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Mass Selection for Adaptation in Antigua Maize (Zea mays L.) Composite¹

F.M. SAN VICENTE and A.R. HALLAUER²

Tropical maize (Zea mays L.) germplasm has had limited use in temperate areas because of photoperiod sensitivity. Antigua germplasm from the island Antigua was introduced to Iowa because of its resistance to important pests of maize and its heterosis expressed in crosses with other tropical varieties. Mass selection procedures were used to adapt the Antigua Composite germplasm to Iowa conditions. After six cycles of mass selection for earlier silk emergence, the selected Antigua Composite flowered 17 days earlier than the original composite. Grain yield and other agronomic traits of the adapted strain of Antigua were similar to those of adapted varieties. INDEX DESCRIPTORS: Corn, tropical germplasm, recurrent selection.

Maize (Zea mays L.) breeders have the challenge to continuously increase grain yield through the genetic improvement of hybrids. Hybrids have been improved in the U.S. Corn Belt primarily with use of adapted germplasm (Russell, 1986). Maize breeders generally have not incorporated exotic tropical germplasm into temperate area breeding programs to improve yield and other agronomic traits. Exotic tropical germplasm has been considered primarily because of the concern of genetic vulnerability. Problems with use of exotic germplasm in the U.S. Corn Belt are that it is not adapted to major production areas of the United States, and their use in breeding programs presents formidable problems (Goodman, 1985). Use of recurrent selection methods that increase frequencies of favorable alleles in exotic germplasm can provide unique sources of genetic variation for continued genetic improvement of lines and hybrids.

The increased use of productive and uniform hybrids in the U.S. Corn Belt has led to a reduction of the maize germplasm base in the United States (Gracen, 1986). The genetic diversity among and within the tropical and semitropical maize germplasm collections has been recognized (Brown, 1975; Wellhausen, 1965). The major difficulties in use of tropical germplasm in the U.S. Corn Belt breeding programs have been its poor adaptation to temperate areas and a lower mean performance level than of elite Corn Belt breeding germplasm. To overcome the problems of poor adaptation and unacceptable performance standards, long-term selection programs are required.

Mass selection is a breeding method in which individual plants are chosen on the basis of their phenotype, and a balanced seed bulk from the selected plants is composited to propagate the next cycle of selection. Successful mass selection depends on the level to which individual phenotypes reflect breeding values, on the importance of environmental effects in the expression of the trait under selection, and on the magnitude of genotype by environment interaction because selection is usually practiced in one environment per cycle. Mass selection has been used successfully by maize breeders to increase yield (Gardner, 1977; Zorilla and Crane, 1982), prolificacy (Lonnquist, 1967; Coors and Mardones, 1989), and components of yield (Salazar and Hallauer, 1986; Odhiambo and Compton, 1987). Mass selection for earlier flowering has been used effectively to adapt populations that included exotic germplasm to temperate areas (Hallauer and Sears, 1972; Troyer and Brown, 1976; Compton et al., 1979).

A composite of landrace collections from the Caribbean island of Antigua combines well with U.S. Corn Belt Dents (Goodman and Brown, 1988). Antigua germplasm has resistance to important maize pests, has earlier maturity, and has shorter plant height compared with other tropical varieties. Because of the potential value of Antigua germplasm for temperate breeding programs, Antigua germplasm was introduced and adapted to the U.S. Corn Belt.

Objectives of our study were to evaluate effectiveness of mass selection for earlier flowering in Antigua Composite (100% exotic germplasm), to determine whether correlated responses to selection for earlier flowering occurred for other agronomic traits, and to compare changes associated with mass selection in Antigua Composite with three populations with different proportions of exotic germplasm.

MATERIALS AND METHODS

Wellhausen (1965) reported that Antigua germplasm had good combining ability with Tuxpeño and U.S. Corn Belt Dents. Goodman and Brown (1988) suggested that the Antigua materials belonged to the race Tusón. Tusón was included in three of the heterotic patterns (Tusón x Tuxpeño, Tusón x Chandelle, and Tusón x U.S. Southern Dents) suggested by Goodman (1985) for potential use in temperate areas. Samples of 500 seeds of the composites Antigua Grupo 1 and Antigua Grupo 2 were obtained from the International Maize and Wheat Improvement Center (CIMMYT) in 1975. Each lot of 500 seeds was increased by hand-cross pollinations in 1975. In 1976, 1,000 seeds of Antigua Grupo 1 and Antigua Grupo 2 were bulked, planted in isolation, and allowed to intermate by open pollination. A bulk sample of ears (ca. 1000) was harvested from the central portion of the isolation field and equal quantities of seed (ca. 100) of each ear were bulked to form Antigua Composite.

Mass selection for adaptation of the Antigua Composite for temperate environments was initiated at Ames, IA, in 1977. Mass selection was for the date individual plants had visible silks on the uppermost ear. Plots were planted in fields isolated (at least 220 m) from other maize fields. The protocol for mass selection was the same for each cycle of selection except that the date of silk was earlier in successive cycles of selection. Approximately 20,000 seeds were sown in the isolated field. The field was examined periodically throughout the growing season, and tags indicating date of visible silk were attached to 300 plants with the earliest dates of visible silk. Ears of the 300 earliest silking plants were harvested, dried at 35 C to about 1400 g kg⁻¹ grain moisture, and shelled individually. Two samples of 100 seeds from each ear were bulked from the 300 individually shelled ears; one bulk sample was placed in cold storage as reserve, and the second bulk used to plant the isolation field the following year. Six cycles of mass selection for earlier flowering were completed before Antigua Composite was considered to have maturity appropriate for U.S. Corn Belt environments.

The unselected Antigua Composite and the six mass selected cycles for earlier flowering were evaluated to determine the effectiveness of the selection methods. Three breeding populations (BS16, BS2, and BSTL), each with different proportions of exotic germplasm, were included as checks. BS16 was developed from ETO Composite after six cycles of mass selection for earlier flowering (Hallauer, 1978). BS2 was developed by crossing 40 ETO Composite plants to each of six early

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maturity lines (A251, A554, A575, A619, Mt42, and ND203), followed by five generations of intermating (Hallauer, 1978). BSTL was developed by crossing the Mexican landrace Tuxpeño with the U.S. landrace Lancaster Sure Crop, backcrossing to Lancaster Sure Crop, and intermating the backcross population to form BSTL (Hallauer, 1978). The 10 entries (Antigua Composite, six mass selected cycles, and three checks) were evaluated in a randomized completeblock experiment with three replications conducted in 1987 and 1988 at five locations (environments) each year. Experimental units were two-row plots that were 5.5 m long with 76.2 cm between rows. Plots were overplanted and thinned to a stand of 57,000 plants ha-1. Conventional fertilizer and weed control practices for optimum grain production were used at each location. Warm, dry conditions occurred at all locations for both years. Four locations were harvested by machine in 1987; one location in 1987 and all locations in 1988 were harvested by hand.

Data were collected for 17 traits, but data were not taken at all locations for all traits. Stand (number of plants at harvest), percentage of root (plants leaning more than 30° from vertical) and stalk (plants broken at and below top ear node) lodging, percentage of ears detached from plants, and grain yield (t ha-1) were collected at 10 locations. Plant and ear height (cm) were recorded for 10 similarly spaced plants within each plot for five and six locations, respectively. Total leaf number, ear leaf number, ear length (cm), ear diameter (cm), and number of kernel rows per ear were taken for 10 competitive plants within each plot at five locations. Leaves at the fifth and tenth leaf stage were marked and used to make total leaf number and the ear leaf number (node of ear) counts. Number of tassel branches for 10 similarly spaced plants and grain moisture (g kg-1) of harvested grain were recorded at four locations. Number of days from date of planting to date when 50% of plants exhibited visible silks was recorded at three locations. Number of days from date of planting to date 50% of plants within each plot were shedding pollen and ear leaf width (cm) for 10 plants within each plot were recorded at two locations. Stand data were taken before flowering at all locations. Number of plants that were root and stalk lodged and that had dropped ears were recorded immediately before harvest and converted to percentages by dividing by the final stand for each plot. Plants were measured about one week after flowering. Ears were measured from hand-harvested plots after drying ears to 60 g kg-1 ear moisture.

Analyses of variance were computed either on plot totals or on plot means for a randomized complete-block design at each location. A combined analysis of variance across locations and years was computed for each trait by assuming that locations within each year were a sample of environments. Entries were considered fixed effects, and all other variables were considered random effects for making F-tests. The entry x environment interaction mean square was used in calculation of standard error of means. Sums of squares and degrees of freedom for entries and entries x environment interactions were subdivided orthogonally for Antigua Composite entries, check entries, and Antigua Composite entries vs. check entries.

The changes in performance of Antigua Composite with cycles of mass selection for earlier flowering were determined by a quadratic regression model. Cycle means across environments were used in the regression analyses for each trait. Standard errors (S.E.) of the regression coefficients were calculated by the methods of Draper and Smith (1966).

RESULTS AND DISCUSSION

Highly significant ($P \le 0.01$) differences were detected among environments for all traits evaluated except percentage of dropped ears and kernel-row number (analyses not shown). Severe drought conditions at all locations during the 1988 growing season contributed to the differences among environments. Differences among the 10 entries were either significant ($P \le 0.05$) or highly significant for all traits measured except for percentage of stalk lodging and ear leaf width. The same trends occurred with the effects of cycles of selection. Entries by environment interaction effects were significant or highly significant for eight (yield, root lodging, dropped ears, ear diameter, kernelrow number, tassel branch number, silking date, and pollen shed date) of the 17 traits measured. Mass selection for earlier silking was emphasized within Antigua Composite. Changes in flowering date (plants showing visible silks) are direct estimates of response to selection, whereas changes in other traits are correlated responses to selection for earlier flowering (Table 1).

Mass selection for early silk emergence was effective for developing an earlier-flowering Antigua Composite. The linear regression of silk date on selection cycles was highly significant and accounted for 91.2% of the variation among cycles. The linear model adequately explained the response to selection for earlier flowering. The average change in number of days-to-silk over cycles of selection was -3.2 days per cycle (Table 1), which would be encouraging, especially if no unfavorable correlated responses occurred in other important agronomic traits during selection for earlier flowering.

The greatest decrease in number of days to silk emergence occurred in the second cycle of selection with rate of decrease tending to be reduced with additional cycles of selection (Table 1). The sixth cycle of selection flowered 17 days earlier than the original population and had a silking date similar to those of the three check populations (BS16, BS2, and BSTL) with different proportions of exotic germplasm (Table 1). These results suggest that selection was effective in adapting Antigua Composite to central Iowa conditions. Hallauer and Sears (1972) successfully used mass selection to develop BS16 from ETO Composite. ETO Composite was obtained from Colombia. South America, but some U.S. Corn Belt germplasm was included in the synthesis of ETO Composite (Chavarriaga, 1966). The effectiveness of selection for earlier flowering in ETO Composite may have been due to selection of alleles from the U.S. Corn Belt germplasm for earlier flowering. To our knowledge, Antigua Composite includes no U.S. Corn Belt germplasm, and the effects of selection for earlier flowering were similar to those for ETO Composite. Seemingly, the problems related to recombination before initiation of intense selection in adapted x exotic crosses can be overcome by directly selecting productive exotic gene pools before intermating with adapted germplasm.

Most of the variation among cycles for grain yield was explained by a linear relationship (81.4%), though the quadratic and lack-of-fit mean squares were highly significant. Expressed as a deviation from the estimated intercept, the rate of indirect response per cycle of selection was 7.8 q ha⁻¹. Antigua Composite had an increase in grain yield until the fourth cycle, with a tendency to level off in further cycles of selection. The lack of increase after the fourth cycle of selection could explain the significance of the quadratic term and also would suggest that a plateau was attained for yield. The sixth cycle of selection yielded 43.9 q/ha more than the original population, and its yield did not differ significantly from that of the three checks.

It is important to emphasize the good agronomic performance of the cycle 6 population in comparison with the three check breeding populations with different proportions of exotic germplasm. Yield, as an indirect response to selection for earliness, increased to a level similar to that of BS16CO (100% exotic germplasm), BS2CO (50% exotic germplasm), and BSTLCO (25% exotic germplasm), which is very encouraging in terms of new breeding material to broaden the genetic base of the U.S. Corn Belt maize hybrids.

Mass selection for earlier flowering was not nearly as effective for increasing yield in previous studies (Troyer and Brown, 1972, 1976; Troyer and Larkins, 1985) in which average gain per cycle fluctuated between 1.0 and 1.7 q/ha. In one instance, a yield decrease was reported as a correlated response (Sudfana, 1984). It seems that selection for earlier flowering in late-flowering (less adapted) and,

Table 1. Means of 16 traits for six cycles of mass selection for earlier flowering in Antigua Composite and three check populations averaged over environments.

	Traits															_
	Days 50%									Number			Ear	Ear ^e		
		Pollen	C	Grain	Hei	ght	Lodg	ingc	Dropped	Total	Ear	Tassel	leaf			Kernel
Entry	Silkª	$shed^{b}$	Yield ^c	Moistured	Plante	Earf	Root	Stalk	ears ^g	leavese	leafe	branches ^d	$width^{b}$	Diameter	Length	rows
	f	10	q/ha	%	CI	n		%			n o)		cm		no.
Antigua CO	91	100	7.0	20.5	226.1	142.9	35.8	13.5	0.2	25	18	24	10.3	3.1	13.4	13.3
Antigua C1	91	99	12.5	19.7	228.0	146.1	32.2	13.1	0.0	24	18	24	10.6	3.4	14.3	13.7
Antigua C2	82	88	37.2	18.2	224.5	137.4	20.8	15.8	0.6	22	16	23	10.2	3.9	16.5	15.2
Antigua C3	79	85	46.1	17.3	221.6	132.6	13.4	15.2	0.3	22	16	21	10.3	3.9	15.6	15.4
Antigua C4	76	81	50.9	16.8	209.8	120.9	9.2	15.1	0.2	21	15	21	10.4	3.9	16.5	15.4
Antigua C5	74	79	50.4	16.0	204.7	116.9	6.8	15.1	0.9	20	15	20	10.3	3.9	16.5	15.4
Antigua C6	74	79	50.9	16.4	213.8	123.8	5.2	18.3	1.3	21	15	21	10.4	3.9	16.4	15.5
b _o ^h	92.4	101.3	3.3	20.7	229.5	145.7	37.8	_	0.0	24.7	18.0	24.0	·	3.1	13.4	13.2
Ь _/	-3.2	-7.3	19.3	-1.5	-4.2	-4.7	-9.9		0.2	-1.2	0.9	-0.7		0.4	1.4	1.0
Ь _q	—	0.6	-1.9	0.1		_	0.7			0.1	0.1		·	-0.1	-0.2	-0.1
Checks																
BS16CO	76	79	49.4	17.5	214.7	122.7	6.7	17.9	0.7	21	15	20	10.5	4.1	16.3	15.1
BS2CO	74	77	47.0	15.6	205.0	119.8	14.2	15.7	1.1	20	14	23	9.7	3.9	14.8	15.6
BSTLCO	76	79	48.8	16.5	210.8	114.1	4.3	15.1	1.0	20	14	19	9.9	3.8	17.3	13.7
Mean	79.2	84.3	40.0	17.4	215.9	127.7	14.9	15.5	0.6	21.5	15.4	21.6	10.3	3.8	15.8	14.8
C.V. (%)	1.5	1.2	19.8	8.6	3.7	6.2	59.6	46.8	204.5	3.0	4.3	8.9	3.7	4.6	7.4	5.0
LSD (0.05)	1	1	4.0	1.4	5.8	5.2	4.5	3.7	0.7	1	1	2	0.4	0.1	0.9	0.5

^aBased on three environments and three replications per environment.

^bBased on two environments and three replications per environment.

^cBased on ten environments and three replications per environment. ^dBased on four environments and three replications per environment.

Based on four environments and three replications per environment.

Based on six environments and three replications per environment.

^gBased on nine environments and three replications per environment.

 b_0 is the intercept, b₁ is the linear effect, and b₀ is the quadratic effect estimated from the regression analyses.

therefore, lower yielding populations may produce positive correlated responses in yield. Negative correlated responses in yield may occur in populations only moderately late-flowering (more adapted). The increase in grain yield in Antigua Composite was directly related to earlier flowering from selection. The lower yield in the original, unselected Antigua Composite occurred because of the day-length sensitivity, commonly observed in tropical germplasm grown in temperate environments. The lower yields of the unselected Antigua Composite were caused by later flowering.

Selection for earlier flowering effectively decreased plant and ear height (Table 1). For plant height, linear regression was highly significant and accounted for 71.5% of the variation among cycles. Plant height was reduced 12.3 cm after six cycles of selection. Other correlated reponses to selection for earlier flowering were less root lodging, fewer leaves, fewer tassel branches, lower grain moisture, longer ears, more kernel rows per ear, and increased ear diameter (Table 1).

Mass selection for adaptation, or less photoperiod sensitivity, was effective in developing an earlier, shorter, and greater-yielding population, with an agronomic performance similar to that of BS16CO, BS2CO, and BSTLCO. It seems that selection for earliness removed some of the negative photoperiod effects on yield and other important agronomic traits. The improved population of Antigua Composite could be incorporated into plant breeding programs for the U.S. Corn Belt. The improved population can be used as a source population of exotic germplasm in a reciprocal recurrent selection program with another population that represents the heterotic patterns of the U.S. Corn Belt (e.g., Lancaster Sure Crop) or the tropical regions (e.g., an adapted strain of Tuxpeño).

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