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STUDIES WITH BULKED HYBRID POPULATIONS OF BARLEY
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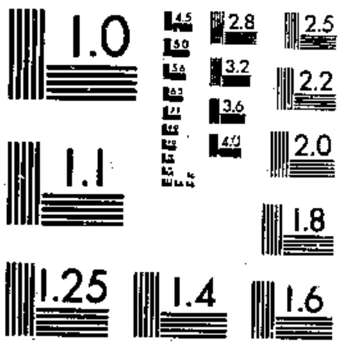

MICROCOPY RESOLUTION TEST CHART
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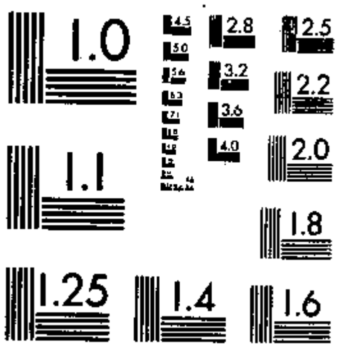

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NATIONAL BUREAU OF STANDARDS-1963-A

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Studies With Bulked Hybrid Populations of Barley[1]

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United States Department of Agriculture in cooperation with the agricultural experiment stations of California and Idaho

CONTENTS

During the period in which cereal breeding methods were being developed in North America, the late H. V. Harlan, of this Bureau, became the chief designer and advocate of the complex bulk population method of breeding—an extended form of the bulk population method of breeding. He emphasized the efficiency of this method for advancing selection material to a homozygous state. He also pioneered in its use for study of survival under competitive selection.

The studies here reported grew out of the writers' association with this work. Six different composites were grown for 6 to 24 generations. This permitted observations on the persistence of specific characters, the probable causes of nonrandom survival in the hybrid mixtures, and the progressive changes in the yield of 3 composites grown for 13 to 24 generations. Companionate studies on the survival of varieties in mixtures have aided in making the interpretations.

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[1] Submitted for publication February 4, 1953.

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REVIEW OF LITERATURE

Most of the literature on bulk populations has been concerned with detecting, in early generations, crosses that are potentially good selection stocks. Varied conclusions have resulted from studies with barley (*6*),[2] wheat (*7*), and soybeans (*8*). The work with Composite Cross II of barley indicates that bulk populations are at least as effective as pedigree selections in perpetuating superior genetic recombinations (*6*). In three similar bulk populations of rice grown in Arkansas, California, and Texas for eight generations, "all degrees of maturity, height, grain type, and awn development survived" in sufficient number for selection (*1, pp. 714–716*). Furthermore, (*1, p. 716*) "the association of the characters studied . . . was not of such a nature as to interfere seriously with the survival of desirable plant types . . .". This statement implies that some limitations on survival were imposed by linkage.

A distinction between variety performance in pure stands and survival capacity in mixtures must also be recognized. Survival in a mixture may not relate to either yield or disease resistance (*14*). Of the 11 parent varieties included in Composite Cross I and grown in mixtures at 8 stations for 5 to 13 years, the varieties Trebi, Coast, and one other variety comprised 62 to 99 percent of the mixture in the last year grown (*5*). Only 5 of the 11 varieties remained among the best 3 survivors at any of the 8 locations.

The information on the yield of the random recombinations of certain characters recovered from both bulk and pedigree populations (*6*) has been useful in these investigations.

Anderson's work (*2*) supports the writers' general findings and their departure from the more usual methods of analyzing hybridization in seeking to establish the relative importance of hybridization in evolution.

MATERIAL AND METHODS

Composite Cross I (C. I. 4116)[3] was compounded by H. V. Harlan from 32 crosses involving 11 varieties. These same 11 varieties also were used in a parallel study of survival in mixtures (*5*). The 11 varieties were crossed with 1 to 3 of the other varieties. After harvest of the F_3 generation plants, equal parts by weight of each cross were mixed together to form the Composite. The F_1 to F_3 generations were grown at Aberdeen, Idaho, and subsequent generations were grown at 10 locations for various periods. Cooperators provided random seed lots from these generations for a study of character survival under competition. From these seed lots 500 plants were grown and classified annually at Sacaton, Ariz., or Aberdeen, Idaho.[4] The maximum measure of changes involved 12 generations (1925–36). Short-term data from Pullman, Wash., and Arlington, Va., did not seem to merit inclusion.

Composite Cross II (C. I. 5461) has been under continuous culture in California from the F_2 to F_{24} generations, with only limited ex-

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[2] Italic numbers in parentheses refer to Literature Cited, p. 13.

[3] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

[4] These data were obtained by H. V. Harlan, M. L. Martini, H Stevens, G. A. Wiebe, and L. L. Davis.

traction of material for plant-breeding use. This stock consisted of progenies from 28 varieties crossed in all possible combinations—a total of 378 crosses (*4*). The parents were chosen to provide broad genetic and ecologic diversity. The successive generations were grown in consecutive years in drilled plots ranging from 1/50- to 1/10-acre in size. Planting rates varied from 55 to 70 pounds of seed per acre. In most seasons the plantings were made before mid-December. The plants were harvested with a binder when fully ripe, and the seed was given a minimum of selective screening before replanting. The objective was long-term cumulative natural selection under normal cultural conditions.

A random lot of seed was set aside after harvesting the F_{10} generation in 1936. The residual seed was then subjected to selection for extremes in size. Thus, from the F_{11} to F_{19} generations the largest and smallest seeds were sorted out each year by means of screens and an air blast. The selected large and small seeds comprised less than 10 percent of the total production of the previous generation. These separates were grown in each successive year under the same conditions as the stock subjected only to natural selection. The large-seed fraction consisted of predominantly two-rowed types that were not wanted. The F_{20} generation, therefore, was deliberately reconstituted by hand-selection of enough six-rowed heads to provide 65 percent of the seed of that type. These selected six-rowed type seeds weighed 57.7 mg., which is truly large for six-rowed barley. The seeds were not sized from the F_{20} to F_{23} generations, but the three separate stocks were continued for comparison.

Through the use of reserve F_2 seed, it was possible to reconstitute the F_3 and F_4 generations of Composite Cross II for both census counts and yield determinations in 1937–38. An attempt to repeat this in 1947 failed, owing to the poor germination of the small reserve seed sample.

Other Composite Crosses tested also were grown on areas of 1/50 acre or more in each generation. These are briefly described as follows:

Composite Cross III (C. I. 5530) was a mixture of Harlan's crosses from 13 winter- and spring-type varieties. Winter types of barley are generally unadapted in California.

Composite Cross V (C. I. 6620), also developed by H. V. Harlan, is a bulk of F_1 plants derived from crossing 31 varieties, and then crossing the resulting F_1 plants in increasing numbers through 4 successive pairings to give a "complete" recombination.

Composite Cross XII (C. I. 6725), developed by G. A. Wiebe, is in part a modified backcross in which Lion, Atlas, and Club Mariout germ plasm predominate. Actually 26 varieties were combined through a series of 4 pairings of F_1 plants, and the residual then crossed with the F_1 of Atlas × Vaughn.

Composite Cross XV (C. I. 7133) was compounded by the senior writer from a bulk of F_1 plants from 625 pollen parents chosen at random for crossing on a male-sterile strain. Various degrees of continuing recombination are afforded by the presence of male-sterile plants in every generation (*12*).

Census data on the California-grown Composite Crosses were based on counts of the different types among the plants or reserve seed lots.

Yield data were obtained from replicated three-row nursery plots 16 feet long, in which the center row was harvested for yield. The variability in yield differences is indicated by the number of superior-yielding replications among each of the paired stocks.

SURVIVAL OF FIVE COMMON CHARACTERS IN COMPOSITE CROSSES

Specific characters, like varieties (*5*), exhibit differential survival capacity when grown in mixtures in different parts of the United States. Some environments are more selective than others (table 1). Of the five characters recorded, hooded and deficiens [5] plants at all locations became progressively less numerous under continued competitive selection. The Meloy and Deficiens parents produced this same pattern in the census study of the Mechanical Mixture (*5*). Two-rowed types increased at Aberdeen, Moccasin, Fargo, St. Paul, North Platte, and Moro, but declined rapidly at Davis and Ithaca. This trend was previously reported for two-rowed parent varieties when grown at these stations (*5*). The percentage increase of the rough-awned portion of the two-rowed types was equal to that of the smooth or semismooth types, or even greater. Black recombinations at Davis followed the pattern of an unadapted variety and were reduced in number in a very short time. This character at the other seven locations showed the trend typical of a variety well enough adapted to remain in competition for many years. Smooth-awned segregates persisted at original frequencies or increased at six stations. This character decreased at Fargo and North Platte.

The smooth-awned parent varieties, which did not have good competitive ability (*5*), did not foreshadow the result of this test. There are two factors affecting the inheritance in a cross of rough and completely smooth-awn barleys. The rough-awned versus smooth-awned cross produces three types; namely, rough, semismooth or half-smooth, and completely smooth. The smooth- and semismooth-awned barleys were classed as smooth, however. These two types may have different ranges of adaptation. Since three of the five characters under review were neutral at some locations and sharply divergent at others, as selection progressed, it seems likely that the basis of the difference may not lie in the character itself but may be caused by adaptation factors linked with it. H. V. Harlan, in conversations and in subsequent crossing programs, evidenced concern over the inadequacy of recombinations in Composite Cross I. This may not have been serious, because the data generally substantiate those developed independently by the writers from other material. The actual crosses bulked in F_3 to form Composite Cross I are shown in table 2.

Four plant census enumerations involving the F_4, F_{12}, F_{15}, and F_{23} generations of Composite Cross II are shown in table 3. None of the four characters persisted at or near the levels to be expected from random recombination. Low yields of hooded types, as established by Harlan and coworkers (*6*), may account for the small number of

[5] The "deficiens" barleys are described in Technical Bulletin 907, Classification of Barley Varieties Grown in the United States and Canada in 1945, p. 6.

TABLE 1.—*Progressive changes in the composition of Composite Cross I when grown successively at various stations, 1925–36*

Test station	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936
TWO-ROWED PLANTS												
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Davis, Calif	21.0	26.6	24.2	24.4	19.8	20.0	17.2	----	12.8	11.8	5.8	5.4
Aberdeen, Idaho	21.8	23.2	21.6	25.8	24.0	22.0	25.6	25.6	29.8	35.2	35.4	27.6
Moccasin, Mont	20.4	20.2	18.8	22.8	16.8	21.8	26.8	27.0	23.6	27.4	24.6	28.8
Fargo, N. Dak	23.2	29.6	20.8	23.2	23.4	27.4	----	----	----	----	----	----
St. Paul, Minn	15.2	18.5	26.1	24.6	30.4	29.6	----	----	----	----	----	----
Ithaca, N. Y	21.5	22.4	19.4	20.4	11.1	8.0	----	----	----	----	----	----
North Platte, Nebr	18.3	21.4	----	21.6	20.0	24.2	----	----	----	----	----	----
Moro, Oreg	18.9	----	24.8	----	30.6	44.8	----	----	----	----	----	----
DEFICIENS PLANTS												
Davis, Calif	7.8	6.2	6.6	3.2	2.4	1.0	3.0	----	1.0	0.6	0.8	1.0
Aberdeen, Idaho	5.1	5.6	5.4	4.1	4.8	2.0	1.6	2.2	1.8	.6	.8	.2
Moccasin, Mont	5.7	3.6	4.6	5.0	4.6	3.0	3.8	1.8	.8	.4	----	1.2
Fargo, N. Dak	6.1	3.6	1.8	1.4	1.0	1.6	----	----	----	----	----	----
St. Paul, Minn	5.6	4.8	3.4	2.4	2.4	2.6	----	----	----	----	----	----
Ithaca, N. Y	11.1	10.1	4.8	5.6	2.4	.8	----	----	----	----	----	----
North Platte, Nebr	9.1	6.6	----	5.4	3.0	2.8	----	----	----	----	----	----
Moro, Oreg	8.3	----	6.9	----	4.2	.6	----	----	----	----	----	----
BLACK PLANTS												
Davis, Calif	12.0	10.0	4.8	5.4	1.4	2.4	2.2	----	1.6	0.2	0.2	0.8
Aberdeen, Idaho	10.7	10.0	11.4	11.2	10.2	9.2	8.0	6.8	6.0	5.8	4.2	6.6
Moccasin, Mont	12.9	13.0	11.2	12.6	13.9	9.2	9.2	9.2	12.2	9.8	6.2	9.2
Fargo, N. Dak	13.4	11.6	17.0	11.0	12.2	9.0	----	----	----	----	----	----
St. Paul, Minn	11.7	15.3	12.2	10.0	11.0	10.8	----	----	----	----	----	----
Ithaca, N. Y	9.9	11.5	10.8	9.6	9.0	10.4	----	----	----	----	----	----
North Platte, Nebr	13.0	15.8	----	11.8	14.4	13.0	----	----	----	----	----	----
Moro, Oreg	8.4	----	14.9	----	9.4	9.8	----	----	----	----	----	----
HOODED PLANTS												
Davis, Calif	9.6	7.2	5.8	3.4	3.8	2.0	3.6	----	2.4	1.4	0.4	1.4
Aberdeen, Idaho	8.3	6.0	4.6	2.1	3.0	3.0	1.6	1.6	.8	.6	1.0	2.4
Moccasin, Mont	9.4	9.4	6.8	5.8	3.8	3.8	3.6	4.4	4.2	2.2	1.0	2.6
Fargo, N. Dak	3.5	3.4	.8	.8	1.2	0	----	----	----	----	----	----
St. Paul, Minn	5.1	5.6	2.2	1.4	2.8	1.6	----	----	----	----	----	----
Ithaca, N. Y	6.6	4.1	1.6	1.8	1.8	0	----	----	----	----	----	----
North Platte, Nebr	6.6	7.8	----	6.6	3.8	4.0	----	----	----	----	----	----
Moro, Oreg	7.4	----	4.8	----	4.4	3.0	----	----	----	----	----	----
SMOOTH-AWNED PLANTS												
Davis, Calif	9.6	14.8	13.4	10.0	20.2	17.8	16.6	----	12.2	19.0	20.8	25.8
Aberdeen, Idaho	9.9	14.2	13.6	14.2	10.4	10.2	11.6	13.6	7.4	14.8	11.0	9.6
Moccasin, Mont	11.5	14.8	14.0	9.4	13.8	15.0	15.8	19.8	11.2	21.2	21.6	19.2
Fargo, N. Dak	11.0	15.2	16.3	8.0	10.8	8.8	----	----	----	----	----	----
St. Paul, Minn	11.4	15.5	13.6	15.0	11.2	13.6	----	----	----	----	----	----
Ithaca, N. Y	13.5	14.0	12.6	10.8	18.7	19.2	----	----	----	----	----	----
North Platte, Nebr	14.0	13.8	----	12.6	11.9	8.8	----	----	----	----	----	----
Moro, Oreg	10.0	----	17.4	----	17.6	23.0	----	----	----	----	----	----

TABLE 2.—*Description of the parents and listing of the 32 hybrids mixed in equal parts by weight after harvest of the individual F_3 populations to form Composite Cross I (C. I. 4116)*

Parent (P_1)	C. I. No.	Genotype [1]	Parent (P_2): Coast	Manchuria	Gatami	Smooth Awn	Lion	White Smyrna	Hannchen	Svanhals	Deficiens	Meloy
Trebi	936	vv bb RR kk	X	X	X	X	-	-	X	X	X	X
Coast	690	vv bb RR kk	-	-	-	-	-	-	-	-	-	X
Manchuria	2259	vv bb RR kk	-	-	X	X	X	-	X	X	-	-
Gatami	2276	vv BB RR kk	X	-	-	-	-	X	-	-	-	X
Smooth Awn	2256	vv bb rr kk	X	-	X	-	-	-	-	-	-	-
Lion	2238	vv BB rr kk	-	-	-	-	-	-	-	-	-	-
White Smyrna	195	VV bb RR kk	-	-	-	-	-	-	-	-	-	-
Hannchen	531	VV bb RR kk	X	-	-	-	-	X	-	-	X	X
Svanhals	187	VV bb RR kk	X	-	X	X	-	-	-	-	X	X
Deficiens	2225	V^tV^t bb RR kk	X	-	X	X	-	-	-	-	-	X
Meloy	2289	vv bb RR KK	-	-	-	-	-	-	-	-	-	-

[1] vv=6-rowed, VV=2-rowed, V^tV^t=deficiens, BB=black, bb=nonblack, RR=rough awn, rr=smooth awn, KK=hooded, kk=awned.

hooded barleys in the final population. The same reason was given for the small number of two-rowed types (*6*), but the data from Composite Cross I and Mechanical Mixture (*5*) showed that this character has a high survival at some locations. Yield inferiority of smooth-awned selections was not established by Harlan and others and probably does not exist, because a large number of smooth-awned varieties have been produced by recombination and are now being grown in all parts of America.

The black-seed character disappeared most quickly from the mixture (table 3). Unlike smooth awn, it is a character for which there is no recognized economic value. Percentage of black seeds in the F_{10} to F_{23} generations of Composite Cross II are given in table 4. Conclusive proof that the character generally has a poor survival capacity is shown by early generations of Composite Crosses V and XV (table 4). Composite Cross XII, which is really a modified backcross and thus might provide a more favorable gene environment for the black character, is the only possible exception. In this cross black seed persisted at approximate expectancy levels through the F_9 generation.

Some further support for the theory that black seeds in themselves do not influence survival is shown by the comparative kernel weights of black and white seeds (table 5). No consistent weight advantage for either black or white seeds is shown, and, hence, no probable difference in the synthesis or deposition of materials in the different colored kernels. The black pigment is a mature plant character that develops as the seeds ripen.

TABLE 3.—*Decline of 4 characters in Composite Cross II derived from intercrossing 28 varieties grown at Davis, Calif.*

Generation	Test year	Plants observed	Composition of linkage group [1]			
			I, 2-rowed, 7	II, black, 1	IV, hooded, 1	V, smooth-awned, 3
		Number	*Percent*	*Percent*	*Percent*	*Percent*
F_4	1933	500	22. 0	3. 4	2. 6	13. 0
F_{12}	1938	230	15. 0	0	. 4	9. 6
F_{15}	1941	2, 000	8. 0	. 1	. 1	4. 9
F_{23}	1949	4, 000	. 5	0	. 02	2. 4

[1] First item=linkage group; second item=genetic character; third item=number of parents contributing character to Composite Cross.

TABLE 4.—*Black seeds taken from various generations of 4 composite crosses grown at Davis, Calif., 1936–49*

[Based on samples of 2,000 seeds]

Composite Cross II (C. I. 5461)				Composite Cross V (C. I. 6620)		Composite Cross XII (C. I. 6725)		Composite Cross XV (C. I. 7133)	
Generation	Black seeds: Random seed stock	Black seeds: Directed selection for— Largest seeds	Black seeds: Directed selection for— Smallest seeds	Generation	Black seeds	Generation	Black seeds	Generation	Black seeds
	Percent	*Percent*	*Percent*		*Percent*		*Percent*		*Percent*
F_{10}	0. 3	-----	-----	F_1	19. 5	F_2	2. 3	F_2	3. 1
F_{11}	. 2	0. 2	0. 5	F_2	13. 1	F_3	2. 1	F_3	2. 6
F_{13}	. 2	. 05	. 6	F_6	7. 2	F_7	1. 7	F_4	1. 9
F_{14}	. 05	0	. 5	F_7	7. 0	F_8	2. 2	F_6	1. 3
F_{16}	0	0	. 4	F_8	5. 9	F_9	1. 5	sib_2F_2	1. 9
F_{17}	0	0	. 4	-----	-----	-----	-----	sib_3F_1	. 9
F_{21}	0	0	. 01	-----	-----	-----	-----	sib_5F_1	. 6
F_{23}	0	0	. 01	-----	-----	-----	-----	-----	-----

TABLE 5.—*Kernel weight of randomly separated black and white seeds from various stocks grown in 1948 or 1949*

Stock	Generation	Kernel weight [1]	
		White	Black
		Mg.	*Mg.*
Composite Cross V	F_8	33.46	35.72
Composite Cross XII	F_9	33.72	31.20
Composite Cross XV	F_5	32.87	31.94
Do	sib_1F_2	34.21	35.33
Do	F_6	48.22	49.20

[1] Based on samples of 1,000 kernels.

SELECTION FOR SEED SIZE

Large- and small-seed separates of Composite Cross II were developed by subjecting the F_{11} to the F_{19} generations to annual grading toward the respective seed-size extremes (table 6). From the F_{20} to the F_{23} generations all three lots were grown without further grading. The large-seed separates consisted primarily of kernels from the central (large) florets, whereas the small-seed separates were largely from lateral (small) florets.

Black seeds were most numerous and persistent in the small-seed separates, and least persistent among the large seeds (table 4). The two-rowed types comprised 27 percent of the large-seed separates in 1939 and 65 percent in 1945. Despite such character differences, the three stocks remained similar.

TABLE 6.—*Kernel weight of 3 seed lots from an F_{10} generation of Composite Cross II stock, 2 of which were selected for seed size from the F_{11} to the F_{19} generations*

Selection variable from F_{11} to F_{19}	Kernel weight [1] by year and test generation						
	1939	1940	1941	1942	1943	1947	1949
	F_{13}	F_{14}	F_{15}	F_{16}	F_{17}	F_{21}	F_{23}
	Mg.	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Mg.*	*Mg.*
No selection for seed size	42.3	42.3	46.3	48.6	52.5	45.9	50.5
Only largest seeds sown	55.0	55.5	60.0	73.5	61.5	55.2	57.7
Only smallest seeds sown	34.3	21.3	39.1	23.6	36.0	34.6	41.6

[1] Based on samples of 600 kernels.

PERSISTENCE OF HETEROZYGOUS PLANTS

Plants heterozygous for 1 or more of the 4 characters given in table 3 persisted in advanced generations of Composite Cross II. In the

F_{12} generation heterozygous plants comprised 6 percent of the control stock, and 12 percent and 32 percent, respectively, of the small-seed and large-seed separates. Since observed heterozygosity involved only 4 characters, the total heterozygosity was even greater. Ten percent of heterozygous plants persisted in the large-seed separate in the F_{23} generation. Some of the continued segregation no doubt resulted from natural crossing, the influence of which may have been increased by 10 generations of continuous selection for large seed. Some of it apparently had a cytological basis, as is indicated by various types of sterility.

Some heterozygous plants may gain a selective advantage from yield or competitive ability. Such an advantage did not accrue from the heterozygous Vv genotype as constituted in Composite Cross I, however. In this stock the proportion of Vv plants was over half in F_1, only 2 percent in F_5, and 0.2 percent in F_{15}. The same terminal value occurred at Davis, Aberdeen, and Moccasin.

ENVIRONMENT-INDUCED ALBINISM

Linkage with lethal characters is a recognized cause for nonrandom recovery of characters, but losses from conventional lethals are generally confined to the first segregating generations. It therefore seems fitting to call attention to a group of near-lethal seedling color deficients, including flash deficiencies in green color that are recognizable for only a few days but involve up to 40 percent of the population, as well as persistent deficiencies in color that are recognizable even in the early jointing stage of growth. In some years these can be found in all varieties and hybrids grown at Davis, Calif. Only rarely have any stocks shown more of these albinos than has Composite Cross II.

Collins (*3*) reported a simply inherited form of albinism, expressed only when the plants were grown at mean temperatures below 45° F. Its most common expression was a first green leaf, 3 to 6 white or partly white leaves, and normal color in all succeeding leaves. This gene may be one of the group reported herein.

Color-deficient seedlings were observed in abundance during the years 1937, 1942, 1945, and 1949, the more persistent nonlethals comprising from 2 to 8 percent of the total population of Composite Cross II in those years. Some plants of this type actually may sometimes function as lethals, owing to their greater susceptibility to frost, but this is a secondary effect of relatively minor importance. The real problem involves the ultimate impotence of the temporary albino plants in mixed stands (table 7). These randomly chosen paired plants had equal opportunities, except as the environment temporarily slowed the growth rate of one. In effect, the temporary albinos might behave like later seeds sown in a situation in which total yield of the area was not improved by the increase in stand. All progenies from the albino plants (table 7) that matured seed had normal color and growth in 1950.

Pairs similar to those shown in table 7 had been observed in 1937. The progenies of those plants were all normal in 1938 and 1939, and their yields in 1939 were no different from the 1937 normals. These data were compiled to illustrate an extreme case of plant suppression by competition. A character linked with vulnerability to this type of suppression might have little chance to survive.

TABLE 7.—*Examples of extreme selectivity in a single season resulting from low temperature-induced temporary nonlethal seedling albinism in March 1949, at Davis, Calif.*

Variety or cross	Matured tillers and kernels,[1] on plants paired for equality of opportunity when albinism was first expressed									
	Pair 1		Pair 2		Pair 3		Pair 4		Pair 5	
	Normal	Albino	Normal	Albino	Normal	Albino	Normal	Albino	Normal	Albino
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
C. I. 5461 (F_{23})	5-264	2-66	4-219	1-9	5-243	1-0	5-180	1-1	3-123	1-11
Atlas	12-579	1-33	5-270	1-21	5-238	2-75	3-165	1-6	5-330	1-9
Arivat	5-300	1-0	4-186	1-48	5-234	1-9	4-210	3-1	4-210	1-2
Hanna	5-131	1-20	7-156	2-27	11-396	1-14	7-231	1-12	11-352	1-24

[1] First number denotes matured tillers; second number, the number of kernels.

OTHER EXAMPLES OF NONRANDOM RECOVERIES

The common conception that disease-susceptible plants are readily eliminated from mixtures through operation of the principle of survival of the fittest was not confirmed by these experiments. Barley scald (*10, p. 926*) has been considered the most destructive disease to barley in California, yet only 17 resistant progeny were found among 356 progeny randomly chosen from the F_{12} generation plants of Composite Cross II. Of the 28 parents used in making this composite, 3 had resistance (*10*). The recovery, therefore, was less than half of the expectancy, even if scald resistance held no selective advantage. In the F_{23} generation there remained 7 percent of highly scald-susceptible plants with an extreme degree of susceptibility. Disease resistance, therefore, is not necessarily a potent determiner of survival in a mixture. These findings support the previously observed demise of Vaughn and the dominance of Atlas in a mixture despite the superior yield and leaf-disease resistance of Vaughn (*14*).

Much of the progress in breeding small grains in America has come from the production of earlier maturing varieties (*11*). With Composite Cross II, more than 5 percent of the F_3 generation plants headed 5 days earlier than any plants in the F_{11} generation. Thus, there was complete elimination of the earliest recombinations in 8 generations. This trend continued, because in the F_{11} to F_{13} generations the composite was 3 days earlier than Atlas, but in the F_{21} to F_{23} generations the composite was 1 day later than Atlas. This mass expression does not reveal the complete behavior. In the F_{23} generation, 13 percent of the population headed more than 10 days later than Atlas, and only 2 percent of the population was more than 3 days earlier than Atlas. Among the 28 parents, 6 were more than 10 days earlier and 6 more than 10 days later than Atlas.

YIELDS OF COMPOSITE CROSSES

Many investigators have used early-generation yield evaluation of hybrids as an index of the potential value of crosses for later selection. The three Composite Crosses reported in table 8 probably would have been discarded early by that standard. Even later, when 356 random F_{12} selections were taken from Composite Cross II and then gradually eliminated over a 5-year period, not one agronomically desirable selection yielding more than Atlas was recovered. It is clear, therefore, that the initial material was predominantly low-yielding.

Continuous improvement apparently was effected in the three composites by the elapse of time and natural selection (table 8). The

TABLE 8.—*Progressive changes in the yield of three composite crosses and Atlas barley grown at Davis, Calif., 1924–50*

Generation	Test year	Yields per acre				Superior-yielding replicates when paired			
		Composite Cross II	Composite Cross I	Composite Cross III	Atlas barley	Composite Cross II	Composite Cross I	Composite Cross III	Atlas barley
		Bu.	*Bu.*	*Bu.*	*Bu.*	*No.*	*No.*	*No.*	*No.*
F_3–F_4	1937–38	58.3	----	----	86.2	2	----	----	6
F_7–F_8	1933–34	71.3	----	----	83.8	3	----	----	7
F_{11}–F_{14}	1937–40	72.6	----	----	81.7	6	----	----	10
F_{15}–F_{20}	1941–46	75.1	----	----	70.8	13	----	----	10
F_{21}–F_{23}	1947–49	56.8	----	----	49.9	14	----	----	6
F_{24}	1950	51.3	----	----	37.8	10	----	----	0
F_4–F_8	1924–28	----	61.7	----	86.4	----	2	----	9
F_{15}–F_{18}	1938–40	----	82.4	----	78.7	----	7	----	6
F_4–F_7	1933–34	----	----	61.6	90.0	----	----	0	10
F_{10}–F_{13}	1937–40	----	----	68.7	82.4	----	----	7	9

proof for continual improvement in yields of the composites has been built primarily on relationships to the Atlas variety. The possibility that Atlas yields have declined is recognized, but the summary of long-time yields reported by Laude (*9*) suggests that any change that may have occurred is comparatively small. A direct comparison between the F_3 to F_4 and the F_{11} to F_{12} generation yields also was made. The latter group yielded 15 percent more and was superior in 6 of 8 replications.

During the years 1937–45 and 1948–49, three previously mentioned stocks of Composite Cross II were grown in paired tests. During this period the random stocks gave a 4-percent higher yield than did the large-seed separate, and were superior in 8 of the 11 years. The small-seed separate yielded 12 percent less than the random stock and had a better average yield in only 2 of the 11 years. All the stocks showed progressive improvement when compared with Atlas. Thus, despite wide diversity as regards a few characters, similar basic adaptation seemed to dominate in all three stocks of Composite Cross II.

DISCUSSION

Cereal breeders in California have been occupied predominantly with backcross breeding projects for 20 years (*13*). Consequently, there has been no strong urge to exploit the various Composite Crosses for selection material. These crosses have been advanced each year with limited effort, while recognizing the need for a reasonably large population in each generation.

The unequal survival of characters at different locations, the impotence of disease resistance and early-maturity characters, and the tendency for progeny predominantly like the most adapted parents to survive best all point to character associations, rather than specific characters, as the determiners of survival in a mixture. They impose heavy statistical odds against recovery of a truly superior recombination from an early generation selection.

The question might be raised as to whether superiority based on comparative testing is a better measure of "a superior variety" than is survival capacity. The senior writer was not convinced that Vaughn was superior to Atlas, despite the fact that it gave higher yields in 12 of 15 years and showed greater resistance to prevailing diseases (*14*). Atlas practically eliminated Vaughn from a mixture during the same years and remained the favorite with farmers, despite the publicity given to the higher yields for Vaughn. This example is not unique in California or America.

The evidence of cohesive linkage that cannot be resolved to precise descriptions is also very striking. There are many type or appearance characters among the 28 parents used in Composite Cross II that have disappeared as completely as have the black seeds. In this connection, the experiments reported have not established the significance of black seeds, early maturity, smooth awns, or any other character as they individually may affect yield or survival. Either isogenic or backcross-derived lines will be particularly useful for determining these roles more precisely, although even these techniques do not completely eliminate linkages.

Since long-term natural selection within bulk populations recovers associations of characters predominantly from the most adapted parents, it produces essentially the same results as backcross breeding. This perspective of the two breeding methods is important.

SUMMARY AND CONCLUSIONS

Six different Composite Crosses of barley were grown in $\frac{1}{80}$- to $\frac{1}{10}$-acre plots at Davis, Calif., from 6 to 24 generations. Selection within any of these stocks was limited. They were grown primarily to study progressive-population and yield-relationship changes. Natural selection, under conditions approximating normal barley culture, was the chief goal, although selection for two extreme seed sizes and continuous recombination of characters through male-sterile plants also were included among the goals.

Deficient nonrandom survival of four genetically independent factors was observed. The characters that show low survival were (1) the two-rows; (2) the hoods, from which characters inherent yield disadvantages might result; (3) the smooth-awns, for which variable survival was observed; and (4) the black seeds. The rate of disappearance of black seeds was rapid. It could not be explained by a seed-size difference.

Selection for extreme seed sizes, beginning in the F_{11} generation, markedly influenced the proportion and persistence of such characters as two-rows and black seeds. It also revealed a high frequency of heterozygous types in later generations among the two seed-size extremes of the population.

Though scald has been the disease most destructive to barley in California, less than half the normal expectancy of disease-resistant progeny were recovered in the F_{12} generation. Extremely early recombinations were also quickly eliminated from the bulk populations.

Environment-induced seedling albinism, which generally is not lethal and persists for only a relatively short period, retarded the growth of afflicted plants sufficiently to make them poor competitors in a mixed population.

The data developed at Davis from Composite Cross II are supported by data involving Composite Cross I and its parent varieties from eight locations, as developed by H. V. Harlan and associates. Genetic characters, like varieties, do not survive equally in mixtures, nor similarly at different locations. Particularly, at the more selective locations, progenies recovered from prolonged natural selection are predominantly like the few best adapted parents.

Yield data for three Composite Crosses suggest that there is a continuous improvement in their yield level when grown over long periods. This may be extremely important, because most breeders discard their bulk hybrids after they become sufficiently homozygous to give stable selection lines.

This experiment demonstrates conclusively that there is a nonrandom survival of recombination characters in hybrid mixtures. The complete loss of some characters, the impotence of disease-resistance factors, and the general cohesiveness of the populations all suggest that the limitations on recombination into a favorable adaptation complex imposed by linkages are larger than most barley breeders have realized. This suggests that all breeders should employ more backcrossing or grow bulk populations for long terms to insure more complete recovery of proved gene associations.

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FOREWORD

The research on which this report is based was authorized by two projects conducted under the Agricultural Marketing Act of 1946 (RMA, Title II): (1) Effects of New Oilseed and Fats and Oils Processing Techniques on the Industry, Market Outlets, and Returns to Growers; and (2) Analysis of Factors Affecting Consumption of Food Fats, and Analysis of Competition Among Food Fats and Oils.

Mr. Armore, the author, left the Bureau in July 1951, after completing the research and preparing the first draft of this bulletin. Comments and suggestions of various specialists in the Department were considered in making slight modifications in some sections and in condensing and reorganizing several portions of the bulletin.

These revisions were carried out by Richard J. Foote, Assistant Head for Commodity Research. Mr. Foote completely revised and prepared new material for the section headed, "Factors that Affect Prices of Food Fats and Oils Other than Butter and Lard." He redeveloped the analysis of factors affecting the average price of food fats and oils other than butter and lard, demonstrating statistically the price inelasticity of demand for this group of fats and oils. In addition, Mr. Foote prepared Appendix notes 5, 6, and 11.

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END