPULATIONS IN INTRA- AND INTERSPECIFIC COMPETITION

T. E. MILLER

Department of Biological Science, Florida State University, Tallahassee, Florida 32306–2043

Abstract.—Populations of *Brassica rapa* were grown for three generations in each of two environments: intraspecific competition, with four surrounding *Brassica rapa* neighbors per pot, and interspecific competition, with two *Raphanus sativus* neighbors per pot. In each environment, the largest (by flower number) 10% of the plants were outcrossed and provided seeds for the next generation. As a control, a randomly chosen 10% of the plants in each environment were outcrossed to produce seed for the next generation. Each of these four treatments, the selected lines in intra- and interspecific competition and the corresponding control lines, was maintained for three generations. After a single generation of growth in a common, no-competition environment, replicate plants from each treatment were grown with no competition and with intra- and interspecific competition for determination of growth responses.

After two generations of selection, flower number in the intraspecific-selection line had increased by more than 50% over that in the control line and by more than 19% over that under interspecific selection. After a common-environment generation, plants from the intraspecific-selection line were shown to have significantly faster growth in height and flower number as seedlings. Plants in the interspecific-selection line showed similar but nonsignificant trends. No differences in seed mass, emergence time, or photosynthetic rate were found between control and selected lines in either intra- or interspecific competition. Some differences between control and selected lines were noted in biomass allocation related to differences in phenology. The results demonstrate that performance in competitive environments can evolve through changes in plant development but that rates of evolution will differ in intra- and interspecific competition.

Key words.—*Brassica rapa*, competition, interspecific competition, intraspecific competition, phenotypic selection, plants

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Competition among plants has long been recognized as a major ecological force (see reviews by Harper 1977; Connell 1983; Schoener 1983). Because of the well-documented ecological importance of competition, many studies have suggested or assumed that competition is also an important evolutionary force. Supportive evidence is circumstantial: although a number of selection experiments on competition among animals have been conducted (see Law and Watkinson 1989; Mueller 1988a,b), I know of no previous direct studies of the evolution of plants as a result of competition.

Evolution of competitors has received a great deal of theoretical attention, primarily focused on limiting similarity (e.g., MacArthur and Levins 1967) and the evolution of character displacement in animals (e.g., Roughgarden 1976; Lawlor and Maynard Smith 1976; Abrams 1987). It has been suggested, however, that these concepts may be less appropriate for the evolution of plant competitors because of inherent differences in the nature of animal and plant resources (Aarssen 1983). Generally, plant resources such as water, light, and nutrients are not “partitionable” in the same way as seed or prey size, suggesting that the expected evolutionary role of competition may be different for plants and animals (Aarssen 1983; Abrams 1987). Certainly plants do vary in competitive ability: genetic variation in fitness under competition has been demonstrated for many plant species (e.g., by Sakai 1955; Solbrig and Simpson 1977; Donald 1981; Langton 1985; Clay and Levin 1986; Shaw 1986; Goldberg 1988; Jordan 1989; Tonsor 1989), but the mechanistic basis for variation in competitive performance is generally unknown.

Patterns of character divergence have been presented as evidence for evolution resulting from competitive selection. For example, competition has been inferred from differences

among species in root depth distribution (e.g., Berendse 1981), phenology (see, e.g., Grubb 1977; Fowler and Antonovics 1982), root or stem morphology and placement (see, e.g., Parrish and Bazzaz 1976; del Moral et al. 1985), and water use (Werner 1979). All of this evidence is correlative: it is consistent with the concept that limiting similarity and competition may lead to the evolution of resource-use patterns among species, but it does not necessarily indicate how or when such evolution will occur.

Further evidence for the evolutionary importance of competition comes from studies comparing genotypes derived from different competitive environments. Martin and Harding (1981, 1982) studied *Erodium cicutarium* from two different populations, one with primarily intraspecific competition and the other with both intra- and interspecific competition. They found that genotypes from the population with interspecific competition generally had a higher fitness when grown in either intra- or interspecific competition. Turkington and Harper (1979) demonstrated extreme local adaptation (specialization), apparently as a competitive response to the genotypes of neighboring species. *Trifolium* genotypes from different areas of the same field grow best when competing in the greenhouse against the species with which they were originally growing. Similar studies by Aarssen and Turkington (1985) found that genotypes of *Trifolium* had the highest yield when grown with genotypes of *Lolium* from the same microsite; genotypes of *Lolium*, however, had their lowest yield when grown with their natural *Trifolium* neighbor genotypes.

Such examples of genotypic specialization to different types of competitive environments (Martin and Harding 1982; Turkington and Harper 1979; see also Evans et al. 1985; Joy and Laitinen 1980; Aarssen and Turkington 1985) could

be due to historical establishment events, correlations of both genotype and competitive environment with other factors (see Turkington and Mehrhoff 1990), or to evolution and adaptation to specific competitive environments.

What is lacking is direct evidence of evolution in different competitive environments, as well as a theoretical framework for understanding the general evolutionary role of competition as a function of the nature of the limiting resources. As a first approach, I present here the results of three generations of selection comparing the evolution of performance of mustard species grown under intraspecific and interspecific competition.

METHODS

Experimental System

Brassica rapa L. (Cruciferae), rape or field mustard, and *Raphanus sativus* L. (Cruciferae), radish, are cosmopolitan annuals of temperate zones used in agriculture and found as common weeds. *Brassica* seedlings develop as rosettes but rapidly bolt to an upright growth form. *Raphanus* has a similar growth form but generally has a longer, less upright stem, larger leaves, and, in these experiments, a higher growth rate. Both species are hermaphroditic and have sporophytic self-incompatibility systems.

Rapid-cycling stocks of these species were obtained from the Crucifer Genetics Cooperative at the University of Wisconsin (*Brassica*, CRCG stock #1, Aaa; *Raphanus*, CRCG #7, Rrr; Williams 1985). The stock for each species was derived by the cooperative through initial combination of diverse early-flowering types followed by recurrent selection for minimum time from sowing to flowering, rapid seed maturation, absence of seed dormancy, and high female fertility (Williams and Hill 1986). These stocks appear to contain substantial genetic variation; considerable isozyme variation remains after selection for rapid-cycling characteristics (Williams 1985; Williams and Hill 1986).

Previous studies with rapid-cycling *Brassica* have identified several traits that are heritable in given environments and that may be related to competitive performance. Evans (1989, 1991) measured the heritability of a number of physiological and morphological traits using full-sib and half-sib families. Number of flowers per plant, time of first flower, height at first flower, carbon-nitrogen ratios in leaves, specific leaf weight, and flower production all demonstrated significant heritable variation in some environments. Miller and Schemske (1990) found significant variation in biomass and flower number among maternal half-sib families of *Brassica* grown in each of three environments—no competition, intraspecific competition, and interspecific competition—with *Raphanus*.

Design of Selection Experiments: Overview

Two rather different designs have been used in previous selection experiments, depending on the questions being addressed. In the first type of design, studies compare lines developed through selection for some specific trait with lines developed through random “selection” (see Falconer 1981, pp. 181–182), or lines selected to maximize a trait are com-

pared to those that minimize the trait (“divergent” selection; e.g., Falconer 1953; Ågren and Schemske 1992). This approach allows a quantification of the magnitude of evolution of a trait in a given environment but does not directly demonstrate what aspects of the environment would lead to such a change. In the second type of design, lines selected according to the same criteria but developed in different environments are compared to reveal which environmental factors contribute to evolutionary change (e.g. Mueller 1988a,b). Such designs are commonly used in studies of density-dependent selection (see Law and Watkinson 1989). The absence of a significant difference between lines does not indicate a lack of evolutionary change, but only that the two lines changed (or did not change) in a similar fashion in the two environments.

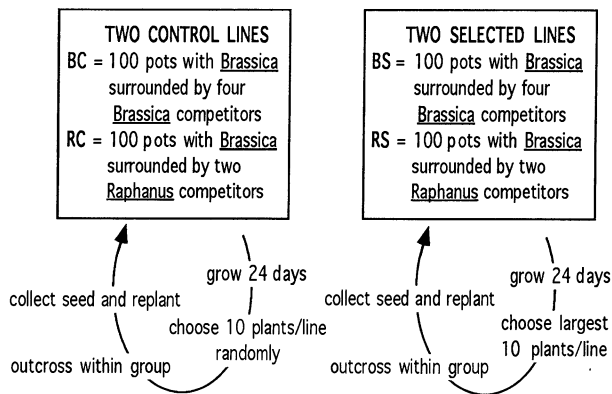
My experimental design incorporates both types of designs. Experimental lines were developed by selection for high performance in two environments (intra- and interspecific competition) and compared both to each other and to control groups in which individuals were randomly selected in both environments. This design allows me to address three questions: (1) Does performance evolve (improve) in environments with intra- and interspecific competitors? (2) If so, what phenotypic changes also occur? (3) Is evolution in intraspecific competition different from that in interspecific competition? Note that, unfortunately, my design does not include a control group consisting of plants selected for performance when not grown in competition. Any evolutionary changes I may observe cannot be shown necessarily to have evolved as a result of competition, but only to result in increased performance when the plants are grown in competition.

Four “lines” were created by growth of control plants and selected plants in environments of both intraspecific and interspecific competition (fig. 1A). For each line, 100 plants were grown each generation. In the control lines for intraspecific and interspecific competition (BC and RC, respectively), 10 of the 100 plants were chosen randomly each generation and randomly intercrossed to produce seed for the next generation. In the selected lines for intraspecific and interspecific competition (BS and RS, respectively), the 10 largest individuals, defined as those with highest flower number (10% hard selection), were randomly intercrossed to produce seed each generation.

Only a single line of each treatment was used because time and growth-chamber space were limited. Because replicate plants are used within lines, I can determine whether lines differ in performance when grown in competition or in any measured traits. However, the lack of replicate lines makes it difficult to determine the relative importance of selection and drift to any difference between treatments. I have addressed this deficiency in the experimental design by first estimating the maximum possible drift in each environment (Lande 1976). All observed changes are then discussed in light of the maximum possible effects of drift.

Ideally, the criterion for selection in these experiments would be the expected fitness of individuals. Seed number per plant could not be obtained because specific hand-pollinations had to be performed to produce seed for the next generation. Similarly, destructive harvesting to obtain plant

A.



B.

	BC	BS	RC	RS
Alone				
Intraspecific competition		3 replicates from each of ten maternal lines per cell		
Interspecific competition				

FIG. 1. Experimental procedure for (A) each generation of growth in intra- and interspecific environments and (B) common-environment study used to quantify changes in plants from control and selected lines.

biomass as an estimate of fitness was not possible. Preliminary experiments had shown that flower number is highly correlated with both plant biomass ($r = 0.92$) and plant height ($r = 0.90$). These correlations remained high in the final generation of plants grown for this experiment (flower number with height, $r = 0.84$; flower number with biomass, $r = 0.86$).

Design of Selection Experiments: Details of Experimental Design

Four hundred 8- \times -8- \times -8-cm plastic pots were filled with ProMix BX (a standard soilless mix of sphagnum moss, vermiculite, and perlite) and divided into four treatment groups of 100 pots each. A single *Brassica* seed was planted in the center of each pot. For intraspecific-competition lines, four neighboring *Brassica* individuals were planted in the same pot surrounding the center *Brassica* individual, each midway between the center plant and a corner of the pot. For the interspecific-competition control and selected lines, two *Raphanus* individuals were planted, each midway between the center *Brassica* individual and opposite corners of the pot. Pots in which center individuals failed to germinate were replaced with extra pots established for this purpose. Competitor *Brassica* and *Raphanus* individuals that failed to ger-

minate were replaced with individuals transplanted from separate trays.

The intra- and interspecific densities used were based on the results of preliminary experiments in which plants were grown at a variety of densities. At any given density, *Raphanus* had a much greater competitive effect than *Brassica*. The densities used (four *Brassica* neighbors or two *Raphanus* neighbors per pot) both resulted in target plants whose growth was approximately 35% the growth of a plant grown with no neighbors.

All plants were grown in an enclosed room illuminated 24 h/d with fluorescent lights (approx. $240 \mu\text{E m}^{-2} \text{s}^{-1}$) at a constant 24.5°C . The plants were watered at the first sign of wilting and were fertilized once 10 d after planting with 50 ml of a weak solution of soluble fertilizer (20-20-20, Peter's Peat-Lite). Positions of the pots were rearranged into a new random pattern on the benches approximately every 2 d.

After 24 days of growth, center plants were censused for number of flowers and fruits and for plant height and were then fertilized as before. Competing neighbor plants were clipped off at the base and discarded. In the selection treatments under both intraspecific (BS) and interspecific (RS) competition, the 10 largest plants (on the basis of flower number) were chosen to be outcrossed to produce seed for the next generation (fig. 1A). Three flowers on each selected plant were hand-pollinated with pollen from three individuals chosen at random from the other nine selected plants within that treatment. At the same time, 10 plants from the control treatments under both the intraspecific (BC) and interspecific (RC) competition were randomly chosen from the original 100 per treatment. Each plant had its neighbors removed and was then measured. Plants were then outcrossed among each other by hand-pollinations as above to produce seed for the second generation of control lines.

This growth and outcrossing design was repeated for a total of three generations. For each generation, seed from the 10 plants selected from each of the four lines was used to produce 100 new plants of that line, which were grown under the same competitive environments as their parental generations.

Mean seed mass for each generation was determined before planting as the mean of five seeds per plant from the previous generation. Mean flower numbers for control and selected lines were compared by ANOVA. Selection intensity (sensu Falconer 1981) in each line in each generation was determined as $i = (\text{mean flower number of chosen individuals} - \text{mean flower number for all individuals}) / \text{standard deviation in flower number of all individuals}$ (Falconer 1981).

Responses to Selection

It has been shown that plants grown under high resource levels or low competition often produce larger seeds (Roach and Wulff 1987) and that larger seeds can provide a competitive advantage under some circumstances (e.g., Stanton 1984; Wulff 1986). These nongenetic differences among individuals attributable to the environment of their parents are an example of environmental maternal effects (Fenner 1985; Roach and Wulff 1987). Such effects may have occurred

during the selection portion of this experiment because of the confounding of treatment and resulting plant size.

To minimize environmental maternal effects, a "common-environment" generation was grown after three generations of selection, in which plants from each of the four lines were grown for one generation with no competition or selection. Environmental maternal effects may persist for more than a single generation (e.g., Alexander and Wulff 1985). However, in this experiment environmental maternal effects were not expected to be great, as all lines were grown under identical conditions; a single common-environment generation was thought to be sufficient to minimize environmental maternal effects.

Ten plants chosen from each line at the end of the third generation of selection were used to produce seed for two offspring each. The offspring were grown in individual pots, fertilized every 7 d (20–20–20, Peter's Peat-Lite), and watered as needed. Three flowers on each plant were pollinated with pollen from three different randomly selected individuals from the same line. Seeds harvested from these flowers were grouped together into 10 maternal families per line, each derived from one of the 10 plants selected at the end of the third generation.

I weighed 10 randomly chosen seeds per maternal family to determine mean seed mass per family. Then seeds chosen randomly from each of the 10 families in each of the four selected lines were used to grow three replicate plants in each of three environments: Alone (no competition), Intraspecific Competition, and Interspecific Competition (10 families \times 4 lines \times 3 environments \times 3 replicates = 360 plants; fig. 1B). Conditions in the Alone treatment were identical to the conditions described above in the intra- and interspecific environments, but with no competitors. The two competition environments were identical to those used for the three generations of selection.

Pots were examined every 6 h after planting. Emergence time for each center plant was noted when the emerging cotyledons had separated. Height and number of leaves were determined at 7, 14, and 24 d from planting. After 24 d, all center plants were harvested. Area-based photosynthetic capacity (Model LCA-3 infrared gas analyzer, Analytical Development Co.) was determined for each plant in the Alone treatment. The newest fully expanded leaf was excised and immediately placed in a Parkinson chamber, where photosynthetic capacity was estimated from per-area CO₂ uptake. All plants were divided into leaves, stems (+ flowers), and roots, then dried at 60°C and later weighed. Roots were carefully washed before drying.

Values for the three replicate plants from each maternal plant in each competitive environment (fig. 1B) were averaged. Emergence time, number of leaves, height, flower number, and biomass allocation in control lines and selected lines within each environment were then compared by means of ANOVA (df = 1). Lines selected for performance in intraspecific (BS) and interspecific (RS) competition were also compared in each environment by ANOVA.

Estimating Effects of Drift

The maximum effect of drift can be estimated if the heritability (h^2), effective population size (N_e), and phenotypic

variation in the trait (σ^2) are known (Lande 1976). Heritability can be estimated as $h^2 = R/S$, where R is the response to selection, measured as the difference in mean number of flowers produced by the offspring of the selected individuals and the whole of the parental generation before selection, and S is the selection differential, measured as the mean number of flowers produced by the selected individuals expressed as a deviation from the population mean. The number of breeding individuals in each generation was 10. However, because each self-incompatible individual produced the same number of progeny for the next generation, $N_e = 2N - 2 = 18$ (Crow and Kimura 1970, p. 362). Then, the maximum drift in flower number (z^*) can be estimated as:

$$z^* \equiv \frac{1.96\sigma(h^2)^{0.5}}{\sqrt{N_e}}.$$

If the observed change in flower number (z) is greater than the maximum possible through drift alone (i.e., $z > z^*$), then the hypothesis that drift alone can account for the change in flower number can be rejected with 95% confidence (Lande 1976).

Maximum possible drift was determined for both intra- and interspecific-selection lines and compared to the actual change in flower number. This approach has several unresolved statistical problems having to do with sampling errors for z , σ^2 , and h^2 (Turelli et al. 1988), and the conclusions of this analysis should be treated cautiously.

RESULTS

Selection for Performance

Flower number in *Brassica* increased in response to selection in both intraspecific and interspecific competition (fig. 2). Under intraspecific competition, the selected (BS) line produced 8.2 (55%) more flowers per plant than the control (BC) line after a single generation of selection (i.e., in generation 2). This difference was maintained but did not increase after a second generation of selection. Under interspecific competition, the selected line (RS) produced significantly more flowers (1.7 more flowers, 22%) per plant than did the control line (RC) after a single generation of selection. This difference between the selected and control lines was maintained through two generations of selection. Both control (RC) and selected (RS) lines produced fewer flowers in the second generation than in the first (fig. 2).

Control and selected lines did not, however, differ in seed size in either intra- or interspecific competition in any generation. Seed size remained relatively constant in generations 1 and 2, but all lines produced larger seeds in generation 3 (fig. 3).

Selection intensity (i) in the BS and RS lines ranged from 1.59 to 1.96 (table 1). The BS and RS lines did not differ significantly in selection intensity, but it was somewhat higher in the second generation than in the first or third.

Final Response to Selection

After the single "common-environment" generation to reduce environmental maternal effects, seed sizes in all lines were significantly higher than for seeds from the original seed

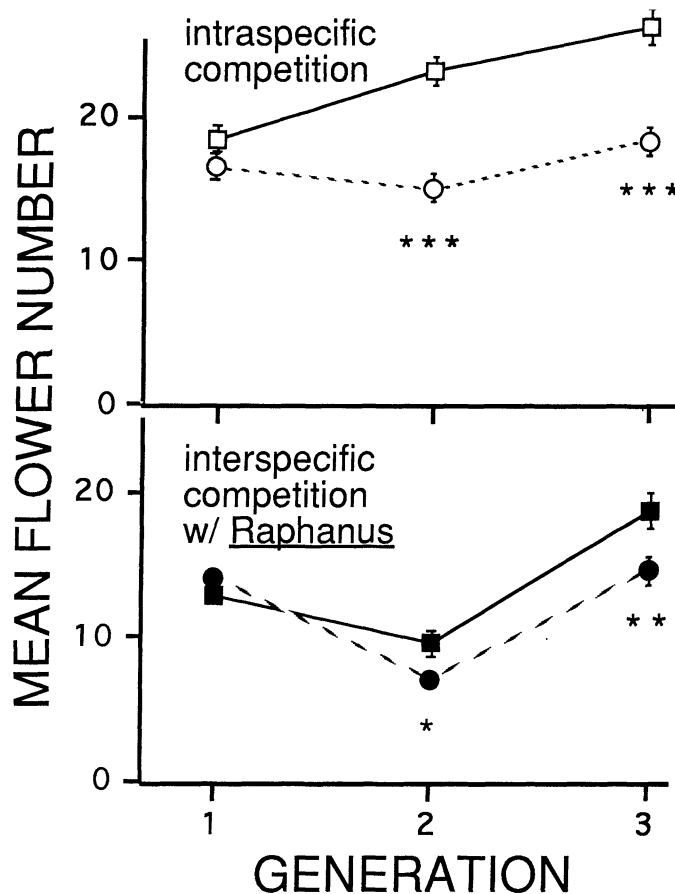


FIG. 2. Mean flower number (\pm SE) in *Brassica campestris* after one and two generations of selection for performance under intraspecific and interspecific competition. Squares represent lines selected for higher flower number; circles represent control lines in which parents were randomly selected. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

stock (fig. 3). However, there were no significant differences in seed mass between control and selected lines in either competitive environment.

When the seeds produced in the common environment were then grown alone and in intraspecific competition, random and selected lines did not differ significantly in emergence time (table 2). However, when grown under interspecific competition, seeds from the line selected under intraspecific competition (BS) emerged more than 5 h earlier than did those from the control line (BC) and more than 9 h earlier than those from the line selected under interspecific competition (RS).

Individuals derived from the BS line appeared to grow faster than those derived from the BC or RS line in both competitive and noncompetitive environments. When grown in the no-competition environment, BS-derived plants were taller at 24 d and had more leaves at 16 d than did the BC-derived plants and had more leaves at all ages than did the RS-derived plants (table 3). When grown under intraspecific competition, BS-derived plants were again taller and had more leaves than did control, BC, plants. Under interspecific competition, BS-derived plants were taller and had more

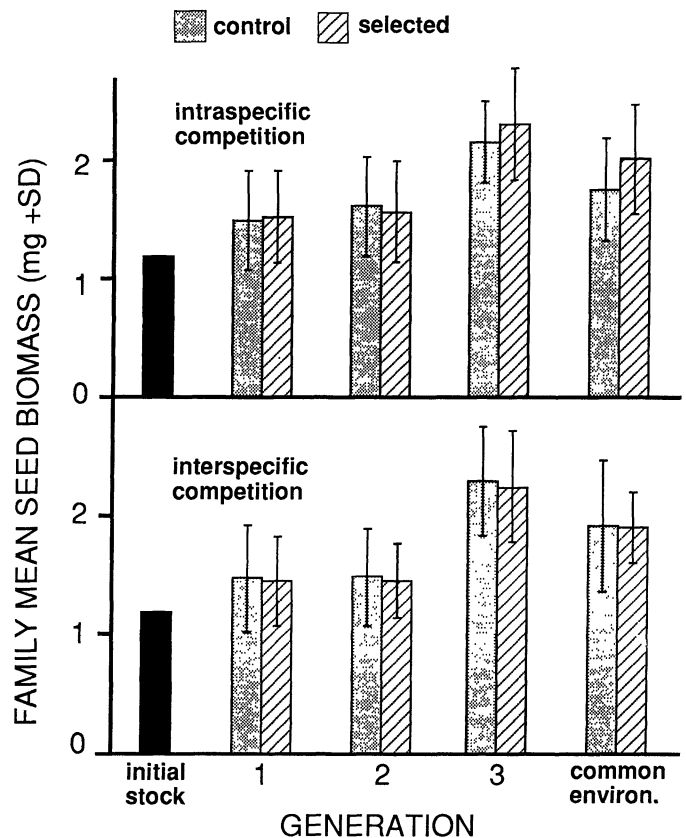


FIG. 3. Mean biomass (and SE) of seeds produced by the initial seed stock, after each generation of selection, and after growth in a common environment. Except in the initial seed stock, values represent averages of family means.

leaves than did either BC- or RS-derived plants. Note that number of leaves declined from day 16 to day 24 for all lines when the plants were grown in competition (table 3): many plants lost some leaves apparently as plant resources were shifted to reproduction.

Plants derived from the RS line were generally taller and had more leaves than plants from the control, RC, line (table 3), but these differences were generally nonsignificant. Mean

TABLE 1. Intensity of selection (i) for flower number for plants each generation for control and selected lines under intraspecific and interspecific competition.

Generation	Line	Intensity of selection
1	BC	-0.333
	BS	1.746
	RC	0.257
	RS	1.590
2	BC	-0.470
	BS	1.958
	RC	0.467
	RS	1.906
3	BC	-0.116
	BS	1.790
	RC	-0.259
	RS	1.860

TABLE 2. Emergence time and flower number per plant (\pm SE) of each treatment line when grown in three different competitive environments. Comparison of control and selected lines and the two selected lines were by analysis of variance (df = 1).

Competition	Line	Emergence time (h \pm SE)	Flower no. per plant (\pm SE)
None	BC	NS ^[35.0 (1.2)]	* ^[25.67 (4.92)]
	BS	NS ^[36.6 (2.6)]	^[35.20 (2.52)]
	RC	NS ^[40.0 (1.5)]	NS ^[18.19 (4.01)]
	RS	NS ^[42.7 (3.0)]	NS ^[26.24 (4.37)]
Intraspecific	BC	NS ^[34.1 (1.9)]	* ^[9.12 (1.79)]
	BS	NS ^[34.4 (3.0)]	^[13.39 (1.84)]
	RC	NS ^[40.0 (3.4)]	NS ^[10.18 (2.00)]
	RS	NS ^[37.6 (1.8)]	NS ^[14.76 (2.06)]
Interspecific	BC	* ^[37.7 (1.6)]	** ^[8.88 (1.40)]
	BS	^[32.1 (1.9)]	^[15.04 (1.65)]
	RC	NS ^[41.4 (3.7)]	NS ^[9.06 (2.16)]
	RS	NS ^[41.3 (2.4)]	NS ^[10.85 (1.54)]

* $P < 0.05$, ** $P < 0.01$, NS, not significant.

number of leaves on day 16 was significantly greater for the RS line than for the RC line.

In general, plants grown without competition produced 2–3 times more flowers than those grown under either intraspecific or interspecific competition (table 2). Mean flower number was always higher in the selected lines than in the control lines. The BC and BS lines differed significantly in flower number when growing in any of the three environments, but the RC and RS lines did not differ in any competitive environment. Plants derived from the BS line produced significantly more flowers than those from the RS line when grown alone or in interspecific competition.

At 24 d, photosynthetic rates were determined for all plants growing without competition. In intraspecific competition, no significant differences were found between control and selected lines (4.02 and 3.76 mg/m²/s, respectively; $F = 0.94$, $P = 0.35$). Similarly, in interspecific competition, no significant differences were found between control and selected lines (4.07 and 3.74, respectively; $F = 1.925$, $P = 0.19$).

Under intraspecific competition, the BS line allocated a higher percentage of biomass to stem than did the BC line

(fig. 4). The same pattern was evident in no-competition and interspecific-competition treatments but was not significant. The RS line allocated a significantly lower percentage of biomass to roots than did the RC line when grown under interspecific competition. In the no-competition and intraspecific-competition environments, the RS line allocated significantly more biomass to stem and less to leaves. No significant differences in biomass allocation were found when the BS and RS lines were compared.

Estimating Effects of Drift

In the intraspecific competitive environment in the first generation, the maximum change in flower number due to drift, z^* , can be estimated as

$$z^* = \frac{1.96(7.89)(0.61)^{0.5}}{\sqrt{18}} = 2.85.$$

In this case, the observed change in mean number of flowers between generations 1 and 2, 8.20 flowers per plant, was much greater than z^* , 2.85, suggesting that drift was not primarily responsible for differences in flower number.

For interspecific competition,

$$z^* = \frac{1.96(5.04)(0.22)^{0.5}}{\sqrt{18}} = 1.09.$$

The observed change in flower number was 1.7 flowers per plant, some 50% greater than the maximum effect of drift ($z^* = 1.09$).

DISCUSSION

The performance of *Brassica rapa* does increase significantly within three generations in response to selection when it is grown in competitive stands (fig. 2). Flower number increased in the selected line relative to that in the control line under both intraspecific and interspecific competition after a single generation of selection. The selected lines appear to have higher growth rates at the earliest measured stages (7-d seedlings). They matured and flowered earlier

TABLE 3. Mean plant height and number of leaves of each treatment line when grown in three different competitive environments. All comparisons of control and selected lines and comparisons of the two selected lines in each environment were done by analysis of variance (df = 1).

Competition	Line	Mean plant height (cm)			Mean no. of leaves		
		day 7	day 16	day 24	day 7	day 16	day 24
None	BC	NS ^[1.68]	NS ^[8.91]	** ^[28.91]	NS ^[1.82]	*** ^[4.45]	NS ^[5.73]
	BS	NS ^[1.85]	NS ^[10.61]	^[36.16]	NS ^[2.27]	^[5.87]	NS ^[6.12]
	RC	NS ^[1.74]	NS ^[6.61]	NS ^[25.09]	NS ^[1.79]	NS ^[4.44]	NS ^[5.35]
	RS	NS ^[1.70]	NS ^[9.72]	NS ^[31.68]	NS ^[1.72]	NS ^[4.94]	NS ^[5.17]
Intraspecific	BC	NS ^[1.83]	* ^[6.76]	* ^[15.37]	* ^[1.72]	** ^[3.82]	NS ^[3.22]
	BS	NS ^[2.09]	^[11.52]	^[21.42]	^[2.17]	^[4.96]	NS ^[3.52]
	RC	NS ^[1.87]	NS ^[7.32]	NS ^[18.38]	NS ^[1.81]	NS ^[4.04]	NS ^[3.48]
	RS	NS ^[1.63]	NS ^[10.06]	NS ^[21.75]	NS ^[1.91]	NS ^[4.56]	NS ^[3.20]
Interspecific	BC	** ^[1.67]	*** ^[7.82]	*** ^[15.63]	NS ^[1.85]	*** ^[3.72]	** ^[2.88]
	BS	^[2.23]	^[13.70]	^[23.05]	NS ^[2.15]	^[5.30]	^[3.72]
	RC	NS ^[1.62]	NS ^[7.58]	NS ^[16.68]	NS ^[1.57]	*** ^[3.72]	NS ^[2.83]
	RS	NS ^[1.63]	NS ^[8.95]	NS ^[16.86]	NS ^[1.85]	*** ^[4.63]	NS ^[3.63]

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant.

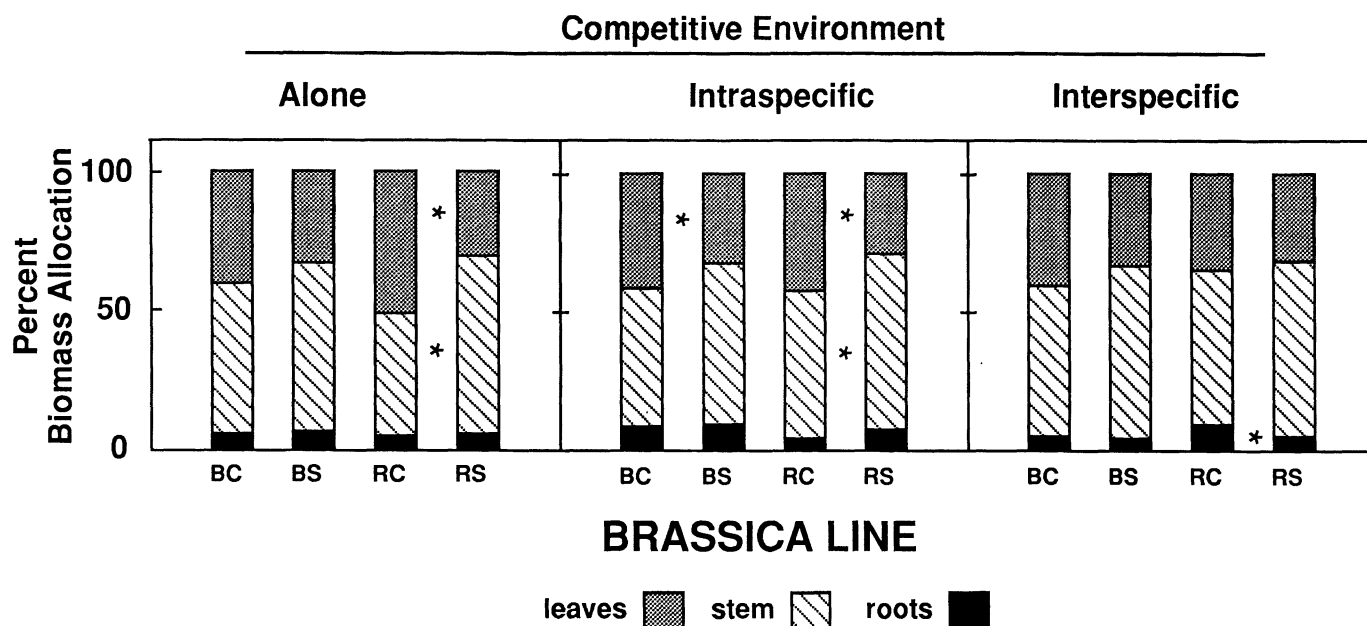


FIG. 4. Mean percent allocation of biomass to leaves, stems, and roots for each treatment line when grown in each competitive environment. Asterisks indicate significant differences between control and selected lines for that morphological feature ($P < 0.05$).

than control lines both when grown in competition and when grown alone.

Response to selection when plants were grown in intraspecific competition was much stronger than that when they were grown in interspecific competition, even though plants were generally more competitively suppressed under the latter (fig. 2) and selection intensities were similar in the two cases (table 1). Under both intraspecific and interspecific competition, plants appeared to increase in height and leaf number faster in the selected than in the control lines (table 3), but these patterns were generally significant for only the lines developed under intraspecific competition. In many cases, BS-derived plants grew faster than both control (BC) plants and those developed under interspecific competition (RS).

The BS line not only produced 47% more flowers than the control line when grown in intraspecific competition (table 2) but also produced more flowers than the control line when grown in interspecific competition (69%) and alone (37%). This same pattern appears in plant height and in leaf number. These results suggest that the traits that bestow greater performance under intraspecific competition are the same as or at least correlated with those that do so under interspecific competition and, to a lesser degree, no competition. This pattern is consistent with the results of Miller and Schemske (1990), who suggested that the growths of different genotypes under intra- and interspecific competition were strongly and positively correlated and that the growths of different genotypes without competition were weakly but positively correlated with growth under competition.

Three possible explanations can be advanced for these results. First, selection acting on heritable variation may have resulted in the evolution of increased performance. Second, the differences between control and selected lines may have occurred as a result of genetic drift. Third, environmental

maternal effects may have resulted in a phenotypic but not a genotypic increase in the performance of the selected lines when they were grown in competition.

I argue that these results for the line derived in intraspecific competition are most probably due to evolution of increased performance in a competitive environment. The effects of drift must be considered because of the small population size selected each generation ($N_e = 18$ individuals), but the observed changes in flower number in intraspecific competition were far greater than the maximum effects of drift as predicted according to the methods of Lande (1976). Further, the correspondence between the direction of selection and the direction of the response, as well as the similarity between the two control lines, BC and RC, suggests that drift was not responsible for the increased performance in the selected lines when they were grown in competition.

Environmental maternal effects were minimized by growth of all lines in a common environment, without competition, for one generation before a final generation was grown for comparison of selected lines. In this final generation, the difference in flower number between the BC and BS lines remained undiminished, but the differences between the RC and RS lines were no longer significant. This result suggests that selection under intraspecific competition did result in the evolution of increased performance but that in interspecific competition the observed differences between the control and selected lines after three generations were, in part, due to environmental maternal effects.

There was some variation in flower number within control lines from generation to generation (fig. 2). This variation is probably due to uncontrolled differences between generations in environmental conditions, especially between generations 1 and 2. Although light, temperature, and soil were constant over all generations, small differences in time of watering or

in humidity may have caused the differences in plant size in different generations.

It is difficult to attribute the increased performance of the selected lines to specific traits. The increased height and number of leaves in the BS line as early as day 7 (table 3) documents that more rapid growth was correlated with the development of better competitors. The more rapid decline in leaf number in the BS line by day 24 suggests that these plants are phenologically ahead of the BC line. *Brassica*, like many annuals, begins to drop leaves as resources are shifted to reproductive structures. This pattern of advanced phenology in the selected line relative to the control line was found under interspecific competition as well, although most differences between plant traits in RC and RS lines were not significant.

It has been hypothesized (e.g., by Tilman 1988) that changes in biomass allocation may increase competitive performance when resources are limiting. For example, if competition is for light, juvenile plants may allocate more resources to above ground biomass and less to roots, thus increasing light-garnering abilities. Ballaré et al. (1990) have suggested that changes in red to far-red light ratios (R:FR) caused by the presence of competitors may provide a proximal cue for changes in biomass allocation. The possibility for this response may have been somewhat limited in my experiments, as the primary source of light was fluorescent. Fluorescent lights have very high R:FR, to which plant pigment systems are not very sensitive (C. Ballaré pers. comm.). The control and selected lines did appear to allocate more biomass to stems (fig. 4), which may aid in light competition and canopy preemption by the BS and RS lines. However, because many plants had begun to drop leaves by the harvest at day 24, the biomass-allocation data shown in figure 4 are difficult to interpret.

Some traits did not exhibit any change after three generations of selection for performance. Both seed mass (see, e.g., Black 1958; Winn 1988) and emergence time (see e.g. Ross and Harper 1972; Kalisz 1986; Miller 1987) have been shown in other studies to have significant effects on competitive performance. Seed mass exhibited no response to selection in this study (fig. 3). Emergence time was earlier for BS-derived plants in the interspecific environment, but not when they were grown alone or under intraspecific competition (table 2). Several physiological traits have also been shown to be heritable in *Brassica* (Evans 1991) and could be important for growth in competitive environments yet showed no significant change over the three generations of selection studied here.

Note that, although early growth and a shift in phenology improve performance in competitive environments, they also, to a lesser degree, increase growth when plants are alone (see discussion above). One way to increase performance in competition may be to have high initial growth rates, which will increase performance with or without neighbors present. Therefore, the response to selection observed in this study could be due to selection for increased size, independent of true competitive "ability."

Law and Watkinson (1989) reviewed 17 experiments on selection for competitive performance, virtually all on *Drosophila* spp., *Tribolium* spp., or *Musca domestica*. A majority

(10/17) of the studies reviewed found significant density-dependent selection in some cases. On a per-trial basis (where a "trial" follows changes in an individual species or strain in competition for a number of generations), only 16 of 72 trials found significant evolutionary increases in competitive performance in response to density. The authors are unsure whether this relatively low number (22% of trials) truly reflects the "real state of nature" or is an artifact of the small number of studies (Law and Watkinson 1989). Because of a lack of appropriate controls, it is also unknown whether any of the studies that did not find density-dependent selection might still have found significant evolution for increased performance in competition. That is, if populations maintained at different densities (e.g., with and without competition) increased in potential performance in the same fashion, many previous studies would not have detected a difference between treatments and would conclude that density-dependent selection had not occurred. However, they could not conclude that the performance in competition had not evolved.

In summary, these experiments demonstrate the evolution of performance in intraspecific competition. This increased performance is correlated with an increase in leaf number and height in seedlings as young as 7-d old and in adults, but it is not known whether these traits are a cause or a result of increased performance. Similar but less substantial trends were found for the evolution of performance in interspecific competition. These experiments were conducted in a limited set of environments with a derived experimental system (rapid-cycling *Brassica rapa*). Until a wider variety of environments and species are studied, the generality of these conclusions cannot be evaluated. The results do suggest that the evolution of performance in competition may involve important phenological changes and may differ with the identity of the competitor.

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