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Within-family Selection in *Avena fatua* and *A. barbata*

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Summary. Twenty families each of *Avena fatua* and *A. barbata* drawn from a natural population were used for measuring the response to within-family selection for the two extremes in heading date and seed size. The estimates of the relative amounts of between- and within-family variation were interpreted in relation to the realized responses to show that *A. fatua* has greater genetic variability than *A. barbata* which, on the other hand, has more phenotypic plasticity. These results support our model on the alternative adaptive strategies in the two species discussed earlier.

Two species of *Avena*, *A. fatua* (common wild oat) and *A. barbata* (slender oat), occur in pure or mixed stands as a stable component of the California annual type vegetation. Extensive population surveys have provided evidence for widespread polymorphism in *A. fatua* and none or a low degree of polymorphism in *A. barbata* over a large region for both phenotypic marker loci and electrophoretic variants (Marshall and Jain, 1969; Marshall and Allard, unpublished). A preliminary analysis of quantitative genetic variation at three sites further showed that *A. barbata* populations have relatively less genetic variability than *A. fatua* (Jain and Marshall, 1967; see Jain, 1969, for a review of comparative ecogenetic studies in *Avena*). The relative amounts of between- and within-family variability provide measures of the level of genetic heterogeneity and heterozygosity respectively and can be estimated by using the classical approach of selection between- and within-families for quantitative characters. Both species have predominant inbreeding (95–97% selfing) which theoretically maintains almost all genetic variability among an array of homozygous lines, and therefore, our primary interest in the present study was to estimate within-family genetic variation through response to selection (see Allard, Jain and Workman, 1968, for a review on the population genetics of inbreeding species). Such a comparative study is of direct relevance to our earlier discussions of the adaptive strategies postulated to involve greater phenotypic plasticity in *A. barbata* versus greater genetic variability in *A. fatua*.

Seed samples for individual plants drawn from site *H* in region *I* (Jain and Marshall, 1967) were grown as individual plant families in a field nursery and bulk seed was harvested from 20 random families in each species (Spring of 1965). From each family bulk, S_0 families were grown in 1966 (12 to 15 plants per family) and individual plant data were taken for flowering time (number of days after March 31 for heading) and seed size (mean length of top five seeds on the primary panicle). Selection for highest and lowest values within each family was practiced independently, for two cycles in the case of heading time (1967, 1968) and one cycle in the case of seed size (1967). S_0, S_1 and S_2 families were grown undee comparable greenhouse conditions of temperature, photoperiod, pot culture and sowing time over the three year period. Within each year, the response to selection is given by paired plot comparisons between high and low selection lines (10 plants per family) and an approximate measure of the genetic determination (heritability, in broad sense) is obtained by the regression of mean values (parent-progeny means or rank correlation over families) since year to year variations were minimized as much as possible.

On the basis of our previous studies and the postulated difference in the adaptive strategies of *A. fatua* and *A. barbata*, it is possible to make the following predictions with respect to the present experiment:

(a) Both the within- and between-family components of variation for the S_0 families should be greater for *A. fatua* than *A. barbata*.

(b) If the between family variation in *A. fatua* has a larger genetic component, the regression of S_2 on S_1 means should be higher in *A. fatua* than *A. barbata*.

(c) If the within-family variation in *A. fatua* has a greater genetic component, this species should show a greater selection response, as measured by the mean response over families, or the number of families which show a significant response, than *A. barbata*.

(d) If much of the within family variation in *A. barbata* is nongenetic as predicted, it should remain relatively constant in this species throughout the selection experiment.

The results of within family selection are summarized for heading date in Table 1 and for seed size in Table 2. The estimates of between- and within-family components of variance (σ_B^2 and σ_W^2) are based on natural logarithm transformation because of the marked difference between the means of two species and correlation between means and variances (cf. Lewontin, 1966; Marshall and Jain, 1968). For both heading date and seed size, the estimates of

Table 1. *Selection within Avena families for heading date*
(Recorded as days after March 31)

Species	Generation	Mean of Family Means $\bar{X}$	$S_B^{2\prime}(\ln X)$	$S_W^2(\ln X)$	$\bar{d}$		Proportion of Families With $\bar{\bar{d}} > 0$
A. fatua	S_0	51.9	0.100	0.009	21.9		
	S_1 – High selection	46.6	0.055	0.006	8.60	1.8	14/20
	S_1 – Low selection	44.8	0.053	0.006			(1)*
	S_2 – High selection	42.4	0.075	0.007	13.95	2.5	(15/19)
	S_2 – Low selection	40.0	0.068	0.007			(1)*
A. barbata	S_0	75.7	0.078	0.003	21.3		
	S_1 – High selection	67.4	0.036	0.003	12.3	1.6	11/19
	S_1 – Low selection	65.8	0.031	0.003			(1)*
	S_2 – High selection	57.5	0.055	0.005	8.4	1.2	11/18
	S_2 – Low selection	56.3	0.052	0.005			(1)*

$S_B^2(\ln X)$ = variance among family means
$S_W^2(\ln X)$ = variance within families
based on natural logarithms of measurements

$\bar{d}$ = mean difference between the highest and lowest scores within families.

$\bar{\bar{d}}$ = difference between the high and low family means.

($\bar{d}$ represents average difference between the selected plants; $\bar{\bar{d}}$ is the average difference between their progeny, or the realized response).

* Number of families in which response was statistically significant.

Table 2. *Selection for seed size*
(Based on mean length of five seeds)

Species	Generation	Mean of Family Means $\bar{X}$	$S_B^2(\ln X)$	$S_W^2(\ln X)$	High-Low $\bar{d}$	Response in S_1 $\bar{D}$	Proportion of Families With $\bar{D} > 0$
A. fatua	S_0	1.44	.0057	.0036	0.25		
	S_1 – High	1,51	.0074	.0028	0.20	0.10	13/20 (13*)
	S_1 – Low	1.41	.0063	.0030			
A. barbata	S_0	1.73	.0044	.0032	0.22		
	S_1 – High	1.74	.0037	.0031	0.17	0.05	12/19 (7*)
	S_1 – Low	1.69	.0032	.0031			

* Number of families showing significant response ($P < .01$) based on one-tailed t-test, and using pooled error variance

σ_B^2 and σ_W^2 in S_0 are larger in *A. fatua* than *A. barbata*, thus confirming our expectation (a) above. The form of distribution of heading date is different in the two species as shown by plotting the family means in Fig. 1. *A. fatua* shows an almost continuous distribution whereas the distribution is markedly bimodal in *A. barbata* suggesting a threshold response to the conditions of greenhouse culture by one or a few major genes. Similar bimodality was also observed in the case of segregating generations of interpopulation hybrids in *A. barbata*. It is likely that in natural populations different alleles are nearly fixed at such major loci, allowing relatively less genetic variability within sites but more between sites.

In order to test the relative ranking of the family means in S_1 and S_2 generations (heading date), Spearman's rank correlation coefficients (r_s) were estimated for both high and low selection (i.e. High 1968/High 1967 and Low 1968/Low 1967). The estimates are given below:

	A. fatua	*A. barbata*
High	0.81*	0.64*
Low	0.66*	0.78*

(* Significant at $P = .001$ level)

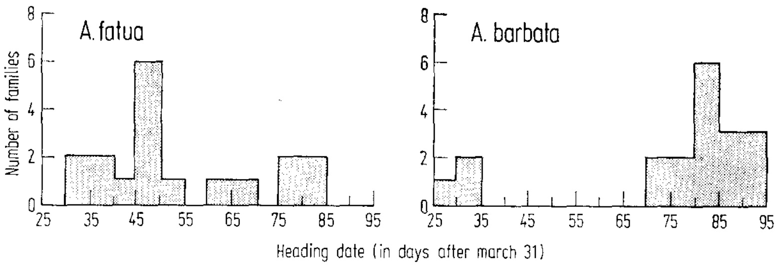

Fig. 1. Histograms showing the distribution of family means for heading date in S_0 generation

Thus, these data indicate that the between family genetic component is large indicating that heading date is a highly heritable character in both species. Similarly, high correlations are obtained between the S_0 and S_1 family means for seed size in both species.

The response to selection as given in the last two columns of Tables 1 and 2 is clearly larger in *A. fatua* than *A. barbata* for both heading date and seed size. The Mann-Whitney U test showed that the response as measured by values of D (= high−low) is significant ($P < .05$) taken over all families. Tests of difference between high and low pairs of individual families (using Student's *t*-test, with pooled S_W^2 as error variance) showed that the number of families with significant response ($P < .05$) in case of seed size is larger in *A. fatua* than *A. barbata*. Thus, these results taken overall support our postulate about greater genetic variation in *A. fatua* in terms of both between- and within-family components. The within-family variance decreased proportionately in the case of *A. fatua* whereas it remained unchanged or even increased in *A. barbata* presumably due to yearly differences in the environment, in line with our expectation (d) above.

Thus, in general our findings suggest that within-family selection provides a useful measure of the potential genetic variability stored in heterozygous families and that comparative results from the two *Avena* species confirm our earlier observations. *A. fatua* relies more on genetic variability whereas *A. barbata* has greater plasticity in the sense of "environment-induced" nongenetic variation as a source of adaptability to the varying environments. The presence of some major threshold factors as noted for heading date in *A. barbata* would provide further basis for selection studies involving the interpopulation hybrids.

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Zusammenfassung

Je 20 Familien von *Avena fatua* und *A. barbata*, die aus natürlichen Populationen entnommen worden waren, wurden zur Messung der Reaktion auf intrafamiliäre Selektion auf die beiden Extreme des Schoß-Termins und der Samengröße verwendet. Die Schätzungen der relativen Beiträge der Variation zwischen und innerhalb der Familien wurden in Beziehung zu der erzielten Reaktion interpretiert, um zu zeigen, daß *A. fatua* eine größere genetische Variabilität und *A. barbata* eine größere phänotypische Plastizität als die jeweils andere Art besitzt. Die vorliegenden Ergebnisse stützen unser früher diskutiertes Modell der alternativen adaptiven Strategien in diesen beiden Spezies.

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