ture (*1*). It cannot be said that the N-tropic variant of MuLV from the BALB/c mouse is nononcogenic in the BALB/c host because it is possible that with high doses neoplasm induction could take place. In order to maintain the "natural state" of the MuLV in the neoplasms used we elected, however, not to attempt passage to build up titer and chance artificial selection or alteration of the C-type RNA virus genome (or genomes) that might be present.

ROBERT L. PETERS
GERARD J. SPAHN, LOUISE S. RABSTEIN
Microbiological Associates, Inc.
Walkersville, Maryland 21793
GARY J. KELLOFF, ROBERT J. HUEBNER
Viral Carcinogenesis Branch,
National Cancer Institute,
Bethesda, Maryland 20014

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Viability versus Fecundity Selection in the Slender Wild Oat, Avena barbata L.

Abstract. *Estimates of relative selective values of different genotypes in natural populations of predominantly self-pollinated plants have consistently shown a net heterozygote advantage. Heterozygote advantage is further analyzed in the present study by estimating components of selective values corresponding approximately to viability and fecundity. The results show that a higher proportion of heterozygotes than of homozygotes survive from seedling to adult stages and that this viability selection accounts for the overall excess of heterozygotes.*

A central problem of experimental population genetics is the estimation of selection intensities in natural populations. The difficulties associated with such measurements are manifold and their paucity has been cited as one of the major shortcomings of the field (*1*).

Annual plant species offer a number of technical advantages for the estimation of selection. Their chief advantage is monoecism featuring simple mating systems that can be described precisely, thus satisfying the assumptions of simple selection models. Other advantages are ease of collection, and sedentary habit which allows precise identification of population units and accurate description of ecological relationships. Thus it is not surprising that annual plants have been the basis of several studies to measure selection intensities (*2*). Each of these studies has revealed intense selection featuring reproductive advantage of heterozygotes, which was often twice that of homozygotes. The present report describes a preliminary effort to apportion this intense selection over life-cycle stages in the slender wild oat species, *Avena barbata* L.

The population studied occupies a 10-acre site (1 acre = 0.4047 hectare), near Geyserville, California, which supports a vigorous stand of nearly pure *A. barbata* numbering several millions of individual plants. In a previous study of this site (*3*) significant excesses of heterozygotes were found for four esterase loci (E_1, E_4, E_9, and E_{10}), whose assay techniques and formal genetics have been described (*4*). The present study was based on three of these loci (E_4, E_9, and E_{10}).

To partition estimates of selective values into components corresponding approximately to viability and fecundity, census data taken prior to and following the operation of viability selection are required (*5*). In this study, census data were taken on seedlings in the fall of 1969 (generation n prior to viability selection), on adults in the spring of 1970 (generation n after viability selection), and on 1970 seedlings (generation $n+1$ after generation n fecundity selection but prior to generation $n+1$ viability selection). Two weeks after the first wetting rain in the fall of 1969, 140 randomly chosen *A. barbata* seedlings collected in nature were transplanted individually into peat pots. Selection was minimized by growing these seedlings under optimal conditions in a greenhouse for a month and then transplanting them into a garden plot in which conditions were also optimal. At maturity, selfed seeds were harvested from 66 randomly chosen plants among the 133 survivors, and the esterase genotype of each adult plant was inferred from electrophoretic assays of six of its seedling progeny [probability of correct identification $> .995$ (*6*)]. Estimates of genotypic frequencies in 1969 seedlings were made from these data. Genotypic frequencies in 1970 adults were obtained from assay of seven seedlings grown from seed harvested from individual plants in nature at maturity in the spring of 1970. An estimate of genotypic frequencies for 1970 seedlings was obtained from a census of seedlings grown from seeds collected from the ground in the late summer of 1970, before the first fall rain.

Table 1 gives estimates of allelic

Table 1. Allelic frequencies, fixation indices, and their standard errors. N refers to numbers of families examined for the 1969 seedling (S69) and 1970 adult (A70) censuses and to numbers of seedlings examined for the 1970 seedling census (S70).

Census	N	Allele 1	Allele 2	$\hat{F}$
		Locus E_4		
S69	66	0.303	0.697 ± 0.05	0.856 ± 0.07
A70	85	.329	.671 ± .05	.841 ± .06
S70	200	.300	.700 ± .03	.893 ± .03
		Locus E_9		
S69	66	0.227	0.773 ± 0.05	0.914 ± 0.06
A70	101	.208	.792 ± .04	.760 ± .08
S70	211	.206	.794 ± .03	.868 ± .05
		Locus E_{10}		
S69	66	0.204	0.796 ± 0.05	0.861 ± 0.08
A70	101	.232	.768 ± .04	.806 ± .07
S70	212	.172	.828 ± .02	.884 ± .04

Table 2. Estimates of relative selective values over the entire life cycle ($\hat{w}_{ij}$) and approximate estimates of viability ($\hat{v}_{ij}$) and fecundity ($\hat{l}_{ij}$) components.

Locus	Estimates of selected values								
	$\hat{v}_{11}$	$\hat{v}_{12}$	$\hat{v}_{22}$	$\hat{l}_{11}$	$\hat{l}_{12}$	$\hat{l}_{22}$	$\hat{w}_{11}$	$\hat{w}_{12}$	$\hat{w}_{22}$
E_4	1.00	1.22	1.13	1.00	0.99	0.85	1.00	1.21	0.96
E_9	1.00	2.63	0.80	1.00	0.91	1.00	1.00	2.39	0.80
E_{10}	1.00	1.61	1.15	1.00	0.72	0.65	1.00	1.16	0.77

frequencies and of Wright's fixation index [$\hat{F}$ (*7*)], and their standard errors (*8*), for each locus. The fixation index is defined for the *i*th and *j*th alleles at a locus by $\hat{F}_{ij} = 1 - f_{ij}/p_i p_j$, where $2f_{ij}$ is the observed frequency of the heterozygote and p_i and p_j are allelic frequencies. A consistent feature of these data is a decrease in $\hat{F}$ from seedling to adult stages for each locus. This decrease is significant [$P \approx .05$ (*9*)], indicating that there were relatively more heterozygotes at the adult stage than at the seedling stage and thus that heterozygotes have an advantage in viability.

Characterization of the mating system provides a second means of testing for selection. The mating system of this species is one in which a proportion s of the matings is due to selfing and a proportion t $(= 1 - s)$ is due to outcrossing. Maximum likelihood estimates of t (*10*) over the three enzyme loci were homogeneous in the Geyserville population; hence, the mean value, $\bar{t} = 0.022 \pm 0.007$, is used in the subsequent analysis.

It is reasonable to assume that this population, which is known to have occupied this site for many years, has reached inbreeding equilibrium, $F_e = s/(1 + t)$. The approach to equilibrium is given by the recurrence relation $F_{(n)} = [s/(1 + t)] [1 - (s/2)^n] + (s/2)^n F_{(0)}$, where $F_{(0)}$ is the inbreeding coefficient in some initial generation. A population selfing to the extent of the Geyserville population is expected to approach $F_e = s/(1 + t)$ closely by generation $n = 6$, even if it were originally in inbreeding disequilibrium. In the absence of selection, mutation, and migration, the fixation index, $\hat{F}$, is thus expected to equal $F_e = 0.957$ for $t = 0.022$. Since F_e is calculated from $\bar{t}$, which is a function of random variables, it is inappropriate to treat F_e as a constant in the significance test. Consequently, a lower bound for F_e was calculated from $\bar{t} + 2\sigma_t$ and this was used to test the null hypothesis, $\hat{F} = F_e$. The result shows that $\hat{F}$ is significantly smaller than F_e ($P < .0025$), indicating that heterozygotes are in excess. Evidently this excess is attributable to selection, since the isolation of the Geyserville population from other populations of *A. barbata* and the low mutation rates for enzyme loci in grasses (*11*) eliminate migration and mutation as factors of more than trivial importance.

To quantify the impact of selection over the seedling to adult and adult to seedling transitions, we have calculated relative selective values for these life-cycle stages. Maximum likelihood estimators for viability selection, defined relative to the most frequent homozygote, are $\hat{v}_{ij} = S_{11}A_{ij}/A_{11}S_{ij}$, $i,j = 1,2, \ldots, k$, in which $2S_{ij}$ and S_{ii} and $2A_{ij}$ and A_{ii} denote the frequencies of heterozygotes and homozygotes in seedling and adult stages, respectively. In estimating fecundity selection from the adult to seedling transition, it is assumed that all selection occurs between the census point and mating, that is, that no gametic selection occurs and that no selection occurs in the interval from formation of zygotes to the seedling census. Under these assumptions estimators for fecundity selection are

$$\hat{l}_{ij} = \frac{2A_{11}[S'_{ij} - tp_i p_j]}{A_{ij}[2S'_{11} - p_1(1 - t + 2tp_1)]} \qquad \begin{array}{r} i \neq j \\ i,j = 1,2, \ldots, k \end{array}$$

$$\hat{l}_{ii} = \frac{A_{11}[2S'_{ii} - p_i(1 - t + 2tp_i)]}{A_{ii}[S'_{11} - p_1(1 - t + 2tp_1)]} \qquad i = 1,2, \ldots, k$$

in which the S'_{ij} denote relative frequencies in the second seedling census (*10*),

$$p_i = \sum_j S'_{ij} = \frac{1}{\bar{L}} \sum l_{ij} A_{ij}$$

and

$$\bar{L} = \sum \sum l_{ij} A_{ij}$$

The selection coefficient over the S to S' transition is $\hat{w}_{ij} = \hat{v}_{ij}\hat{l}_{ij}$. The $\hat{v}_{ij}$ and $\hat{l}_{ij}$ are negatively correlated so that a high $\hat{v}_{ij}$ value implies a low $\hat{l}_{ij}$ estimate relative to $\hat{w}_{ij}$, and vice versa. Variances of selective values are not reported because these statistics provide a less powerful test of the significance of the increase in proportion of heterozygotes from seedling to adult stages than analysis of F statistics (selective values utilize information from only one set of seedling census data whereas F statistics utilize information from both sets). The results (Table 2) bring out dramatically that superior survival ability of heterozygotes from seedling to adult stages, rather than differences in fecundity (number of seeds produced by adults of different genotypes), account for the excess of heterozygotes.

Recent studies of the genetic structure of natural populations of *A. barbata* have demonstrated strong correlations in allelic state over loci, indicating that selection acts to structure the genetic resources of this species into highly interactive allelic complexes (*3*). A consequence of this organization is that an individual heterozygous at one locus is much more likely to be heterozygous for other loci. Thus the observed excesses of heterozygotes almost certainly result from the entire correlated multilocus complex with which the allozymes are associated. Evidently, therefore, viability interactions in which individuals heterozygous for these coadapted complexes are favored are a major component of natural selection in *A. barbata*.

M. T. CLEGG*
R. W. ALLARD

Department of Genetics,
University of California,
Davis 95616

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* Present address: Division of Biological and Medical Sciences, Brown University, Providence, Rhode Island 02912.

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