

2000

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Abstract

Use of adequate effective population size in maize (*Zea mays* L.) recurrent selection programs is important because of random genetic drift and inbreeding depression. The objectives of this study were to (i) evaluate the performance of the BS11 Cycle 0 (C0) and the BS11 Cycle 5 (C5) populations from four S₁-progeny selection programs each with a different effective population size (5, 10, 20, or 30) but with a common selection intensity of 20%, and (ii) compare the additive genetic variance among the C0 and C5 populations. Five cycles of selection were conducted by intermating 5, 10, 20, or 30 lines. One hundred thirty C5 S₁ lines from each of the selected populations (i.e., C5-5, C5-10, C5-20, and C5-30) and 100 C0 S₁ lines were topcrossed to BS11 C0. The resulting half-sib progenies were evaluated at five environments in a replications-within-sets incomplete block design. The four selection programs resulted in significant increases in grain yield, reduced grain moisture, and reduced root and stalk lodging. For yield, the 10-S₁ program showed the highest gain cycle⁻¹ of 0.16 Mg ha⁻¹ followed by the 30-S₁ program with 0.13 Mg ha⁻¹ cycle⁻¹. The 5-S₁ program had a higher gain cycle⁻¹ than the 20-S₁ program. The additive genetic variance for yield did not change significantly. Heritability for yield was highest for C5-20, but no significant differences were observed among populations. These results suggest little to no advantage of using larger effective population sizes to maintain genetic variability for short-term recurrent selection.

Disciplines

Agricultural Science | Agronomy and Crop Sciences | Plant Breeding and Genetics

Comments

This article is published as Guzman, Peter S., and Kendall R. Lamkey. "Effective population size and genetic variability in the BS11 maize population." *Crop science* 40, no. 2 (2000): 338-346. doi: [10.2135/cropsci2000.402338x](https://doi.org/10.2135/cropsci2000.402338x). Posted with permission.

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Effective Population Size and Genetic Variability in the BS11 Maize Population

Peter S. Guzman and Kendall R. Lamkey*

ABSTRACT

Use of adequate effective population size in maize (*Zea mays* L.) recurrent selection programs is important because of random genetic drift and inbreeding depression. The objectives of this study were to (i) evaluate the performance of the BS11 Cycle 0 (C0) and the BS11 Cycle 5 (C5) populations from four S_1 -progeny selection programs each with a different effective population size (5, 10, 20, or 30) but with a common selection intensity of 20%, and (ii) compare the additive genetic variance among the C0 and C5 populations. Five cycles of selection were conducted by intermating 5, 10, 20, or 30 lines. One hundred thirty C5 S_1 lines from each of the selected populations (i.e., C5-5, C5-10, C5-20, and C5-30) and 100 C0 S_1 lines were topcrossed to BS11 C0. The resulting half-sib progenies were evaluated at five environments in a replications-within-sets incomplete block design. The four selection programs resulted in significant increases in grain yield, reduced grain moisture, and reduced root and stalk lodging. For yield, the 10- S_1 program showed the highest gain cycle⁻¹ of 0.16 Mg ha⁻¹ followed by the 30- S_1 program with 0.13 Mg ha⁻¹ cycle⁻¹. The 5- S_1 program had a higher gain cycle⁻¹ than the 20- S_1 program. The additive genetic variance for yield did not change significantly. Heritability for yield was highest for C5-20, but no significant differences were observed among populations. These results suggest little to no advantage of using larger effective population sizes to maintain genetic variability for short-term recurrent selection.

RECURRENT SELECTION contributes greatly to the genetic improvement of maize hybrids in the USA. Recurrent selection in the 'Iowa Stiff Stalk Synthetic' (BSSS) maize population led to the development of widely used maize inbred lines such as B73 and B84 (Hallauer et al., 1983). As a cyclical breeding procedure, recurrent selection is designed to improve population performance and maintain genetic variability for continued selection. Improvement of population performance results from an increase in the frequency of favorable alleles. The increase in the frequency of favorable alleles increases the probability of obtaining inbred lines with superior combining ability.

The number of individuals intermated is the most critical aspect of the intermating phase of recurrent selection programs (Hallauer, 1992). Gain from selection can be increased for any recurrent selection method by increasing selection intensity (Sprague and Eberhart, 1977), which is the ratio of the number of lines selected

for intermating to the number of lines evaluated. For a given number of lines evaluated, the selection intensity increases as the number of lines evaluated increases. Similarly, for a given selection intensity, an increase in the number of lines selected requires an increase in the number of lines evaluated. However, resources for a recurrent selection program usually limit the number of lines evaluated necessitating a trade-off between selection intensity and number of lines intermated. The number of individuals intermated approximates the effective population size, N_e , in recurrent selection programs (Vencovsky, 1978; Labate et al., 1997).

Theoretical studies (Crow and Kimura, 1970) and empirical studies with *Drosophila* and *Tribolium castaneum* (Herbst.) (Kerr and Wright, 1954; Wright and Kerr, 1954; Buri, 1956; Rich et al., 1979) have shown that small population size results in increased genetic uniformity as a consequence of genetic drift. The use of inadequate effective population size in artificial selection programs may result in the loss of genetic variability because of the fixation of alleles caused by genetic drift (Robertson, 1960, 1961; Baker and Curnow, 1969; Rawlings, 1979; Vencovsky, 1978). Fixation may be for either favorable or unfavorable alleles, and unless mutation occurs or germplasm is introduced into the population, genetic variability will not be generated at fixed loci (Hallauer, 1992).

Most of the early studies on the effect of genetic drift on genetic variance assumed a pure additive genetic model. These studies did not consider either intra-allelic or inter-locus interactions. However, some studies (Robertson, 1952; Goodnight, 1987, 1988; Cheverud and Routman, 1996) relaxed the assumption of pure additive gene action and considered non-additive gene action (dominance or epistasis). In the presence of interacting genes, these studies have shown that additive genetic variance could increase with small effective population size or after a population bottleneck.

Weyhrich et al. (1998) evaluated the mean performance of the S_0 populations per se, the S_1 populations per se, and the testcrosses to the C0 after five cycles of S_1 -progeny selection in the BS11 maize population using 20% selection intensity and intermating 5 (5- S_1), 10 (10- S_1), 20 (20- S_1), or 30 (30- S_1) progeny. The S_1 populations per se represent the direct response to S_1 progeny selection. For the S_0 populations per se, Weyhrich et al. (1998) found that the 10- S_1 (0.15 Mg ha⁻¹ cycle⁻¹), 20- S_1 (0.09 Mg ha⁻¹ cycle⁻¹), and 30- S_1 (0.13 Mg ha⁻¹ cycle⁻¹) programs resulted in a significant increase in grain yield

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Abbreviations: BSSS, Iowa Stiff Stalk Synthetic; A × E, additive × environment; GDU, growing degree units.

with no significant difference in the rate of response among methods. There was a significant decrease for grain yield in the 5-S₁ program ($-0.22 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$). In the S₁ populations per se, they reported a significant increase in grain yield for the 10-S₁, 20-S₁, and 30-S₁ programs, but a significant decrease of $-0.11 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$ was reported for the 5-S₁ program. There were significant increases in grain yield, however, for all four programs when the cycles were evaluated in testcrosses with the C0. These results suggest that the lack of progress in the S₀ and S₁ populations per se was due to random genetic drift and that we would expect a loss of genetic variation as a result of recombining only five progeny.

Little information is available concerning the effect of effective population size on genetic variance in plants. Our study was designed in response to the Weyhrich et al. (1998) study to evaluate the effect of population size, under a constant selection intensity, on additive genetic variance. The objectives of our study were to (i) evaluate the performance of the BS11C0 and the BS11C5 populations from four S₁-progeny selection programs each with a different effective population size (5, 10, 20, or 30) but with a common selection intensity of 20%, and (ii) compare the magnitude of additive genetic variance and its interaction with the environment, phenotypic variance, heritability, and phenotypic and additive genetic correlations within the C0 and C5 populations.

MATERIALS AND METHODS

Development of Genetic Materials

BS11 is a genetically broad-based population formed by crossing southern prolific material, Caribbean material, and U.S. Corn-Belt lines (Hallauer, 1967). It was developed by W.L. Brown at Pioneer Hi-Bred International, Inc. and was originally designated as "Pioneer Two-ear Composite." The BS11 maize population was adapted to the central U.S. corn-belt by 10 cycles of mass selection for adaptation and prolificacy.

The number of lines recombined in the study were 5 (fewer than generally used), 10 and 20 (most commonly used), and 30 (greater than normally used). Starting with the BS11 population, five cycles of S₁-progeny selection were conducted by intermating 5, 10, 20, or 30 lines to form a population for the next cycle of selection. The S₁ programs in which 5, 10, 20, or 30 lines were intermated were referred to as 5-S₁, 10-S₁, 20-S₁, and 30-S₁, respectively (Table 1).

Weyhrich et al. (1998) described the sequence of S₁-progeny selection conducted for each program. For 5-S₁, a cycle of selection was initiated by growing the population per se at the winter nursery in Puerto Rico and selfing 25 to 50 plants. Ears were harvested from 25 plants with sufficient seed for testing and that had desirable agronomics. The 25 S₁ lines were evaluated the following season at three locations in Iowa with two replications per location. On the basis of the results of the evaluations, the best S₁ lines were selected and intermated the following season at the winter nursery with their remnant S₁ seeds. The bulk-entry method (Hallauer, 1985) was used to intermate the selected S₁ lines producing the Syn-1 population. Chain-sibbing 300 to 400 Syn-1 plants produced the Syn-2 population. The Syn-2 population was used to initiate the next cycle of S₁-progeny selection.

Table 1. Population name, number of progeny intermated each cycle, number of progeny evaluated each cycle, and the expected level of inbreeding of the five maize populations that were used to estimate additive genetic variance.

Population name	Abbreviation of population	Number intermated each cycle	Number evaluated each cycle	Expected level of inbreeding
BS11C0	C0	–	–	0.00
BS11C5(5-S ₁)	C5-5	5	25	0.38
BS11C5(10-S ₁)	C5-10	10	50	0.22
BS11C5(20-S ₁)	C5-20	20	100	0.12
BS11C5(30-S ₁)	C5-30	30	150	0.08

The selection procedure for the 10-S₁ program was similar to that of 5-S₁, but 50 lines were evaluated and 10 lines were selected for intermating each cycle. For the 20-S₁ program, 20 lines were intermated after evaluating 100 S₁ lines each cycle. Similarly, the 30-S₁ program was conducted by evaluating 150 S₁ lines and intermating the best 30 S₁ lines each cycle. For all four S₁ programs, a constant selection intensity of 20% was maintained. Selection of progenies for intermating from the replicated yield trials was based on an index (Smith et al., 1981) of grain yield, grain moisture at harvest, and resistance to root and stalk lodging. Index selection was used in all programs except for the first two cycles of 5-S₁, 10-S₁, and 30-S₁ where selection was conducted only for grain yield adjusted to 155 g kg⁻¹ grain moisture. The heritabilities used as index weights and the selection differentials for each cycle of selection were given by Weyhrich et al. (1998). The Cycle 5 (C5) population of the 5, 10, 20, and 30 S₁ programs will be referred to as C5-5, C5-10, C5-20, and C5-30, respectively.

In 1993, seeds from the BS11C0 and C5 populations of each S₁ program were planted in the breeding nursery, and plants were randomly selfed to produce S₁ lines. One hundred BS11C0 S₁ lines and 150 S₁ lines for each selected population were produced. In 1994, the S₁ lines were topcrossed to a common tester, BS11C0. Topcrossing was done in isolation plots such that there were four S₁ lines as female rows to two BS11C0 male rows. The S₁ lines were detasseled and ≈ 10 ears from each S₁ line were harvested. Equal quantities of seed were bulked from each ear to produce a half-sib family. One hundred half-sib progenies for BS11C0, and 130 for the C5 of each selected population were produced for a total of 620 half-sib progenies.

Evaluation Procedures and Data Collection

The 620 entries (half-sib progenies) were divided into 10 sets of 62 entries composed of 10 BS11C0 top-crosses and 13 C5 top-crosses of each selected population. The entries were replicated twice, and replications were nested within sets. The half-sib progenies were evaluated in replications-within-sets randomized incomplete block designs at three Iowa locations (Ames, Crawfordsville, and Carroll) in 1995 and 1996. The Crawfordsville location in 1996 was discarded because of severe waterlogging. Each location-year combination was considered as an environment for a total of five environments. A plot consisted of two rows, 5.49 m long with 0.76 m between rows. All plots were over planted by machine and thinned to a uniform stand density of approximately 62 124 plants ha⁻¹ at the five-leaf stage. All yield trials were machine cultivated and/or hand weeded as necessary. Plots were machine harvested without gleaning for dropped ears.

Data collected on plots were machine-harvestable grain yield (Mg ha⁻¹) adjusted to 155 g kg⁻¹ grain moisture (g kg⁻¹) at harvest, final stand (thousands of plants per hectare), root lodging (percentage of plants leaning more than 30° from vertical), stalk lodging (percentage of plants broken at or

below the primary ear node), plant and ear heights (cm), and silk emergence. Plant and ear heights were recorded as the average measurement of five random plants in a plot measured as the distance from the ground to the node of the flag leaf and to the highest ear-bearing node, respectively. Silk emergence was measured as growing degree units (GDU) in °C from planting until 50% of the plants in the plot have emerged silks. GDU were calculated as follows: [(daily maximum temperature + daily minimum temperature)/2] - 10°C, where the minimum and maximum limits for calculation purposes were 10 and 30°C, respectively (Shaw, 1988). Grain yield, grain moisture, stand, plant and ear heights, and root and stalk lodging were recorded at all environments. Silk emergence was recorded at the Ames location only.

Theory

The genetic expectation of the mean of the C0 × C0 topcrosses for a one-locus-two-allele model is $\Sigma(2p - 1)a + 2 \Sigma p(1 - p)d$, where p is the frequency of the favorable allele, a is the average of the homozygote values, and d is the deviation of the heterozygote from the mid-homozygote value. The genetic expectation of the mean for a C5 topcross population is $\Sigma(2p - 1)a + 2 \Sigma p(1 - p)d + 5(\Sigma \Delta p a + \Sigma \Delta p(1 - 2p)d)$, where Δp is the change in the frequency of the favorable allele. The expectation of the C5 topcross mean is a function of Δp , which varies among the selected populations. When Δp is zero, then the expectation equals that of the C0 × C0 topcrosses implying the ineffectiveness of selection.

The genetic expectation of the variance among the half-sib progenies from each of the four selected populations is complicated by the fact that the C5-5, C5-10, C5-20, and C5-30, which were used as females in the topcross, have presumably undergone changes in allele frequency due to selection and drift, whereas the male in the topcross is the unselected C0 population. For C0, the progeny resulting from the topcross are simply half-sib families.

The genetic expectation of the variance among half-sib families can be derived by modifying the genetic variance among testcross progeny, $V(TC) = 1/2p(1 - 2p)[a + (1 - 2r)d]^2$, where p is the frequency of the favorable allele in the population being tested and r is the frequency of the favorable allele in the tester. Because our tester population was the original population that selection was initiated in $r = p$ and we can substitute $p + \Delta p$ for p to account for changes in allele frequency due to selection and drift. Making these substitutions and rearranging we find that the variance among half-sibs in our study can be expressed as

$$\begin{aligned} Cov(HS) = & \frac{1}{2}[p(1 - p) + \Delta p(1 - 2p) - \Delta p^2][a \\ & + (1 - 2p)d]^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{2}[\Delta p(1 - 2p) \\ & - \Delta p^2][a + (1 - 2p)d]^2 \end{aligned}$$

When $\Delta p = 0$, this equation reduces to the variance among intrapopulation half-sib families as it should for the C0 topcrosses.

Statistical Analysis

The analysis of variance for each trait was done by pooling over sets and combining across environments with all effects in the model considered random. The sum of squares of genotypes, genotype × environment, and pooled error were partitioned into sources of variation due to within and among

populations. The among population sums of squares was further partitioned into all possible contrasts among the five population means. Contrast within sets mean squares were tested for significance using the corresponding interaction with environment mean squares. Within-population error mean squares and among-population error mean squares were used to test the significance of the within-population by environment and among populations by environment mean squares, respectively. The within- and among-population mean squares were tested for significance using the appropriate interaction mean squares.

The mean squares calculated from the combined analysis of variance were translated into appropriate genetic components of variance. The within-population variance equals the covariance of half-sibs with the genetic expectation given in the theory section. Approximate 90% confidence intervals were calculated for the additive genetic, additive × environment (A × E), and phenotypic variance estimates by the procedures of Burdick and Graybill (1992). Heritability estimates and their exact 90% confidence intervals (Knapp and Bridges, 1987) were estimated on a half-sib progeny-mean basis. Variance components and heritability estimates were regarded as significantly different from zero if their confidence intervals did not bracket zero. Differences between populations for estimates of variance components and heritability were declared significant if their confidence intervals did not overlap. Additive genetic and phenotypic correlations among traits within populations were calculated as additive or phenotypic covariance estimates divided by the square root of the product of the additive variance or the phenotypic variance estimates of two traits, respectively (Mode and Robinson, 1959).

RESULTS AND DISCUSSION

Means

The environmental means for grain yield ranged from 6.29 (Ames, 1995) to 4.49 Mg ha⁻¹ (Carroll, 1995). The mean and coefficient of variation for grain yield combined across environments were 5.67 Mg ha⁻¹ and 14.5%, respectively. Experiments at Carroll in 1995 and 1996 experienced severe stalk lodging. Silks emerged 48.3 GDU earlier in 1995 compared with 1996.

There were significant differences between the means of the C0 and C5 populations for all traits (data not shown). Mean grain yield averaged across environments ranged from 5.18 (C0) to 5.96 Mg ha⁻¹ (C5-10) (Table 2, Fig. 1). The 10-S₁ program showed the greatest rate of improvement (0.16 Mg ha⁻¹ cycle⁻¹) with the 30-S₁ program producing the second greatest rate of improvement for grain yield (0.13 Mg ha⁻¹ cycle⁻¹). Grain moisture ranged from 232 (C5-10 and C5-20) to 240 g kg⁻¹ (C0). The 10-S₁ and 20-S₁ programs showed the greatest reduction in grain moisture (2 g kg⁻¹ cycle⁻¹). Resistance to root and stalk lodging traits improved significantly for all S₁ selection programs. Root lodging ranged from 0.3 (C5-20) to 2.6% (C0), and stalk lodging ranged from 12.5 (C5-20) to 17.3% (C0). The reduction in root (0.8% cycle⁻¹) and stalk lodging (1.6% cycle⁻¹) was greatest in the 20-S₁ program. Rates of improvement for stalk lodging were similar for all selection programs ranging from 1.2 (5-S₁) to 1.6 (20-S₁) % cycle⁻¹. The C5-5 population had the tallest plant and ear heights while the C5-20 population was the shortest. The num-

ber of GDU required for silk emergence decreased significantly in all S₁ programs. The C5-5 population had a significantly later emerging silks than the other selected populations.

The testcrosses to the C0 do not represent the direct response to S₁ selection, but are a measure of the response to selection in the absence of genetic drift (Smith, 1983). Response per cycle for grain yield was largest for the 10-S₁ program, and the selection response for the 5-S₁ program was comparable to the 20-S₁ and 30-S₁ programs. Response per cycle for grain moisture, root lodging, and stalk lodging for each S₁ program was calculated on the basis of the number of cycles of selection conducted on those traits. For grain moisture and stalk lodging, the best response was obtained in the 20-S₁ program while the 10-S₁ and the 30-S₁ programs had a more favorable response than the 5-S₁ program. The 5-S₁, 10-S₁, and 30-S₁ programs gave comparable responses for root lodging. The selection programs for increased grain yield, reduced grain moisture, and reduced root and stalk lodging also resulted in significant changes in other traits. The number of GDU required to reach mid-silk decreased significantly in all four S₁ programs. The three larger effective population size programs showed a greater reduction in plant and ear height than the 5-S₁ program.

Our results agree with those of Weyhrich et al. (1998) for the testcrosses to the C0 in which all S₁ programs showed a significant increase in grain yield. Although they found greater response for grain yield in the 30-S₁ program, the 5-S₁ and 20-S₁ programs had comparable responses, which was consistent with our findings. The difference between the responses of the S₀ and S₁ populations per se and the crosses to the C0 for the 5-S₁ program in the study of Weyhrich et al. (1998) is evidence of genetic drift. Despite evidence of substantial inbreeding depression due to genetic drift, genetic progress for grain yield has been made in the 5-S₁ program as indicated by the crosses to the C0.

Our data support the conclusion of Weyhrich et al. (1998) that intermating an additional 10 or 20 progenies does not contribute enough favorable alleles to the population to affect short-term selection response. Weyhrich et al. (1998) suggested that response could be increased by increasing selection intensity for a given population size. The results of our study also agree with the conclusions of Baker and Curnow (1969) and of Brim and Burton (1979). Baker and Curnow (1969) showed that there is little to be gained in going beyond an effective population size of 16 when the issue of interest is the progress to be realized in a reasonable number of generations. Brim and Burton (1979) concluded that reduced effective population size and number of lines tested per cycle had little effect on progress. For the populations used in their study, Brim and Burton (1979) inferred that the use of larger effective population size over the short term was unwarranted. On the other hand, Frankham et al. (1968) found that greater responses to selection were obtained with larger effective population sizes at the same selection intensity. The differences in results could be attributed to the number of cycles to which the response was evaluated (Weyhrich

Table 2. Mean, error variance ($\hat{\sigma}^2$) and coefficient of variation (CV) for yield and other agronomic traits of S₁ lines from the C0 and the C5 each selected maize population topcrossed to the C0 population combined across five environments.

Trait	Topcross population	Mean ± S.E.		CV
		Mean ± S.E.	($\hat{\sigma}^2$) ± S.E.	
				%
Grain yield (Mg ha ⁻¹)	C0	5.18 ± 0.02	0.47 ± 0.03	13.2
	C5-5	5.74 ± 0.02	0.46 ± 0.03	11.8
	C5-10	5.96 ± 0.02	0.49 ± 0.03	11.8
	C5-20	5.66 ± 0.02	0.49 ± 0.03	12.4
	C5-30	5.81 ± 0.02	0.47 ± 0.03	11.8
Grain moisture (g kg ⁻¹)	C0	240 ± 0.41	168.34 ± 10.14	5.4
	C5-5	236 ± 0.32	134.96 ± 7.79	4.9
	C5-10	232 ± 0.32	132.64 ± 7.65	4.9
	C5-20	232 ± 0.32	129.19 ± 7.45	4.9
	C5-30	233 ± 0.31	124.78 ± 7.19	4.8
Root lodging (%)	C0	2.6 ± 0.11	12.30 ± 0.82	136.9
	C5-5	1.1 ± 0.06	5.30 ± 0.31	212.4
	C5-10	1.0 ± 0.06	4.10 ± 0.24	203.8
	C5-20	0.3 ± 0.02	0.70 ± 0.04	297.7
	C5-30	1.1 ± 0.06	4.70 ± 0.27	195.8
Stalk lodging (%)	C0	17.3 ± 0.22	46.80 ± 3.11	39.6
	C5-5	13.8 ± 0.15	30.90 ± 1.78	40.3
	C5-10	13.2 ± 0.15	29.30 ± 1.69	41.1
	C5-20	12.5 ± 0.16	33.20 ± 1.91	46.1
	C5-30	13.3 ± 0.16	33.30 ± 1.92	43.5
Plant height (cm)	C0	234 ± 0.32	101.70 ± 6.76	4.3
	C5-5	237 ± 0.27	97.40 ± 5.61	4.2
	C5-10	226 ± 0.29	116.90 ± 6.74	4.8
	C5-20	220 ± 0.28	99.10 ± 5.71	4.5
	C5-30	226 ± 0.27	98.30 ± 5.67	4.4
Ear height (cm)	C0	121 ± 0.29	85.50 ± 5.69	7.7
	C5-5	121 ± 0.26	86.40 ± 4.98	7.7
	C5-10	111 ± 0.25	83.10 ± 4.79	8.2
	C5-20	107 ± 0.25	78.80 ± 4.54	8.3
	C5-30	111 ± 0.25	81.20 ± 4.68	8.1
Silk emergence [†] (GDU °C)	C0	878 ± 0.70	195.50 ± 20.49	1.6
	C5-5	869 ± 0.54	154.60 ± 14.05	1.4
	C5-10	852 ± 0.61	196.60 ± 17.87	1.6
	C5-20	843 ± 0.62	196.90 ± 17.90	1.7
	C5-30	851 ± 0.63	206.00 ± 18.73	1.7

[†] Evaluated at two environments.

et al., 1998). Frankham et al. (1968) evaluated response over 12 cycles whereas in our study and that of Weyhrich et al. (1998) response was observed for only five cycles.

Variance, Heritability, and Correlation Estimates

All variance and heritability estimates for grain yield were significantly different from zero except for the A × E variance of the C5-20 population (Table 3). The additive genetic variance estimates for grain yield ranked C5-5 > C5-20 > C0 > C5-30 > C5-10; however, differences among populations were not significant. The A × E variance estimates were less than the corresponding additive genetic variance estimates in the selected populations. The A × E variance estimate for C5-20 was significantly less than for the C0 population. Phenotypic variance estimates for grain yield were not significantly different among populations. Heritability estimates ranked C5-20 > C5-5 > C5-30 > C0 > C5-10, but the differences among the populations were not significant.

The variance and heritability estimates for grain moisture were significantly different from zero for all populations and ranked C0 > C5-20 > C5-10 > C5-30 > C5-5. The additive genetic variance of the C0 population was significantly different from C5-5 but not from the other

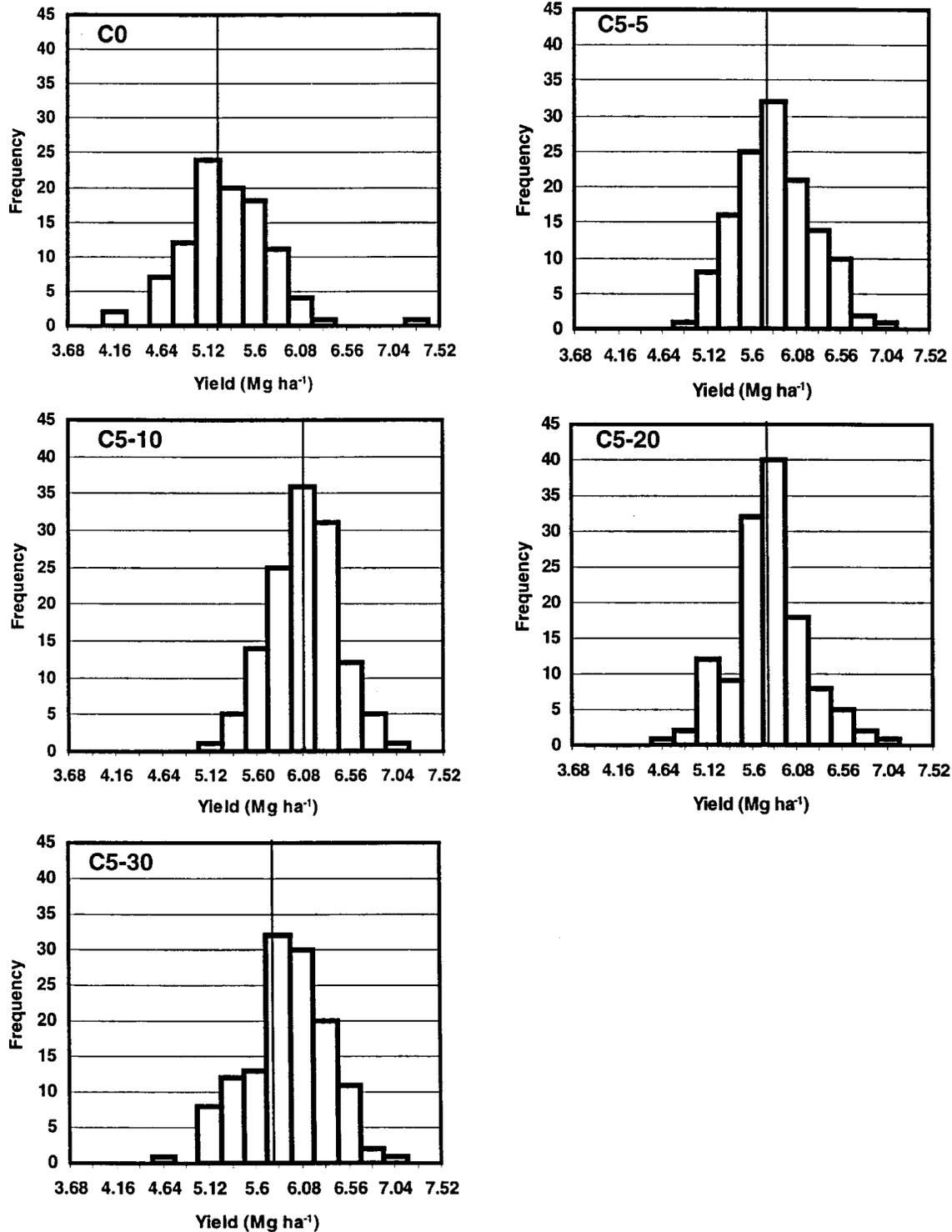


Fig. 1. Frequency distribution for grain yield of S₁ lines from the C0 and C5 of each selected maize population topcrossed to the C0. Distances between class intervals are one-half the phenotypic standard deviation of the C0 S₁ topcross population. Vertical lines represent the population means.

selected populations. The additive genetic variance for C5-5 was significantly less than the estimate for C5-10 and C5-20, but not for C5-30. The additive genetic variance and heritability estimate of the C5-20 population was not significantly different from zero for root

lodging. The additive genetic variance estimate of the C0 population was significantly greater than the selected populations for root lodging. All variance and heritability estimates were significantly different from zero for stalk lodging, except for the A × E variance component

Table 3. Estimates of additive variance ($\hat{\sigma}_A^2$), additive \times environment variance ($\hat{\sigma}_{AE}^2$), phenotypic variance ($\hat{\sigma}_P^2$), and heritability (\hat{h}^2) for yield and other agronomic traits of S_1 progenies from the C0 and the C5 of each selected maize population topcrossed to the C0 population evaluated at five environments.

Trait	Topcross population	$\hat{\sigma}_A^2$	Confidence limits†		$\hat{\sigma}_{AE}^2$	Confidence limits†		$\hat{\sigma}_P^2$	Confidence limits†		\hat{h}^2	Confidence limits‡	
			LL	UL		LL	UL		LL	UL		LL	UL
Grain yield§ (Mg ha ⁻¹)	C0	0.3960	0.2507	0.6047	0.5093	0.3153	0.7239	0.1710	0.1200	0.2572	0.58	0.45	0.68
	C5-5	0.4665	0.3371	0.6448	0.2322	0.0855	0.3870	0.1743	0.1273	0.2482	0.67	0.58	0.74
	C5-10	0.3002	0.2000	0.4370	0.1751	0.0234	0.3333	0.1330	0.0971	0.1894	0.56	0.45	0.66
	C5-20	0.4629	0.3366	0.6373	0.1119	-0.0357	0.2641	0.1705	0.1245	0.2427	0.68	0.60	0.75
	C5-30	0.3904	0.2700	0.5556	0.3307	0.1749	0.4974	0.1610	0.1175	0.2292	0.61	0.51	0.69
Grain moisture (g kg ⁻¹)	C0	703.93	539.65	945.83	146.24	79.45	219.22	200.13	140.44	300.92	0.88	0.84	0.91
	C5-5	367.19	285.69	480.64	123.47	76.47	174.35	111.47	81.39	158.72	0.82	0.78	0.86
	C5-10	486.57	382.50	631.61	153.85	105.12	207.21	142.60	104.12	203.04	0.85	0.82	0.89
	C5-20	580.03	460.94	746.18	110.40	66.00	158.31	163.45	119.34	232.73	0.89	0.86	0.91
	C5-30	452.08	355.00	587.36	149.90	103.65	200.65	132.99	97.11	189.37	0.85	0.81	0.88
Root lodging (%)	C0	30.45	22.42	42.22	17.46	11.98	23.61	9.71	6.82	14.61	0.78	0.72	0.84
	C5-5	1.86	1.03	2.98	1.79	0.17	3.47	1.08	0.79	1.54	0.43	0.28	0.56
	C5-10	0.86	0.32	1.58	1.29	0.05	2.58	0.69	0.50	0.98	0.31	0.14	0.46
	C5-20	0.05	-0.03	0.14	0.30	0.09	0.52	0.09	0.07	0.13	0.12	-0.10	0.31
	C5-30	2.02	1.19	3.15	2.37	0.89	3.94	1.09	0.80	1.55	0.46	0.33	0.58
Stalk lodging (%)	C0	61.41	43.42	87.63	31.35	13.56	50.53	21.60	15.16	32.48	0.71	0.62	0.78
	C5-5	35.13	25.55	48.35	21.13	10.91	32.05	12.93	9.44	18.41	0.68	0.60	0.75
	C5-10	24.51	16.79	35.09	24.87	14.82	35.72	10.30	7.52	14.67	0.59	0.49	0.68
	C5-20	24.76	17.40	34.88	7.12	-2.83	17.37	9.87	7.21	14.05	0.63	0.53	0.71
	C5-30	36.93	26.80	50.90	22.06	11.11	33.75	13.66	9.98	19.45	0.68	0.59	0.75
Plant height (cm)	C0	347.89	267.30	466.57	21.23	-13.92	57.56	98.20	68.91	147.66	0.89	0.85	0.91
	C5-5	138.03	105.52	183.18	1.39	-26.66	29.65	44.32	32.36	63.10	0.78	0.72	0.83
	C5-10	258.03	202.16	335.86	6.15	-27.77	40.48	76.51	55.86	108.94	0.84	0.80	0.88
	C5-20	275.82	217.87	356.61	11.91	-17.21	41.59	79.46	58.02	113.14	0.87	0.83	0.90
	C5-30	387.26	309.28	496.10	8.96	-19.76	38.16	107.09	78.20	152.49	0.90	0.88	0.93
Ear height (cm)	C0	305.82	235.13	409.93	22.82	-7.09	53.93	86.15	60.46	129.54	0.89	0.85	0.92
	C5-5	120.95	92.68	160.22	-6.58	-31.07	17.82	38.55	28.15	54.89	0.78	0.73	0.83
	C5-10	141.60	109.49	186.27	3.26	-20.78	27.54	43.87	32.03	62.47	0.81	0.76	0.85
	C5-20	198.48	156.19	257.42	9.16	-13.96	32.73	57.95	42.32	82.52	0.86	0.82	0.89
	C5-30	204.21	160.81	264.70	6.19	-17.46	30.19	59.48	42.43	84.69	0.86	0.82	0.89
Silk emergence¶ (GDU)	C0	1890.81	1473.43	2504.50	-273.80	-699.13	-11.72	507.89	356.42	763.69	0.93	0.90	0.95
	C5-5	936.31	721.46	1229.80	300.00	65.35	589.72	287.74	210.10	409.71	0.81	0.75	0.86
	C5-10	1140.22	897.98	1474.81	-109.97	-347.98	145.98	328.72	240.02	468.06	0.87	0.82	0.90
	C5-20	1005.95	778.51	1317.35	94.58	-165.65	396.27	305.43	223.02	434.90	0.82	0.76	0.87
	C5-30	1662.83	1319.90	2138.18	2.18	-258.93	296.03	467.32	341.22	665.41	0.89	0.85	0.92

† Approximate 90% confidence interval.
 ‡ Exact 90% confidence interval.
 § Evaluated at two environments.

of the C5-20 population. The additive genetic variance estimate of the C0 population was significantly greater than the estimates for the C5-10 and C5-20 populations. There were no differences in estimates of additive variance among selected populations

The additive genetic variance, phenotypic variance, and heritability estimates were significantly different from zero for all populations for plant and ear height. Estimates of A \times E variance were not significantly different from zero for either trait. For plant height, additive genetic variance estimates among C0, C5-10, C5-20, and C5-30 were not significantly different, but all were significantly greater than C5-5. Additive genetic variance estimates for the C5-5 and C5-10 population were significantly smaller than the C0 estimate. The additive genetic variance, phenotypic variance, and heritability estimates for the number of GDU required to reach mid-silk were significantly different from zero in all populations. Except for the C5-5 population, all estimates of A \times E variance were nonsignificant. The additive genetic variance estimate of the C0 population was not significantly different from either C5-10 or C5-30 but was significantly greater than the estimates for the C5-5 and C5-20 populations.

Phenotypic correlations of grain yield with other traits ranged from -0.38 to 0.42 (Table 4). Among the selected populations, a significant negative phenotypic correlation of grain yield with stalk lodging was observed in C5-10 and with dropped ears for C5-5. A significant positive phenotypic correlation of grain yield with plant height was observed in all selected populations except in the C5-5 population. Grain moisture had significant positive phenotypic correlation with silk emergence in all populations. A significant phenotypic correlation of stalk lodging with ear height was observed in the selected populations. There were significant positive phenotypic correlations between silk emergence and plant and ear height in all populations. There were no clear trends in the phenotypic correlations that could be attributed to selection. Positive additive genetic correlations were observed in all populations between grain moisture and root lodging, root and stalk lodging, and between silk emergence and grain moisture. Negative additive genetic correlations between stalk lodging and grain yield as well as between stalk lodging and grain moisture were observed in all populations. There was no trend observed among the selected populations for additive genetic correlation between any two traits.

Table 4. Phenotypic (above diagonal) and additive genetic (below diagonal) correlations among eight traits of S₁ progenies from the C0 and the C5 each selected maize population topcrossed to the C0 population evaluated at five environments.

Trait	Topcross population	Grain yield	Grain moisture	Root lodging	Stalk lodging	Plant height	Ear height	Silk emergence†
Grain yield (Mg ha ⁻¹)	C0		0.02	0.07	-0.28*	0.18	0.10	-0.17
	C5-5		-0.18	0.03	-0.05	-0.16	-0.13	-0.36**
	C5-10		0.20	0.01	-0.38**	0.32**	0.17	0.06
	C5-20		0.18	-0.09	-0.16	0.42**	0.36**	0.08
	C5-30		0.19	0.04	-0.21	0.30**	0.10	-0.13
Grain moisture (g kg ⁻¹)	C0	0.07		0.11	-0.33**	0.21	0.09	0.34**
	C5-5	-0.21		0.05	-0.16	0.22*	0.18	0.34**
	C5-10	0.33		0.02	-0.23*	0.08	0.14	0.36**
	C5-20	0.24		0.18	-0.13	0.27*	0.20	0.32**
	C5-30	0.28		0.05	-0.22*	0.39**	0.31*	0.54**
Root lodging (%)	C0	0.11	0.13		0.18	0.28*	0.24*	0.07
	C5-5	0.06	0.07		0.19	0.14	0.26*	0.06
	C5-10	0.05	0.04		0.07	0.33**	0.35**	0.18
	C5-20	-0.30	0.50		0.04	0.08	0.07	0.04
	C5-30	0.03	0.07		0.05	0.15	0.20	-0.02
Stalk lodging (%)	C0	-0.40	-0.43	0.27		-0.03	0.07	0.01
	C5-5	-0.01	-0.20	0.42		-0.02	0.22*	-0.12
	C5-10	-0.58	-0.33	0.20		0.07	0.29*	0.02
	C5-20	-0.15	-0.18	0.05		0.10	0.26*	0.00
	C5-30	-0.22	-0.31	0.10		0.00	0.26*	0.02
Plant height (cm)	C0	0.19	0.25	0.32	-0.06		0.83**	0.35**
	C5-5	-0.25	0.26	0.23	-0.05		0.80**	0.35**
	C5-10	0.40	0.10	0.65	0.04		0.82**	0.44**
	C5-20	0.51	0.30	0.23	0.08		0.85**	0.39**
	C5-30	0.37	0.45	0.25	-0.01		0.83**	0.37**
Ear height (cm)	C0	0.10	0.11	0.28	0.05	0.85		0.26*
	C5-5	-0.18	0.23	0.44	0.27	0.84		0.27*
	C5-10	0.18	0.17	0.67	0.34	0.86		0.38**
	C5-20	0.45	0.22	0.21	0.31	0.87		0.31**
	C5-30	0.09	0.38	0.33	0.33	0.85		0.32**
Silk emergence† (GDU)	C0	-0.22	0.37	0.08	0.01	0.39	0.29	
	C5-5	-0.47	0.40	0.10	-0.16	0.45	0.33	
	C5-10	0.10	0.42	0.38	0.02	0.51	0.45	
	C5-20	0.12	0.36	0.10	-0.01	0.46	0.37	
	C5-30	-0.17	0.61	-0.03	0.02	0.40	0.36	

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† Evaluated at two environments.

The design of our study allowed us to determine the magnitude of additive genetic variance after five cycles of S₁-progeny selection using four effective population sizes but with a constant selection intensity. There has been interest in determining the number of lines to intermate in maize recurrent selection programs because of the loss of genetic variance and inbreeding depression resulting from small effective population sizes. The loss of favorable alleles limits the gain that can be attained by selection. Smith (1983), Keeratinijakal and Lamkey (1993), and Holthaus and Lamkey (1995) underscored the importance of genetic drift on the response of the population per se to recurrent selection. Nonresponsiveness or lack of observed gain of the population per se to recurrent selection was generally attributed to inbreeding depression associated with genetic drift. Changing to larger effective population sizes, however, would reduce additional allelic frequency drift in future cycles of selection.

Any progeny selection method could have been used to evaluate the impact of effective population size. However, S₁-progeny selection offers the simplest approach because testcrosses are not needed for evaluation and it requires one season less than S₂-progeny selection. The use of testcrosses by half-sib and full-sib recurrent selection methods requires additional resources. We evaluated topcrosses of the C0 and C5 populations to

BS11C0 to provide an estimate of the additive genetic variance unconfounded by dominance variance. In the absence of additive × additive epistatic variance, the genetic variance among half-sibs is entirely attributable to the additive genetic variance. Thus, topcrossing to the C0 gives a direct estimate of the additive genetic variance. The inclusion of the C0 × C0 topcross also enabled us to observe the change in additive genetic variance from C0 to C5.

The within-population sources of variation suggested that significant genetic variation was present in each selected population for all traits except for root lodging in the C5-20 population. Significant genetic variation implies that improvement of the traits is still possible in those populations. Interestingly, additive genetic variance did not decrease for grain yield after selection. This was contrary to the results of Reeder et al. (1987) who observed a decrease in additive genetic variance and dominance variance for grain yield in BS11 after 6 cycles of reciprocal full-sib selection with BS10. Holthaus and Lamkey (1995) also found a decrease in the additive genetic variance for grain yield after 11 cycles of reciprocal recurrent selection in the BSSS maize population and after 6 cycles of S₂ progeny selection in the BS13 maize population. Labate et al. (1997) found a decrease in genetic variation at molecular marker loci within BSSS(R) and BSCB1(R) after 12 cycles of recip-

rocal recurrent selection. The discrepancy between our results and those of Reeder et al. (1987), Holthaus and Lamkey (1995), and Labate et al. (1997) may be due to the number of cycles of selection completed.

We found that additive genetic variance for grain yield did not decrease in the 5- S_1 program after five cycles of selection contrary to the evidence from Weyhrich et al. (1998) for inbreeding depression caused by genetic drift. After five cycles of selection, the expected level of inbreeding in the 5- S_1 program was five times greater than the 30- S_1 program (Table 1). With this magnitude of inbreeding, additive genetic variance should have decreased significantly in the smaller effective population size programs, particularly in the 5- S_1 program, according to the classical theory of genetic drift (Crow and Kimura, 1970). Theoretical studies have shown that genetic variance decreases with small population size or after a "population bottleneck" due to genetic drift. Genetic drift results in fixation of alleles, which is the basis of genetic uniformity. Bryant et al. (1986), however, emphasized that such results apply only to single or independent loci with additive genetic effects. A population bottleneck may not decrease additive genetic variance if the individual effects of alleles do not operate in a purely additive manner (Bryant and Meffert, 1993). The classical model of genetic drift does not consider either intra-allelic interactions (dominance) or inter-locus interactions (epistasis). Robertson (1952) was the first to discover that genetic variation due to recessive alleles may increase temporarily because of inbreeding. Cockerham and Tachida (1988), Tachida and Cockerham (1989), and Jiang and Cockerham (1990) theoretically demonstrated that additive genetic variance can increase after a population bottleneck when there is dominance but no epistasis. The contribution of epistasis to the increase in additive genetic variance following a population bottleneck was also theoretically shown by Cockerham and Tachida (1988), Goodnight (1987, 1988), and Cheverud and Routman (1996). The additive \times additive epistatic variance is transformed into additive genetic variance following a founder event (Goodnight, 1987, 1988). Empirical results of Bryant et al. (1986), and Bryant and Meffert (1993) support the theoretical expectations of increase in additive genetic variance with small population size. Hence, the comparable magnitude of the additive genetic variance estimates among the selected populations for grain yield, grain moisture, and root and stalk lodging in our study may be due to the conversion of non-additive genetic variance into additive genetic variance in the selection programs with small effective population size. However, Cheverud and Routman (1996) noted that there is a limit to the increase in additive genetic variance such that after the maximum limit is reached, it will decrease dramatically in the smaller population because of fixation. The loss of additive genetic variance due to fixation would also occur earlier for populations with smaller sizes (Cheverud and Routman, 1996). Therefore, the increase in additive genetic variance with small effective population size is likely to occur only with short-term selection.

Another plausible explanation for the increase in ad-

divitive genetic variance for grain yield in the 5- S_1 program is that favorable alleles may be at very low frequencies initially in the BS11C0. If that is the case, then the additive genetic variance should increase regardless of the effective population size unless selection is so ineffective that genetic drift is the predominant force altering gene frequency. For plant and ear heights, although the additive genetic variance estimates among C5-10, C5-20, and C5-30 were not significantly different, the estimate of C5-30 was significantly greater than the C5-5. Similarly for the number of GDU required to reach mid-silk, C5-30 was significantly greater than C5-5, but there were no significant differences among C5-5, C5-10, and C5-20. For these traits, there may not be significant transformation of non-additive genetic variance to additive genetic variance due to limited intra or inter-allelic interactions for these traits. The strength of selection for those traits is also probably not as strong as for the main traits.

On the basis of the results of our study, we conclude that the use of smaller effective population size would not compromise genetic progress in a short-term maize breeding program. Genetic drift may not necessarily result in an immediate and drastic decrease in genetic variance. The results of our study suggest little to no advantage of using a larger effective population size to maintain genetic variability for short-term recurrent selection. It should be realized, however, that the use of smaller effective population sizes will lead to more variation in the response to selection (Falconer and Mackay, 1996, p. 208-211).

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Genetic and Agronomic Evaluation of *wp-m* in Soybean

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ABSTRACT

Transposable element systems have been proposed to explain instability in floral pigmentation of several plant species, including soybean [*Glycine max* (L.) Merr.]. Soybean lines with chimeric (purple and pink sectored) flowers are hypothesized to contain *wp-m*, an active transposable element that is able to excise from the *wp* locus during morphological development. The objectives of this research were (i) to determine the inheritance of the chimeric flower phenotype when crossed to stable pink or purple flowered revertant lines and (ii) to determine the effect of *wp* on agronomic traits in stable flowered lines derived from *wp-m*. Chimeric flowers crossed to pink flowered revertant (*wp**) lines produced four F_2 populations with unusual segregation ratios of 52 pink, three purple, and two chimeric flowered plants. Crossing chimeric flowers to revertant purple flowered (*Wp**) lines resulted in F_2 populations that did not have the chimeric flower phenotype evident. In the agronomic evaluations, stable *wp** lines were later in maturity and averaged 4 g kg⁻¹ higher in protein content and 3 g kg⁻¹ lower in oil content than *Wp** lines. The data suggest *wp* acts in a pleiotropic manner to influence protein synthesis, as purple flowered revertant lines from a pink flower source had lower protein content than sister lines with *wp**. Pink flowered lines derived from a purple flower source had higher levels of protein than sister lines with *Wp**. The influence of *wp* on the anthocyanin pathway, plant morphology, and protein accumulation is a unique phenomenon that has not been reported in other plant species.

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Published in *Crop Sci.* 40:346-351 (2000).

TRANSPOSABLE ELEMENT SYSTEMS have been well characterized in maize (*Zea mays* L.) since their initial discovery by Barbara McClintock in 1944 (Peterson, 1987; Fedoroff, 1988; Vodkin, 1989). A transposable element in *Antirrhinum majus* is one of the few systems in a plant species other than maize that has been characterized at the genetic and molecular level. In soybean, transposable element systems have been proposed for *Y18-m* (variegated leaves), *r-m* (chimeric seed coat), and *w4-m* (purple or white chimeric flowers) (Vodkin, 1994). However, the molecular characterization of transposable element presence has only been characterized for *Tgm1*, an element that blocks the expression of lectin (Rhodes and Vodkin, 1988).

A mutation to the *wp* locus (*wp-m*) in soybean is thought to cause pink and purple flowers on the same plant or chimeric (pink and purple sectored) flowers at different nodes of the same plant (Johnson et al., 1998). Lines derived from LN89-5320-8-53 were observed to undergo flower phenotype switching from one generation to the next (Johnson et al., 1998). Lines that were purple flowered in one generation changed to pink flowered in the next. Other lines that were pink flowered in one generation reverted to purple flowered in the next. Since these lines were $F_{6:10}$, and therefore highly homogenous, this observation suggests the presence of an active transposable element system. The exact mechanism of transposition in *wp-m* materials and whether this system is similar to the currently identified transpos-