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Disruptive and Nondisruptive Selection for Bulk Oat Populations¹

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A mixture of F₃ seeds from 75 oat crosses was divided into four lots, with one being propagated in central Iowa for nine generations (i.e., stationary line of descent) and three being propagated in a rotational pattern in central, southern, and northern Iowa in successive generations (i.e., disruptively selected line of descent). An evaluation experiment was conducted to test whether any changes in genotypic frequencies were caused by the two propagation procedures. Increases in the means of yield traits occurred, but the magnitude and timing of the changes varied among lines of descent. The changes in the stationary and rotational lines of descent were indistinguishable. There was some trend for reduced genotypic variances for most traits with advancing generations. Probably the disruptive selection scheme did not cause differential results from the stationary one because the selection pressure due to differences in propagation sites was mild relative to the pressure due to differences in weather patterns during the years of the propagation period.

INDEX DESCRIPTORS: *Avena sativa*, natural selection

The bulk-population method of plant breeding is used extensively for autogamous species because it is inexpensive for managing large numbers of plants in segregating generations. During propagation of bulk population, inbreeding increases homozygosity at segregating loci, and natural selection may change the proportions of surviving genotypes. Changes caused by natural selection may, however, be at variance with a breeder's goals because the ability of a genotype to survive in competition with other genotypes in a bulk may not be a good criterion of its capacity to yield well in pure stands (Suneson, 1949; Jennings and de Jesus, 1968). Likely, competition is more complex in hybrid bulk populations over segregating generations (Jennings and Herrera, 1968; Allard and Adams, 1969).

The results from use of the bulk method for population improvement and the extraction of superior genotypes in advanced generations are mixed. Adair and Jones (1946) found that propagation sites caused differential evolution in a rice bulk hybrid (*Oryza sativa* L.) for heading date, plant height, grain type, and awnedness. In a composite of barley (*Hordeum vulgare* L.) entries, Rasmusson et al. (1967) obtained a yield increase of 9.5% per year during six years of bulk propagation. Florell (1929) extracted high-yielding lines from F₅ and F₆ of bulk populations of wheat (*Triticum aestivum* L.), and Suneson and Stevens (1953), Suneson (1956), and Jain (1961) reported improvements in yield of lines derived from advanced generations of composite crosses of barley in California. Johnson and Singh (1970) found improvements for yield and maturity in a bulk hybrid barley population. Significant improvements in winterhardiness occurred in bulk hybrids from non-winterhardy × winterhardy barley crosses studied by Warnes and Johnson (1972), but no bulk was equal to the winterhardy parents. Finkner (1964) thought that natural selection was inefficient for selecting winterhardy lines of oats. There were increases in grain yield, plant height, and seed number per plant in bulk populations of oats (*Avena sativa* L.) subjected to natural selection by Fatunla and Frey (1974). Gonzalez-Rosquel (1976) studied evolution of bulk populations of oats grown for several generations in northern, central, and southern Iowa and found increases for yield traits in all three lines of descent. The magnitude and timing of the responses differed among lines of descent, however. On the other hand, Frey (1967) found no significant changes for seed weight, plant height, or heading date in an oat bulk grown for five generations in Iowa, and Taylor and Atkins (1954) found no yield

changes in bulk populations of barley grown for several generations at different sites in Iowa.

Borlaug (1968) and Tsai et al. (1967), respectively, reported that disruptive selection (propagation of successive generations in alternate contrasting environments) was effective for improvement of yield and production stability of wheat and soybeans (*Glycine max* L., Merr.).

In this study, we have compared the changes that may have occurred in quantitatively inherited traits when bulk oat populations were propagated at a single site or rotationally at several sites: In plant breeding, these are considered to be nondisruptive and disruptive procedures, respectively.

MATERIALS AND METHODS

Development of Oat Strains

For this study we used oat strains derived from bulk populations that had been propagated under different environmental regimes. A composite of F₂ seeds obtained by mixing 10-g lots from about 75 oat crosses was propagated for one generation to increase seed supply. Subsequently, the F₃ seed was divided into four samples. One sample was propagated from F₃ through F₁₁ at a single site in central Iowa (stationary line of descent). The other three F₃ samples were sown one each in central, southern, and northern Iowa, respectively. In the following years, the bulks were moved in rotational schemes among the locations as shown in Table 1. The rotational patterns constituted the "disruptive environmental selection" schemes. The propagation sites differed in mean seasonal temperatures and precipitation, soil type, productivity, and disease prevalence (Adegoke, 1979).

Table 1. Rotational schemes for the four lines of descent for the oat bulk populations.

Line of descent	Sequence of rotation		
	1st year	2nd year	3rd year ^a
Rotation 1	Central Iowa	Northern Iowa	Southern Iowa
Rotation 2	Southern Iowa	Central Iowa	Northern Iowa
Rotation 3	Northern Iowa	Southern Iowa	Central Iowa
Stationary	Central Iowa	Central Iowa	Central Iowa

^aSeeds from third year were used to start the rotation over again.

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Table 2. Mean squares from analyses of variance for plant, straw, and grain yields, harvest index, heading date, plant height, flag leaf length, and spikelets/panicle.

Source of variation	Degrees of freedom	Mean square							
		Plant yield ^a	Straw yield ^a	Grain yield ^a	Harvest index	Heading date	Plant height ^a	Flag leaf length	Spikelets/panicle
Population	12	49.1**	29.5**	3.9*	256.9**	145.9**	10.24**	12.4	207.4**
Checks vs. strains	1	253.3**	185.4**	5.3*	1143.6**	542.2**	72.03**	1.0	606.9**
Lines of descent (LD)	3	11.5**	5.8**	1.7**	135.4**	108.0*	2.71	4.9	282.8**
Stationary vs. disruptive selection	1	15.5	5.7	2.0	85.4	0.3	4.50	6.6	41.0
Remainder	2	10.0	5.8	1.5	100.9*	161.8	1.82	3.9	403.7**
Generation (G)	2	87.5**	39.3*	11.5**	409.5	180.2	17.49**	38.2	309.9**
G linear	1	158.8**	61.1**	22.0**	343.5	121.0	31.15**	1.8	520.2**
G quadratic	1	16.2	17.5	1.0	475.5	239.5	3.83	74.6	99.7
LD × G	6	21.2**	12.1**	2.3**	119.0*	87.4**	1.30**	9.6*	68.9*
Strains/populations	370	11.8**	7.4**	1.8**	119.5**	41.1**	1.78**	15.0**	77.3**
Error	b	6.7	4.9	0.5	42.1	1.5	0.16	4.2	25.3

^aTimes 10²

^bDegrees of freedom were 1528 for plant, straw, and grain yields and harvest index and 764 for heading date, plant height, flag leaf length, and spikelets/panicle.

*, ** Denotes mean squares were significant at the 5% and 1% levels, respectively.

Each generation within each line of descent was represented by approximately 90,000 plants propagated at a population density of 300 plants/m². The plants in each generation in each line of descent were harvested and threshed in bulk with no artificial selection. A 3-kg lot (ca 3% of seed production) was taken for sowing the following year, and a 1-kg lot was placed in cold storage. In 1977, we space-planted 30 random seeds from each of the generations F₃, F₇, and F₁₁ of each line of descent. The bulk progeny from a single plant was used to establish a derived strain.

Evaluation and Data Collection

In 1978, we conducted an evaluation experiment consisting of 360 derived strains (i.e., 30 from each of the three generations in each of four lines of descent) plus 23 check cultivars. The experiment was sown in a randomized block design with eight replicates at the Agronomy Research Center, Ames, Iowa. A plot was a hill sown with 30 seeds, and hills were spaced 30 cm apart in perpendicular directions.

Three replicates were used for measuring (a) heading date (number of days after May 31 when 50% of the panicles in a plot were completely emerged), (b) plant height (distance in cm from ground level to the panicle tips), (c) flag leaf length (mean of lengths of five leaf blades per plot in cm), (d) number of spikelets per panicle (mean number of spikelets for five panicles per plot). At maturity, each plot from the remaining five replicates was harvested at ground level, and the bundle of plants was air-dried and weighed to obtain plant yield. Next, the culms were threshed, and the seed lot was weighed to obtain grain yield. Straw yield was computed by subtracting grain from plant yield. Harvest index, calculated as a ratio of grain to plant yield, was expressed as a percentage.

Statistical Procedure

The data for each trait were subjected to an analysis of variance, and genotypic variances among oat strains within populations (i.e., a popu-

lation was the 30 strains from a generation within a line of descent) were computed by equating mean square values to expected variance components. Populations were assumed to be fixed, and oat strains within populations were assumed to be random for purposes of these analyses.

RESULTS AND DISCUSSION

Changes in Generation Means

There were significant variations among means for lines of descent, generations, and strains within populations for plant, straw, and grain yields (Table 2). However, the mean square for stationary vs. disruptively selected lines of descent was not significant for any yield trait. Overall, there were net increases in mean plant, straw, and grain yields between F₃ and F₁₁ in all lines of descent.

The general trends of increase for the yield traits over generations were generally linear. The quadratic component mean square was not significant for any yield trait, but significant line of descent × generation mean squares occurred for all three, due to the contrasting patterns of change in means for rotations 1 and 3 vs. rotation 2 and the stationary line of descent. The trends of increase were rather steady in rotation 1 and rotation 3, whereas in rotation 2 and stationary lines of descent, there was a general tendency for yields to decrease from F₇ to F₁₁ (Table 3). Generally, there was a decided increase in number of strains with grain yields better than the F₃ mean.

For harvest index, there were significant differences among populations and strains within populations, and most of the variation among populations was due to checks vs. strains (Table 2). Except in rotation 1, there was no detectable increase in mean harvest index over generations (Table 3).

There were significant mean squares among populations and among strains within populations for heading date, but most of the variation among populations was due to checks vs. strains (Table 2). There was a significant linear trend over generations (Table 2) for plant height to

Table 3. Means for plant, straw, and grain yields, harvest index, heading date, plant height, flag leaf length, and number of spikelets per panicle in oat generations within lines of descent.

Generation	Plant yield (q/ha)	Straw yield (q/ha)	Grain yield (q/ha)	Harvest index (%)	Heading date (days after May 31)	Plant height (cm)	Flag leaf length (cm)	Spikelets/panicle
Rotation 1								
F ₃	88.1	60.4	27.8	31.4	21.0	103.9	16.6	33.0
F ₇	89.7	60.8	28.9	32.3	20.2	105.6	16.4	33.1
F ₁₁	100.3	68.3	32.0	33.4	21.3	108.5	16.4	33.5
Rotation 2								
F ₃	87.4	59.2	28.3	32.5	22.1	105.1	17.0	35.3
F ₇	92.5	64.5	28.0	30.1	23.2	109.4	16.0	34.6
F ₁₁	89.5	60.1	29.4	32.5	21.5	108.2	16.9	37.6
Rotation 3								
F ₃	88.7	61.2	27.6	31.0	20.7	105.3	16.9	34.0
F ₇	92.1	64.4	27.7	29.8	22.9	108.5	16.4	33.8
F ₁₁	94.6	64.2	30.4	32.7	22.3	107.8	16.7	34.6
Stationary								
F ₃	82.2	56.4	25.8	30.9	20.0	101.9	16.6	32.1
F ₇	94.7	64.8	29.9	31.4	23.2	106.1	16.3	33.6
F ₁₁	91.2	62.6	28.6	31.5	22.0	108.4	17.4	36.0
Checks	75.6	49.1	26.5	34.9	18.8	96.0	16.5	31.2

increase in all lines of descent. The change in spikelet number over generations was significantly linear, but there also was a line of descent \times generation interaction (Table 2). Fairly sizable increases in the mean occurred in the rotation 2 and stationary lines of descent, but no changes occurred in the other two (Table 3).

Flag leaf length mean squares were not significant for any source of variation except the line of descent \times generation interaction and strains within populations.

There tended to be increases in the means for the yield traits, heading date, plant height, and spikelet number with advancing generations in all four lines of descent of our bulk oat populations, but the means for the stationary line of descent were not different from those for the rotation ones for any trait. Lines of descent \times generations interactions were significant for all traits, however, which indicates that the trends of change for all lines of descent were not equivalent nor consistent. Likely, the inequivalencies or inconsistencies were caused by the major changes being manifested in different generations. For example, the major increases in yield traits in the rotation 1 line of descent occurred between F₇ and F₁₁, whereas in the stationary one, the changes occurred between F₃ and F₇. This differential timing of changes in trait means suggests that (a) only a few of the propagation environments in which the bulk oat populations were grown caused the major changes and (b) those particular environments caused cataclysmic changes in the bulk population means.

Unfortunately, our experiment was not extensive enough to permit us to discern whether the changes in means were really cataclysmic or whether they occurred gradually over the intervening generations between F₃ and F₇ or F₇ and F₁₁, which were not tested.

Generally, the shifts in means were in the direction of survival of more vigorous genotypes. They had greater plant, straw, and grain yields and greater plant height. These traits are manifestations of vigor, which give genotypes competitive advantages in bulk hybrid populations of oats. Also, the fact that the F₁₁ had a greater proportion of strains with high grain yield than did the F₃ in each line of descent would be consistent with the goal of increasing yielding capacity of oat

cultivars: Thus, natural selection for high grain yield was compatible with breeders' goals. These results are similar to those reported by Suneson (1956), Jain (1961), and Johnson and Singh (1970) for barley and by Fatunla and Frey (1974) and Gonzalez-Rosquel (1976) for oats, but they conflict with those found by Jennings and Herrera (1968) for rice.

Shifts in population means over generations were not discernibly different for the rotational schemes of propagation than for the stationary one. Theoretically, propagation at a single site should cause natural selection to be more consistent and continuous in its effect, than a disruptive scheme which should cause a mix of selection pressures that would lead to inconsistency in trends of shift for a trait. The similar trends of shifts in trait means that we found for the rotational and stationary lines of descent probably means that the selection pressures due to propagation site were relatively small compared with those pressures caused by specific weather and biotic factors that occurred in a given year. Practically, this means that an oat breeder in Iowa, or in a similar research situation with another crop, can have little hope of utilizing natural selection in bulk hybrid populations to his advantage over the short run.

Genotypic Variances

Changes in genotypic variances among oat strains within populations were large in several instances (e.g., for plant and straw yields) but generally were fairly small. For most traits, however, trends were for genotypic variances to decrease from F₃ to F₇ to F₁₁ (Table 4). Exceptions were plant and straw yields and plant height in the stationary line of descent.

Two opposing forces should influence the trend of change in genotypic variance in successive generations of a bulk hybrid population of an autogamous plant species. Inbreeding should increase the genotypic variance, whereas natural selection, if unidirectional, should reduce it by eliminating strains at one end of the frequency distribution of genotypes. Whether the genotypic variance is increased or decreased will depend on which of these two opposing forces exerts the greater

Table 4. *Genotypic variances for plant, straw, and grain yields, harvest index, heading date, plant height, flag-leaf length, and spikelet number per panicle in F₃, F₇, and F₁₁ of bulk oat populations propagated at a stationary site and rotated among sites.*

Trait	Rotational			Stationary		
	F _{3a}	F ₇	F ₁₁	F ₃	F ₇	F ₁₁
Plant yield	122 _a	88	64	245	43	151
Straw yield	71 _a	54	39	93	22	66
Grain yield	26 _a	21	18	49	37	24
Harvest index	17	15	10	23	34	10
Heading date	17	13	10	21	17	12
Plant height	71 _a	56	50	35	44	55
Flag-leaf length	4	4	3	3	5	5
Spikelet number per panicle	23	17	12	20	18	12

^aTimes 10²

influence. In our oat populations, directional natural selection occurred as shown by the shifts in trait means, and oats is autogamous; thus inbreeding occurred. Therefore, because the genotypic variances of our bulk oat populations tended to decline over generations, we conclude that natural selection was the stronger force influencing genotypic variation in the oat populations.

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