An Evolutionary Plant Breeding Method[1]

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SYNOPSIS

A new method of plant breeding has been developed from long-term tests with diversely constituted bulk hybrid populations. These were grown in mass under competitive natural selection for 12 to 29 generations. The production gains effected in these populations equaled those from the conventional and more costly breeding methods now in use.

NEW ideas for expanding world food production are needed. A "new" method of plant breeding that is uniquely efficient, and adaptable to the varied skills and facilities at both central and branch experiment stations is proposed. It requires assembly and study of seed stocks with diverse evolutionary origins, recombination by hybridization, the bulking of the F_1 progeny, and subsequent prolonged natural selection for mass sorting of the progeny in successive natural cropping environments. Accumulated results with four different hybrid populations, continued in bulk far beyond the generation requirement for practical homozygosity, all show extreme progress in increasing yield and adaptation by this method. Previously two other populations gave similar results (13).

LITERATURE REVIEW

Bulk hybrids in F_2 to F_7 have been widely used as sources from which to select predominantly homozygous test material. The early work of Florell at this station (3), the extensive work of Harlan *et al.* (8), and the present emphasis on this approach by workers in Iowa (14), illustrate the chronology of experience and use of the bulk method in America.

The proposed extensions grew from the work of Harlan and Martini who pioneered in increasing the genetic diversity of bulked populations (6), and in observing the effects of diverse natural selection environments on a mixture of barley varieties (7). From additional studies on the survival of wheat and barley varieties in mixtures came a suggestion that survival capacity, though sometimes inverse to production capacity in pure stands, had special significance for determining agricultural fitness (11). The growing of 3 different bulk hybrid populations for 18, 24, and 13 generations, respectively, without appreciable exploitive selection and with continuous improvement in their yield while progressively unbalancing the expected ratios of homozygous and heterozygous recombinations associated with certain marker genes, rationalized the proposed method (13).

The method being proposed has been neglected or overlooked by many plant breeders focusing on techniques for improving man's selecting and testing efficiency, rather than on evolutionary fitness as determined by survival. Some of these have recorded improved yields in F_7 or F_8 without recognizing its significance. A few geneticists with more fundamental interests have explored this field, however. The work of Anderson (2) is singularly suggestive in showing that in wild populations correlations induced by plietropy and linkage and augmented by natural selection, are vital in perpetuating favorable character combinations. From viability differences of mutants, Gustafsson concludes that survival under competition is a very important evolutionary factor (4). Stebbins (10) points out that the most rapid evolutionary changes are occurring in plants under crop cultivation environments. Gustafsson further believes that plant breeders can improve yield by choosing lines that interact to increase vegetative or reproductive fitness (5).

MATERIALS AND METHODS

In this paper, yield results with 1 previously reported bulk hybrid population are extended and results with 3 others are introduced. Throughout the experiments, the breeding and test plots were grown independently. The current advances in generation of the bulk hybrid populations were in 1/50 acre plots. Yield tests were from guarded 16-foot rows and 1/50 acre field plots sown usually during November or December. Recent tests have sought average rather than maximum soil fertility and yield levels.

Atlas was a parent in each of the four composite crosses under study. It is a selection from Coast. Coast was introduced during the Spanish mission era about 200 years ago. In 18 years of testing, 1923–43, Atlas held a 9.6% yield advantage over Coast. Atlas 46 is a product of back-cross breeding for scald and mildew resistance (9). During the period 1947–53 its advantage over Atlas averaged 7.7% at Davis in 68 tests, and 4.9% state-wide in 153 tests. Thus in using Atlas 46 as a check, progress by conventional breeding methods is also in focus.

Composite Cross II, C.I. 5461, has been grown in California from the F_2 through F_{20} generations. It evolved from 28 diverse varieties completely intercrossed, giving 378 separate F_1 combinations which were blended (6).

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Composite Cross V, C.I. 6620, resulted from combining 31 varieties in a succession of expanded crossings to give a "complete" recombination (13). The F_2 to F_{15} generations of C.I. 6620 have been grown.

Composite Cross XII, C.I. 6725, combined 26 varieties by a succession of pairings and finally crossing the F_1 plants therefrom with the F_1 of Atlas × Vaughn (13). The addition of this final cross is of special interest because of the wide difference in survival ability of Atlas and Vaughn (11), and the unusual record of an Atlas × Vaughn bulk population which produced the four commercially grown varieties Arivat, Beecher, Glacier, and Gem (1). The F_2 to F_{15} generations of C.I. 6725 have been grown.

Composite Cross XIV, C.I. 7132, combined 9 California adapted parents. This composite contains a male sterile gene which allows continuing gene recombinations through natural crossing concurrent with natural selection (12). Its more persistent heterozygosity was not considered in this paper. Only 12 generations of this cross have been grown.

RESULTS

In assessing the practicability of crop improvement by this inexpensive and easily executed method for sorting of heterogeneous germ plasm by natural selection, the evidence of progressive yield improvement seems most vital. For measuring this progress various comparisons of composite crosses II, V, XII, and XIV in paired tests with Atlas 46 are shown in table 1. The relationships to Atlas 46 and between the composites are shown in fig. 1 also, using no less than 15 tests to constitute a comparison point for developing the yield curves.

Composite Cross II when paired with Atlas 46 did not differ significantly in yield in 129 comparisons during the period 1947–55. In previous tests using Atlas as a standard, a large yield inferiority of the composite in F_2 through F_8 generations was narrowed to near equality in the F_{11} through F_{20} generations (13). During the 18-year period, 1937–55, Atlas or Atlas 46 has been more variable in yield with a coefficient of variability nearly twice as high as for Composite Cross II. This emphasizes a production penalty inherent in pure line uniformity. That present stocks of Composite Cross II are as productive, and perhaps somewhat more productive than Atlas 46 throughout California from November or December sowing, is also suggested by a mean advantage over Atlas 46 of 19% in tests at 3 diverse locations in 1955. In a fourth test, which was spring sown, a characteristic yield deficiency of 7% was observed. This has previously been observed in spring-sown tests at both Davis and Tule Lake, and evidences a particular suitability for our optimum sowing date. The variety Rojo responds similarly.

The viability of all seed generations of Composite Crosses V, XII, and XIV is still good. They have been compared with Atlas 46 and each other as shown in table 1. As in a previous experiment (12), the early hybrid generations yielded less than the check. The later generation showed a marked yield improvement over the early generations and approximate equality with Atlas 46. The evidence for substantial progressive yield improvement from sustained natural selection was conclusive in a shorter time with these crosses than with C.C. II as shown in figure 1. The rigor of selection pressure is indicated by the decline of black seeds in Composite Cross V from 19.5% in F_1 to 5.9% in F_8 and 0.7% in F_{14}. The precise cause for the elimination of black seeds is not known (13).

Breeding Potentials

Since natural selection can produce populations as productive as breeders' improved varieties, a further use appraisal of the populations was made. In 1951 yellow dwarf virus attacked the F_{25} seed production plot of Composite Cross II with great severity. Seven percent of the plants were killed, 38% produced less than 25 seeds per head, and only 27% produced more than 50 seeds per head. This was the first noted impact of this virus on this population, and probably resulted in the greatest differential survival encountered in 25 years. Yellow dwarf reactions and heading dates of the 28 parents and 500 selected

Table 1.—Yields of Composite Crosses II, V, XII, and XIV in various generations in comparison with Atlas 46.

Test years	Generation	Number paired plots	Acre yield in bushels				
			CC II	CC V	CC XII	CC XIV	Atlas 46
1937–38	F_3-F_4	8	58.3	—	—	—	86.2†
1933–34	F_7-F_8	10	71.3	—	—	—	83.8‡
1937–40	F_{11}-F_{14}	16	72.6	—	—	—	81.7†
1941–46	F_{15}-F_{20}	23	75.1	—	—	—	70.8†
1947–50	F_{21}-F_{25}	35	53.0	—	—	—	52.3
1951–55	F_{26}-F_{29}	94	50.8	—	—	—	49.1
1947–54	F_2-F_3	25	—	42.4**	43.4*	—	51.3
1947–55	F_4-F_8	15	—	41.4*	43.4*	—	49.9
1951–52	F_{11}-F_{12}	15	—	50.2	51.8	—	51.6
1953–55	F_{13}-F_{15}	15	—	52.4	54.0	—	54.1
1952–54	F_2	15	—	46.5*	46.8*	—	54.0
1952–54	F_{12}-F_{14}	15	—	54.7***	56.7***	—	54.0
1947–54	F_2	30	—	—	—	56.5*	64.2
1947–50	F_3	30	—	—	—	52.6*	59.5
1947–49	F_4-F_6	30	—	—	—	50.2*	62.6
1950–52	F_7-F_9	15	—	—	—	56.0	53.5
1953–55	F_{10}-F_{12}	15	—	—	—	51.3	54.1

* Significantly lower yielding than Atlas 46 at 5% level, and ** at 1% level.
*** Significantly higher yielding than F_2 for same years at 5% level.
† Yields are for Atlas as previously reported. See literature citation (13).

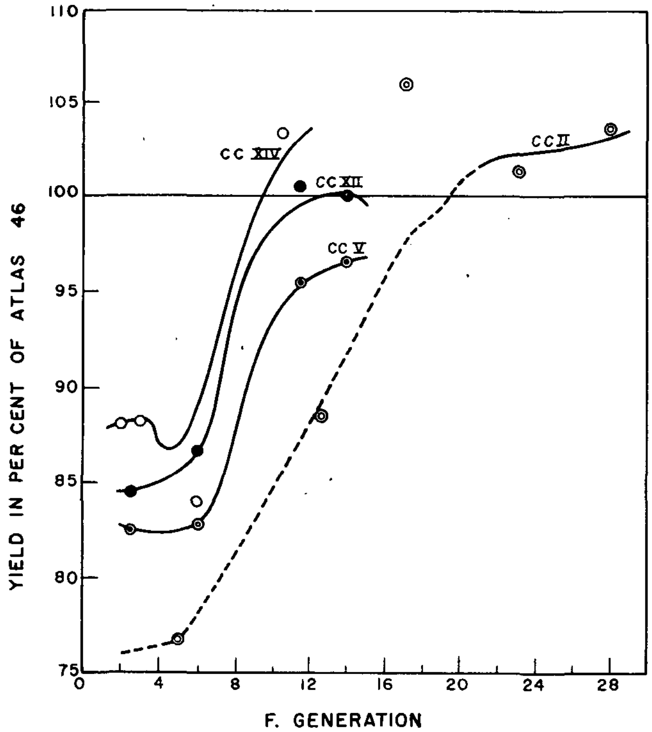

FIG. 1.—Yields of 4 composite crosses compared with each other and Atlas 46 in successive generations.

progenies from the F_{26} generation have been tabulated in table 2. It seems clear that natural selection for yellow dwarf resistance in 1951 favored progeny from the 3 most resistant parents, thus changing the relative frequencies of parental types in the population. Studies of F_{25} vs. F_{26}, and with both bulks and lines selected for extremes of yellow dwarf reaction suggest that while increasing yellow dwarf resistance, yield was slightly reduced. This did not markedly change maturities which continue to average later than presently grown commercial varieties (13). The data in table 2 stress residual diversity and possibilities for further change.

Of particular interest to many breeders is the yielding ability of lines selected from the composites. Sampling has been limited because selection was not a primary interest in the experiment. From 356 F_{12} selections, not one desirable selection yielding more than Atlas was recovered (13). From 50 F_{20} selections screened by 2 years of observation there are 2 promising lines. One (Cal. 1358), in a 7-year advanced nursery test, has outyielded Atlas 46 in each year. It has an average yield advantage of 37% and has averaged 3.5 pounds higher in test weight. It has shown moderate or good resistance to the five principal barley diseases in California. From 66 F_{24} selections first grown in 1951 and selected for contrasts rather than initial yield, 10 have been yield tested for 4 years. From the available yield data it appears that 9 of the 10 will be superior to Atlas 46 in yield. The 3 top yielding selections have a 56% greater average yield than Atlas 46. Better preliminary production records than these are rare. These data and the population curve shown in figure 1 both suggest an ever increasing proportion of superior lines. Figure 1 also shows the very high proportion of poor producing lines in the F_3 to F_7 generations of bulk populations.

Table 2.—Comparative parental differences and residual persistence of this variability for 2 characters among 500 F_{26} progeny.

Class*	Yellow Dwarf reaction		Heading dates	
	Parents	Selections	Parents	Selections
0	0	3	2	3
1	3	91	3	25
2	10	286	6	258
3	11	104	8	188
4	4	16	9	26

* Reaction type to virus, and 5-day intervals for heading.

As shown in figure 1, each succeeding Composite Cross, initially and terminally, gave higher yields. This probably resulted from progressively greater emphasis on parental adaptation. Therefore, these Composite Crosses probably provide a larger diversity of adaptation factors than reside in any collection of adapted varieties. This realization prompted crossing 165 selections from the various Composites in F_{10} to F_{27} to produce Composite Cross XVI, C.I. 10,108, the F_1 of which was grown in 1955.

DISCUSSION AND CONCLUSIONS

The core features of the suggested breeding method are a broadly diversified germ plasm, and a prolonged subjection of the mass of the progeny to competitive natural selection in the area of contemplated use. The prospect of marked progress by competitive sorting of the fittest is challenging because a bulked hybrid population can be advanced through many generations at low cost as compared to conventional and costly early generation line testing techniques. Information available suggests that 15 generations of natural selection seem desirable. Thereafter there can be repeated recourse to three methods of breeding *(1)* continued natural selection with prospects for significant gains in yields to accrue throughout a working lifetime; *(2)* cyclic hybrid recombinations with intervening natural selection to give a kind of recurrent selection; or *(3)* resort to conventional selection and testing (the proportion of well adapted and high yielding lines being a partial function of generation).

Backcross breeding has been perfected and used in California in a way that minimized testing requirements. The evolution-based method now proposed also obtains new varieties at minimum cost and with maximum assurance of adaptability. Significantly, these "new varieties" may be either a superior population, or an outstanding pure line.

The consistently good yields of these advanced generation bulks seem to justify their release for feed production, despite the sharp variance from a "pure line economy" which will result.

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