AN EXPERIMENTAL STUDY OF COMPETITIVE PERFORMANCE IN BRASSICA RAPA (CRUCIFERAE)\textsuperscript{1}

THOMAS E. MILLER\textsuperscript{2} AND DOUGLAS W. SCHEMSKE\textsuperscript{3}

Department of Ecology and Evolution, Barnes Laboratory, 5630 S. Ingleside, University of Chicago, Chicago, Illinois 60637

ABSTRACT

Growth chamber experiments with rapid-cycling Brassica rapa were designed to estimate the signs and magnitudes of the genetic correlations for plant performance in each of three conditions: no-competition (isolated plants), intraspecific competition, and interspecific competition with Raphanus sativa. Biomass and flower number were highest in the no-competition treatment, intermediate under intraspecific competition, and lowest under interspecific competition. Significant among-family variation in biomass and flower number was found under each regime. The mean family performance (biomass or flower number) in the no-competition treatment was significantly positively correlated with the performance in only one of the competitive treatments (for biomass in the intraspecific treatment). For both biomass and flower number there was a significant positive correlation between family means in the intra- and interspecific regimes. These correlations were greater in magnitude than those for the comparison between no-competition and competition (intra- or interspecific) treatments. Our results suggest that the importance of traits affecting plant performance is environment-dependent; the performance of a family grown without competition was a poor predictor of performance with competition, while the performance of families grown under intra- and interspecific competition was positively correlated.

Several previous studies have used analysis of variance to separate the effects of plant genotype, competition, and the genotype × environment interaction on plant fitness (e.g., Kelley and Clay, 1987; Goldberg, 1988). A significant interaction term indicates that the relative performance of a genotype varies with competitive regime (e.g., Gupta and Lewontin, 1982). However, analysis of variance tests the significance of an interaction term in a linear model and does not directly address the distinction between specialized and generalized competitive ability.

The extent to which competitive performance is specialized or generalized can be quantified as the genetic correlation between total fitnesses, or fitness components, under different competitive conditions (Falconer, 1952; Via, 1984; Via and Lande, 1985). A negative correlation implies the existence of “genetic trade-offs” in which biomass allocation or other specializations that lead to superior performance in one competitive environment adversely affect performance under different competitive conditions. If there is local variation in the magnitude of competition or in the identity of competitors within a population, such negative correlations could promote the coexistence of different genotypes (e.g., Schutz, Brims, and Ussanis, 1968; Antonovics, 1978; Kelley and Clay, 1987). On the other

\textsuperscript{1} Received for publication 7 April 1989; revision accepted 6 March 1990.

The authors thank A. Winn and S. Tonsor for comments and discussion and the University of Chicago greenhouse staff for maintaining plants and providing advice and support.

\textsuperscript{2} Corresponding author; current address: Department of Biological Science B-142, Florida State University, Tallahassee, FL 32306.

\textsuperscript{3} Current address: Department of Botany, KB-15, University of Washington, Seattle, WA 98195.
TABLE 1. Yield of Brassica rapa grown in no-competition and in two competitive environments. The skewness of the distribution is given by \( g \), \( H_g = g = 0 \). Positive values indicate skewness to the right of the distribution; negative values indicate skewness to the left.

<table>
<thead>
<tr>
<th>Environment</th>
<th>Biomass (g) Mean</th>
<th>S.D.</th>
<th>No. flowers Mean</th>
<th>S.D.</th>
<th>( g )</th>
</tr>
</thead>
<tbody>
<tr>
<td>No-competition</td>
<td>0.687</td>
<td>0.170</td>
<td>97.90</td>
<td>25.24</td>
<td>0.110</td>
</tr>
<tr>
<td>Competition</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intraspecific</td>
<td>0.073</td>
<td>0.066</td>
<td>12.57</td>
<td>10.99</td>
<td>0.897</td>
</tr>
<tr>
<td>Interspecific</td>
<td>0.012</td>
<td>0.009</td>
<td>2.332</td>
<td>0.82</td>
<td>2.853</td>
</tr>
</tbody>
</table>

\( aP < 0.05. \)

\( bP < 0.01. \)

hand, positive genetic correlations for performance under different competitive conditions would reflect generalized adaptation to a broad variety of competitive regimes and would indicate that traits that improve performance under one regime also do so (or are correlated with traits that do so) under other competitive conditions. Generalized competitive adaptations may provide greater fitness when the competitive regime is spatially or temporally variable (e.g., Hubbell and Foster, 1986).

To establish that competition contributes significantly to the observed variation in fitness among individuals requires that the performance of genotypes grown without competition be a poor predictor of their performance when grown in competitive environments. The strength of this prediction will be revealed by the correlation for performance in competitive and noncompetitive conditions (Martin and Harding, 1982). A strong positive correlation would indicate that a genotype favored in noncompetitive conditions also achieves high fitness when grown under competition. A weak or negative correlation would indicate that a genotype favored in competitive environments is not necessarily favored in noncompetitive environments. Only in the latter case can one unambiguously treat competition as a distinct selective force. This kind of analysis should, therefore, accompany any study that purports to examine the evolutionary dynamics of plant competition.

In this paper, we present the results of experiments designed to estimate the genetic correlations for performance of Brassica rapa grown under three competitive regimes: noncompetition (isolated plants), intraspecific competition (monocultures of Brassica rapa), and interspecific competition (two-species mixtures with Raphanus sativa). Our objectives were to: 1) identify the genetic basis of competitive performance in this species; and 2) provide a general protocol for investigating the evolution of competitive performance in plants.

MATERIALS AND METHODS—Brassica rapa L. (Cruciferae), rape or field mustard, and Raphanus sativa L. (Cruciferae), radish, are cosmopolitan annuals of temperate zones used in agriculture and found as common weeds. Brassica has an upright growth form, whereas Raphanus is relatively prostrate or vine-like and has larger leaves and, in our experiments, a more rapid growth rate. 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 initially derived by 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). Stocks of both species appear to contain substantial genetic variation, including isozyme polymorphism (Williams, 1985; Williams and Hill, 1986) and genetic variation for quantitative characters such as flowering date, ovule number, and trichome density (personal observation). Both species are hermaphroditic and have sporophytic self-incompatibility systems.

Maternal seed families for B. rapa were obtained by outcrossing 48 plants raised in a greenhouse at the University of Chicago. Pollinations were performed for 10 days; on each day, four different randomly chosen plants were designated as pollen donors for each maternal plant. Pollinations were performed using a small piece of felt attached to the end of a toothpick, which was rubbed over the anthers of the four pollen donors, then the mixed pollen load was applied to available stigmas on the maternal plant. Seed was harvested by maternal parent. On the basis of our pollination procedures, we expect that the genetic relatedness among progeny from a given maternal parent was approximately that of half-sibs. Additional populations of both species supplied seeds for neighbor plants in the competition regimes. Bulk seeds for this purpose were obtained by daily random
outcrossing of large populations (100+ individuals) of *Brassica* and *Raphanus* in the greenhouse.

Focal individuals of *Brassica* were grown from seed under three regimes: no-competition, intraspecific competition and interspecific competition. In the no-competition treatment, nine seeds from each family were sown individually in separate 8 x 8 x 12-cm deep plastic pots. In the intraspecific and interspecific treatments, ten seeds from each family were sown in hexagonal arrays in 52 x 22 x 8-cm deep plastic flats such that each focal plant was surrounded by six equidistant neighbors derived from the bulk seed collections.

An 8-cm border of nonsampled plants was used to preclude edge effects. Five flats were used per treatment (two replicate individuals per maternal family per flat), and each flat contained a total of 400 individuals (3,500 plants m⁻²). Seeds that failed to germinate and seedlings that died within 6 days of planting were replaced with transplanted individuals to maintain the uniformity of the competitive regimes, but these individuals were excluded from the analysis. There was no mortality after the 6th day, and no family was left with less than six replicates in each competitive regime; most had eight to ten (mean = 9.3). Each target individual from the half-sib families was surrounded by either six conspecific neighbors from the rapid-cycling seed stock (intraspecific competition) or six individuals of rapid-cycling *Raphanus sativa* (interspecific competition).

Mean weight per seed for each family was determined from unused seed weighed in lots of approximately 20 seeds.

All plants were grown in ProMix BX (a standard soilless mix of sphagnum moss, vermiculite, and perlite) and maintained in a growth room at the University of Chicago. Plants were illuminated 24 hr/day with fluorescent lights (approx. 240 μEm⁻² s⁻¹) at a constant 24.5 C temperature. The plants were watered as needed to prevent wilting and were fertilized at 18 and 28 days with a weak solution of soluble fertilizer (20-19-18, Peter’s Peat-Lite). After 38 days, all plants were harvested, censused for the total number of flowers initiated (number of flowers + developing fruits), dried at 65 C, and weighed. Although no hand pollinations were performed, some pollination occurred when plants bumped together; less than 3% of the flowers had begun developing seed.

For both plant biomass and flower number, we used a mixed model analysis of variance to examine the main effects of treatment (fixed), family (random), and the treatment x family interaction (random). The residuals from ANOVA departed significantly from a normal distribution for these analyses; thus, the significance levels presented should be interpreted with caution. Our purpose in these analyses was simply to establish the presence of a genotype x treatment interaction, which was found to be highly significant for both measures of plant performance (see below). To evaluate the variation in biomass and flower number among families within treatments, we used the Kruskal-Wallis nonparametric analysis of variance in the NPAR procedure of SYSTAT (Wilkinson, 1987). We estimated genetic correlations for performance using pairwise Pearson correlation coefficients (see Via, 1984), calculated from the mean biomass or flower number per family for plants grown in the three different competitive regimes. Confidence intervals for correlation coefficients were determined by means of z-transformations (Sokal and Rohlf, 1981).

**RESULTS AND DISCUSSION**—Plant sizes differed dramatically among the three treatments. Individuals in the no-competition regime were almost an order of magnitude larger than those grown under intraspecific competition and two orders of magnitude larger than those grown under interspecific competition (Table 1). Flower number displayed a similar pattern across the three treatments (Table 1). Although planting densities in the two competitive treatments were equal, interspecific effects on both biomass and flower number were larger than intraspecific effects. The two measures of fitness, biomass and number of flowers, were significantly correlated (P < 0.001) in all three treatments (alone: r = 0.48; intraspecific: r = 0.92; interspecific: r = 0.67).

The three treatments also produced significantly different patterns of variation in biomass and flower number (Table 1). In the no-competition treatments, both biomass and flower number were evenly distributed about the mean and showed no significant skewing (g; Sokal and Rohlf, 1981). Significant skewing was observed in both competitive treatments, with greater skewing in the more extreme interspecific regime. This result suggests that, as competitive intensity increases, a smaller number of individuals will contribute the majority of seeds to the next generation.

There was significant among-family variation in biomass within each treatment (Table 2). Mean biomass within each treatment varied with family by more than an order of magnitude; for example, mean biomass in the intraspecific treatment ranged from 0.011 g to 0.138 g. Mean flower number exhibited similar sig-
significant among-family variation except in the interspecific treatment, where the distribution of flower number/individual was truncated; the majority of individuals did not flower.

The treatment × family interaction was highly significant for both biomass and flower number (Table 3); the relative performance of a family depended on the treatment in which it was growing. The genetic correlation for biomass in the two competitive regimes (intraspecific and interspecific) was significantly greater than those for biomass in the noncompetitive regime and each competitive treatment (Table 4). Flower number showed a similar but nonsignificant pattern (Table 4); the low mean and standard deviation in flower number in the interspecific treatment (Table 1) reduce the likelihood of finding significant differences between treatments.

These results suggest the presence of a "generalized competitive performance" for the two competitive regimes used in this study—traits advantageous in intraspecific competition are also advantageous in interspecific competition. However, the correlation coefficients are significantly less than 1 (Table 4), suggesting that some opportunity exists for evolutionary specialization to each competitive regime.

It is likely that our results are dependent on the intensity of competition and on the identity of the limiting resources in this study. For example, competition for light, where light preemption (shading) by early-emerging or rapidly growing individuals is expected, might lead to a positive correlation between growth without competition and growth with competition. We found a positive, but low, correlation for performance in noncompetitive and competitive regimes, suggesting that relatively little advantage was conferred simply by the potential for rapid growth in our competitive treatments. The significant correlation between family performances in the two competitive treatments may indicate that similar resources were limiting under the intra- and interspecific conditions used in this experiment. Although the competition in this study was created by species with somewhat different growth forms and competitive intensities (competition with Raphanus created a more severe environment), other competitive regimes might have produced different results.

Because we used maternal families, we cannot exclude the possibility that some of the observed differences between families are caused by maternal genetic and/or environmental effects. One way in which environmental maternal effects appear is through seed size. Previous research with other species has shown that the maternal environment can have a large effect on seed size (e.g., Winn and Werner, 1987), and larger seeds may produce larger seedlings and adults, especially in competitive environments (Stanton, 1984; Gross, 1984). In our study, no significant correlation appeared between family mean seed mass and plant biomass, or flower number, in the no-competition or the interspecific treatment (no-competition treatment: biomass, \( r = 0.11 \); flower number, \( r = 0.17 \); interspecific treatment: biomass, \( r = 0.21 \); flower number, \( r = 0.24 \); all \( P > 0.05 \)).

There were significant correlations between mean family seed weight and performance under intraspecific competition for both biomass (\( r = 0.29, P = 0.04 \)) and flower number (\( r = 0.42, P = 0.003 \)).

Several previous studies have shown that the performance of genotypes varies significantly among different competitive regimes, suggesting specialization to particular competitive environments. Martin and Harding (1982) used an experimental design similar to that used in the present study to investigate the performance of families of Erodium cicutarium when grown alone, with intraspecific competition, or with interspecific competition. They found sig-

**Table 2.** Kruskal-Wallis test statistics (H) for effects of family on plant biomass and flower number (df = 47)

<table>
<thead>
<tr>
<th>Environment</th>
<th>Biomass</th>
<th>No. flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td>No-competition</td>
<td>101.2*</td>
<td>99.7*</td>
</tr>
<tr>
<td>Competition</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intraspecific</td>
<td>85.3*</td>
<td>81.5*</td>
</tr>
<tr>
<td>Interspecific</td>
<td>67.13*</td>
<td>50.4</td>
</tr>
</tbody>
</table>

\* \( P < 0.001 \).
\* \( P < 0.05 \).

**Table 3.** Analyses of variance for plant biomass and flower number in Brassica rapa in each environment. All \( F \) values are significant at the \( P < 0.0001 \) level

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Biomass/plant</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Competitive regime</td>
<td>2</td>
<td>59.488</td>
<td>3.021</td>
</tr>
<tr>
<td>Family</td>
<td>47</td>
<td>0.028</td>
<td>2.93</td>
</tr>
<tr>
<td>Regime × family</td>
<td>94</td>
<td>0.020</td>
<td>2.03</td>
</tr>
<tr>
<td>Error</td>
<td>1,118</td>
<td>0.010</td>
<td></td>
</tr>
<tr>
<td><strong>Flowers/plant</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Competitive regime</td>
<td>2</td>
<td>1,198,609.247</td>
<td>2,591.94</td>
</tr>
<tr>
<td>Family</td>
<td>47</td>
<td>641.020</td>
<td>2.84</td>
</tr>
<tr>
<td>Regime × family</td>
<td>94</td>
<td>461.280</td>
<td>2.05</td>
</tr>
<tr>
<td>Error</td>
<td>1,119</td>
<td>225.490</td>
<td></td>
</tr>
</tbody>
</table>
significant among-family differences in performance in the no-competition and interspecific competition treatments, indicating that traits related to performance were heritable. In contrast to the results of our study, they found no significant correlation between family performances in the two competitive treatments. However, the Martin and Harding (1982) study had little statistical power, because of the small number of families investigated (six) and the low replication (two plants/family).

Sakai (1961) found no correlation between the growth of different rice varieties in weeded plots (intraspecific competition) and unweeded plots (intra- and interspecific competition), suggesting that there is specialization for specific types of competitive environments. Turvlington and Harper (1979) did find significant among-clone differences in competitive response of ramets of Trifolium repens to different species of neighboring plants. Aarssen and Turkington (1985) also found significant differences among genotypes of pasture species in response to different genotypes of competitors. Kelly and Clay (1987) measured a similar effect in Danthonia spicata, but the pattern was not reciprocal; the competitive performance of Danthonia spicata depended on both plant genotype and the genotype of the competitor, Anthoxanthum odoratum, but no such pattern was found for the competitive performance of Anthoxanthum when it was grown with Danthonia. Other studies have also found little evidence of specialization (e.g., Goldberg, 1988).

A major purpose of this research was to establish an experimental protocol for evaluating the role of competitive interactions in the evolution of plant populations. Our approach is based in large part on the pioneering work of Sakai (1955, 1961) and Martin and Harding (1981, 1982) which concerned the genetic basis of competitive performance in plants. In Brassica rapa we found that the genetic correlations for performance in competitive and noncompetitive conditions were small compared to the genetic correlation for performance in intraspecific and interspecific competition treatments. These results suggest that the performance of this species when grown under competition is due, at least in part, to traits that confer an advantage only in competitive environments. In addition, there is little evidence of genetic specialization to particular competitive environments. We suggest that these kinds of analyses, once performed for a number of species in different competitive environments, will aid in our understanding of the selective effects of competitive interactions in plants.

LITERATURE CITED


KELLEY, S. E., AND K. CLAY. 1987. Interspecific competitive interactions and the maintenance of genotypic

Table 4. Correlations between mean family performance in each pair of environments. Numbers in parentheses are 95% confidence intervals (after z-transformation, Sokal and Rohlfl, 1981)

<table>
<thead>
<tr>
<th></th>
<th>Biomass</th>
<th>No. flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intra</td>
<td>Inter</td>
</tr>
<tr>
<td>No-competition</td>
<td>0.397*</td>
<td>0.269</td>
</tr>
<tr>
<td>Intraspecific</td>
<td>0.610b</td>
<td>(0.399–0.762)</td>
</tr>
</tbody>
</table>

* P < 0.05.

b P < 0.01.
variation within two perennial grasses. Evolution 41: 92–103.


