

# PLANT GENETIC RESOURCES

## Testcross Performance of Semiexotic Inbred Lines Derived from Latin American Maize Accessions

J. A. Tarter,\* M. M. Goodman, and J. B. Holland

### ABSTRACT

Tropical maize (*Zea mays* L.) represents the most diverse readily available source of germplasm to broaden the limited genetic base of temperate maize in the USA. One objective of this study was to determine if exotic-derived alleles contributing to enhanced testcross agronomic performance were maintained in semiexotic lines created by inbreeding and pedigree selection. A second objective was to determine if first-generation semiexotic lines could produce hybrids with agronomic performance comparable to commercial U.S. hybrids. One hundred sixty-four semiexotic inbred lines were developed from crosses between temperate-adapted inbred line Mo44 and 23 Latin American maize accessions. Mo44 and each semiexotic line were testcrossed to temperate hybrid LH132 × LH51 for evaluations. In first-stage replicated yield trials, testcrosses of 18 semiexotic lines, representing six different races, had significantly greater grain yields than the Mo44 testcross. Advanced yield evaluations were performed on check entries and 33 selected semiexotic line testcrosses in three additional environments. Across 10 environments, 12 semiexotic line testcrosses exhibited significantly greater grain yield than the Mo44 testcross, indicating recovery of favorable exotic alleles. Semiexotic testcrosses were not competitive with commercial hybrids for grain yield but were similar to or better than commercial hybrids for grain moisture and lodging resistance. Many superior accessions represent relatively recent introductions into regions from which they were collected. Tropical landraces seem to be a good source of exotic germplasm that can be used to broaden the genetic base of modern U.S. maize production and improve productivity.

IN THE USA, only limited use is made of the vast supply of available maize germplasm. Only six of the approximately 300 races of maize in the New World are represented in commercial cultivars, and only one of these is used in the USA (Goodman, 1985, 1990). As of 1996, exotic germplasm contributed less than 3% to the pedigrees of U.S. maize cultivars (Goodman, 1999). Interbreeding elite lines derived from a small number of open-pollinated cultivars of the Corn Belt Dent race for 60 yr has further reduced the genetic diversity of commercial U.S. cultivars (Troyer, 1999). For example, a 1984 American Seed Trade Association survey revealed that 16% of new inbred line development came from continually breeding new lines from B73 and 9%

from Oh43 (Darrah and Zuber, 1986). Smith (1988) reported that a small number of lines, including B73, A632, Mo17, and Oh43, were the major contributors to commercial U.S. maize hybrids. Subsequently, Smith et al. (1999) found that pedigree diversity of Pioneer brand inbreds and hybrids were lower in the 1990s than any previous decade.

Tropical maize germplasm likely contains unique alleles that would be useful to temperate breeding programs (Crossa and Gardner, 1987; Holland and Goodman, 1995). Successful incorporation of exotic germplasm has resulted in the creation of new breeding stocks exhibiting increased yields in maize (Goodman et al., 2000) as well as in soybean [*Glycine max* (L.) Merr., Thompson and Nelson, 1998], and wheat (*Triticum aestivum* L., del-Blanco et al., 2001). However, working with tropical maize in temperate environments is hindered by photoperiod sensitivity (Brown, 1975) and linkage between favorable alleles and alleles contributing to maladaptation (Brown, 1953, 1988). Furthermore, choosing appropriate germplasm sources from among the many thousands of available accessions has been hindered, until recently, by inadequate testing and reporting systems (Stuber, 1978; Goodman, 1983, 1999).

A maize germplasm incorporation program, independent of the Germplasm Enhancement of Maize project (Pollak and Salhuana, 1998) and the Latin American Maize Project (Salhuana et al., 1991), has been conducted at North Carolina State University for about 20 yr. This program began by screening 1300 typical Latin American maize accessions for agronomic utility (ear and plant height, lodging resistance, and pollination success rate) in a nearly daylength-neutral nursery in southern Florida for 2 yr (Goodman, 1983). Castillo-Gonzalez and Goodman (1989) advanced the best accessions to replicated yield trials under short-day and long-day photoperiod conditions and identified a subset of accessions that appeared to have sufficient agronomic value to be useful for breeding. The 40 most promising accessions were selected for conversion to photoperiod insensitivity by crossing them to temperate-adapted line Mo44 and then intermating within each segregating population. Following selection for photoperiod insensitivity, four full-sib families were sampled from each of the 40 populations for agronomic evaluation. Holland and Goodman (1995) reported that 24 of these families ranked higher than Mo44 for grain yield in testcrosses to Corn Belt Dent hybrids and concluded that multiple testers were not needed to efficiently identify superior semiexotic populations. Holland and Goodman (1995) suggested that inbred lines with good combining ability

J.A. Tarter and M.M. Goodman, Dep. of Crop Science, Box 7620, North Carolina State Univ., Raleigh, NC 27695-7620; J.B. Holland, USDA-ARS, Plant Science Research Unit, Dep. of Crop Science, Box 7620, North Carolina State Univ., Raleigh, NC 27695-7620. Received 18 Nov. 2002. \*Corresponding author (jatarter@unity.ncsu.edu).

Published in Crop Sci. 43:2272–2278 (2003).  
© Crop Science Society of America  
677 S. Segoe Rd., Madison, WI 53711 USA

for yield could be extracted from superior semiexotic families. Therefore, they selected 69 semiexotic families representing 29 different Latin American accessions as sources for inbred line development.

We hypothesized that favorable alleles would be maintained in some of these semiexotic lines following inbreeding and visual selection. To test this hypothesis, we developed semiexotic inbred lines of 50% tropical parentage and agronomically evaluated them in crosses to a U.S. Corn Belt hybrid. The semiexotic inbred lines, derived from superior semiexotic families identified by Holland and Goodman (1995) were compared with Mo44 in testcrosses. Our objective was to determine if semiexotic inbred lines inherited exotic alleles superior to Mo44 alleles for productivity in a temperate environment. The semiexotic line testcrosses were also compared with commercial hybrid cultivars to assess their potential as germplasm donors to commercial maize breeding programs.

## MATERIALS AND METHODS

### Semiexotic Inbred Line Development

The source populations for inbred line development were 69 photoperiod-insensitive, semiexotic, full-sib families developed from crosses between Mo44 and tropical accessions, as described by Holland and Goodman (1995). Mo44 was derived from a cross between Mo22 and Pioneer Mexican Synthetic 17 and is largely unrelated to either of the two major heterotic groups of maize, Reid Yellow Dent or Lancaster Sure Crop (Gerdes and Tracy, 1993).

Semiexotic inbred lines were developed from the selected families by two generations of full-sib mating, followed by two generations of self-fertilization. At each generation of

inbreeding, visual selection, among and within lines, was conducted for earlier flowering, minimal silk-tassel interval, stay green, lower ear placement, stalk strength, well-filled ears, lower grain moisture at harvest, and resistance to southern corn leaf blight [caused by *Cochliobolus heterostrophus* (Drechs.) Drechs. [anamorph = *Bipolaris maydis* (Nisikado) Shoemaker]], northern corn leaf blight [caused by *Exerohilum turcicum* (Pass.) Leonard and Suggs], gray leaf spot (caused by *Cercospora zea-maydis* Tehon and Daniels), anthracnose stalk rot (caused by *Colletotrichum graminicola* G. W. Wils.), and Fusarium ear rot [caused by *Fusarium verticillioides* (Sacc.) Nirenberg [syn. *Fusarium moniliforme* J. Sheldon]]. Leaf blights were artificially inoculated by applying sorghum seeds infected with pathogenic fungi to the whorl of juvenile maize plants. A toothpick coated with *Fusarium* spores was inserted into the developing ear approximately 1 wk after pollination to promote Fusarium ear rot. Inoculation for stalk rot was accomplished by penetrating the base of the stalk and injecting a liquid solution of inoculum approximately two weeks after pollination.

The final set of selected semiexotic germplasm consisted of 164 lines derived from 36 source families, with 1 to 36 lines developed from each family (Table 1). The selected lines represent 23 of the original accessions, 14 different races, and nine different countries of origin (Table 1). Semiexotic lines were designated by their race (e.g., Tusón), their five to six character accession code (e.g., BAI III), their family of origin (e.g., a, b, c, or d, corresponding to Holland and Goodman, 1995), and a unique line within family number (1–36). The lines were derived from plants in a generation which had an expected inbreeding coefficient of  $F = 0.74$  and the lines had expected homogeneity approximately equivalent to  $F_{4.5}$  lines. The plants within the lines had an expected inbreeding coefficient of  $F = 0.87$ .

**Table 1. Latin American maize accessions from which semiexotic inbred lines were developed, number of source families, number of inbred lines per family, and proportion of lines with significantly greater testcross grain yield than Mo44 × (LH132 × LH51) when tested in seven North Carolina environments in 1999 and 2000.**

Race	Accession	Country of origin	Plant Introduction number	National Research Council number†	Progeny developed from an accession			Lines with greater grain yield than Mo44
					Families	Lines per family	Total lines	
						no	%	
Costeño	ATL 314	Colombia	443992	65	2	1	2	0
Costeño	ATL 329	Colombia	444006	80	2	1–4	5	20
Tusón‡	BAI III	Brazil	449556	NA§	3	4–7	17	29
Cubano Dentado‡	BOV 585	Bolivia	485383	9832	2	1	2	0
Tusón	CUB 57	Cuba	NA	6698	1	11	11	45
Cuban Flint	CUB 63	Cuba	478909	6694	1	3	3	0
Chandelle	CUB 68	Cuba	NA	6699	1	2	2	0
Cubano Amarillo Duro‡	ECU 326	Ecuador	487889	4725	1	2	2	0
Cubano Cateto‡	ECU 339	Ecuador	487899	4737	1	4	4	0
Cubano Tusón‡	ECU 542	Ecuador	487926	7303	1	1	1	0
Cubano Amarillo Duro‡	ECU 653	Ecuador	487939	7403	1	3	3	0
Cubano Amarillo Duro‡	ECU 770	Ecuador	487959	7514	2	1–11	12	17
Cubano Amarillo Duro‡	ECU 904	Ecuador	487994	10381	2	4–36	40	0
Tuxpeño‡	ECU 942	Ecuador	NA	10410	1	2	2	0
Cateto Nortista	GIN I	Guyana	449478	NA	1	1	1	0
Tepecintle	GUA 597	Guatemala	NA	6083	1	2	2	0
Perla‡	LIM 13	Peru	485347	10591	2	2–19	21	0
Puya	MAG 322	Colombia	444898	658	1	3	3	33
Puya	SAN 349	Colombia	445355	7280	4	1–8	14	14
Chandelle	VEN 352	Venezuela	NA	NA	1	5	5	0
Tuxpeño‡	VEN 598	Venezuela	NA	8083	1	4	4	0
Tuxpeño‡	VEN 767	Venezuela	NA	8240	1	3	3	33
Canilla	VEN 981	Venezuela	NA	NA	3	1–2	5	20

† Collection numbers assigned by the Committee on Preservation of Indigenous Strains of Corn (1954, 1955).

‡ Accessions that were introduced to the country from which they were collected.

§ Not available.

### Testcross Yield Trials

Each semixotic line was crossed to the hybrid tester LH132 × LH51 and evaluated in 1999 and 2000. LH132 × LH51 was chosen because of its close relationship to the historically important Corn Belt Dent cross, B73 × Mo17. The semixotic testcrosses were divided into two 90-entry sets, each of which included eight commercial hybrid checks (Pioneer brand hybrids 3165, 32K61, and 31B13; DeKalb brand hybrids 683, 689, 714, and 743; and LH132 × LH51). In 2000, the experimental check Mo44 × (LH132 × LH51) was substituted for DeKalb brand hybrid 683. The experimental design for a set within a location was a 9 × 10 lattice design with three replications in 1999 and with two replications in 2000. In 1999, the experiments were grown at three locations in North Carolina: the Central Crops Research Station at Clayton, the Peanut Belt Research Station at Lewiston, and the Tidewater Research Station at Plymouth. In 2000, a fourth location at the Sand Hills Research Station at Jackson Springs was added. Soils at the experiment sites are classified as Marlboro Loamy Sand (clayey, kaolinitic, thermic Typic Paleudult) at Clayton, Norfolk Sandy Loam (fine-loamy, siliceous, thermic Typic Kandiudult) at Lewiston, Portsmouth Fine Sandy Loam (fine-loamy over sandy or sandy-skeletal, mixed, thermic Typic Umbraquilt) at Plymouth, and Candor Sand (sandy, siliceous, thermic Arenic Paleudult) at Jackson Springs.

At all locations, plots were two 4.86-m rows sown with 44 seeds, with a 1-m length alley at the end of each plot. At Plymouth and Clayton, rows were spaced 0.97 m, resulting in a population density of approximately 57 000 plants ha<sup>-1</sup> within the planted plot area. In Lewiston and Jackson Springs, interrow spacing was 0.91 m, and population density was 60 000 plants ha<sup>-1</sup>.

The number of plants, mean plant height (measured from the ground to the tassel tip in 1999 and to the terminal node in later years), and mean ear height (height to node of topmost ear) were recorded for each plot at all seven environments. Days to anthesis and silking were recorded only at Clayton. Anthesis date was the date on which at least 50% of the plants in the plot were shedding at least 50% of the available pollen. Silk emergence date was the date on which 50% of the plants in the plot were displaying visible silks. Counts were taken of root-lodged plants (leaning greater than 30° from vertical with intact stalks) and stalk-lodged plants (broken below the ear or plants with dropped ears) in all environments except Lewiston and Plymouth in 1999. In 1999, hurricanes Dennis and Floyd made landfall on the coast of North Carolina before harvest and resulted in severe lodging at Lewiston and Plymouth only. Therefore, a visual estimate of percent erect plants was made at these coastal plain locations in 1999. At maturity, plots were machine harvested, and grain yield and moisture content were recorded for each plot. Grain yields were adjusted to 155 g kg<sup>-1</sup> moisture content.

### Advanced Yield Trials

On the basis of the agronomic evaluations in 1999 and 2000, 33 semixotic lines with testcross grain yields greater than the Mo44 testcross, acceptable percentage of erect plants, and acceptable grain moisture were selected for additional testing in 2001. The 33 semixotic entries were tested along with Mo44 × (LH132 × LH51), and eight commercial hybrid checks (Pioneer brand hybrids 3165, 32K61, and 31B13; DeKalb brand hybrids 683, 689, 714, and 743; and LH132 × LH51). The experiment was conducted at Clayton, Plymouth, and Jackson Springs, NC. Experimental design was a 6 × 7 lattice design with two replications per location. Otherwise, the experimental methods were identical to the original experiments conducted in 1999 and 2000.

### Statistical Analysis

Data from seven or 10 environments were combined and analyzed by means of Proc MIXED in SAS version 8.0 (SAS Institute, 2000). Entry (experimental or check hybrid) was considered a fixed factor, whereas all other factors (environment, set, set × environment, entry × set, entry × environment) were treated as random. Percent stand was used as a covariate for grain yield only. Tests for significance of genotype by environment interaction were performed with a chi-square test of the difference between -2 times the logs of the restricted maximum likelihoods of the complete model and a reduced model lacking the genotype by environment interaction factor (Littell et al., 1996). The approximate *P*-value of this test was obtained by dividing the *P*-value of the one degree of freedom chi-square statistic by two (Self and Liang, 1987; Littell et al., 1996). This analysis permitted estimation of experimental line means adjusted for set effects, facilitating presentation of results from both sets simultaneously.

The effect of missing data of Mo44 × (LH132 × LH51) in three of the seven first-stage yield trial environments was investigated by comparing results based on least square means from all seven environments to those based on least square means from only the four environments in which Mo44 × (LH132 × LH51) was included. The conclusions about which semixotic line testcrosses were significantly greater yielding than their temperate parent was consistent across the two analyses. We concluded, therefore, that use of the complete data set was appropriate, and all results reported from the first stage yield trials are based on data from all seven environments.

Obvious spatial trends within locations were observed in the data from the advanced yield trials grown in 2001. A variety of spatial analyses was performed on the data from within each environment of the advanced yield trials. Models with up to fourth-order polynomial effects of rows and columns in the field layout were tested. Trend effects were maintained in the model if significant at *P* < 0.01 (Brownie et al., 1993). Proc MIXED was used to compare the following models within each environment: a model including complete and incomplete block effects, models with row and column trend effects selected as described, a model with correlated errors, and a model with both trend effects and correlated errors (Brownie et al., 1993). Within each environment, the model that minimized Akaike's Information Criterion (Lynch and Walsh, 1997) was chosen. Finally, adjusted entry means for the selected lines were combined from all 10 evaluation environments within each set and analyzed by Proc MIXED.

## RESULTS AND DISCUSSION

### First Stage Yield Trials

Significant (*P* < 0.05) variation among entries was observed for all measured traits except root lodging in the first stage yield trials (1999 and 2000). Overall, 18 semixotic lines had individual mean testcross grain yields significantly (*P* < 0.05) greater than the mean grain yield of Mo44 × (LH132 × LH51) (Fig. 1). These superior lines were derived from eight accessions and six of the 14 races. Among these eight accessions, the proportion of derived lines with significantly greater testcross yield than Mo44 ranged from 14% for lines derived from Puya SAN 349 to 45% for lines derived from Tusón CUB 57 (Table 1). The races from which a relatively high proportion of superior semixotic lines

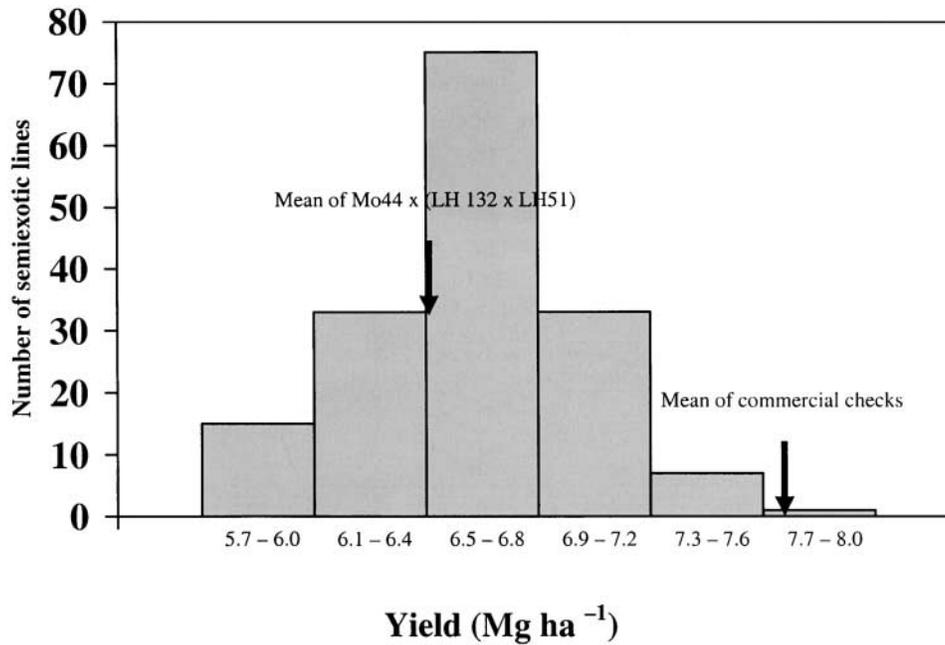


Fig. 1. Histogram of mean grain yields of 164 semiexotic maize lines testcrossed to LH132 × LH51 evaluated in first stage yield trials in seven North Carolina environments in 1999 and 2000. Mean grain yields of Mo44 × (LH132 × LH51) and eight commercial hybrids indicated with arrows. An LSD of 0.7 Mg ha<sup>-1</sup> is appropriate to compare means of one semiexotic line testcross to Mo44 × (LH 132 × LH51) at  $\alpha = 0.05$ . An LSD of 0.6 Mg ha<sup>-1</sup> is appropriate to compare means of one semiexotic line testcross to mean of all seven commercial hybrids at  $\alpha = 0.05$ .

were derived included Tusón, Tuxpeño, and Puya, suggesting that they are excellent sources of germplasm for combining ability with U.S. Corn Belt Dent germplasm. Only one semiexotic line testcross had significantly lower grain yield than Mo44 × (LH132 × LH51).

A commonly observed negative effect of incorporating tropical germplasm into temperate breeding popula-

tions is increased grain moisture at harvest (Hawbaker et al., 1997). This trend also was observed in our experiment, as 61 semiexotic line testcrosses had significantly greater grain moisture than the Mo44 testcross (Fig. 2). Furthermore, no semiexotic line testcross had significantly lower grain moisture than Mo44 × (LH132 × LH51).

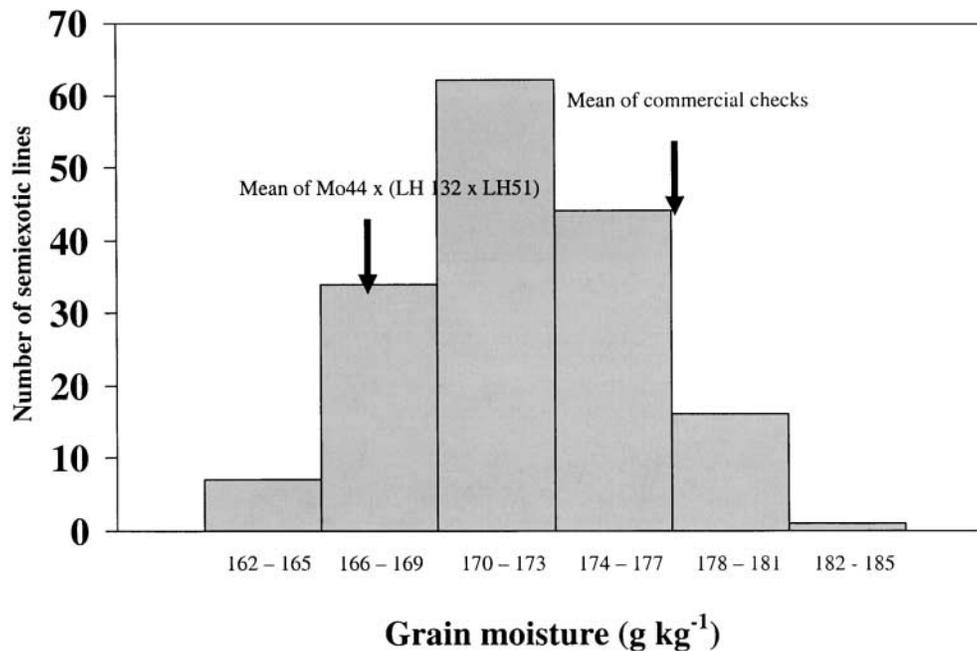


Fig. 2. Histogram of mean grain moisture of 164 semiexotic maize lines testcrossed to LH132 × LH51 evaluated in first stage yield trials in seven North Carolina environments in 1999 and 2000. Mean grain moistures of Mo44 × (LH132 × LH51) and eight commercial hybrids indicated with arrows. An LSD 7 g kg<sup>-1</sup> is appropriate to compare means of one semiexotic line testcross to Mo44 × (LH 132 × LH51) at  $\alpha = 0.05$ . An LSD of 5 g kg<sup>-1</sup> is appropriate to compare means of one semiexotic line testcross to mean of all seven commercial hybrids at  $\alpha = 0.05$ .

**Table 2.** Least square means of best performing semiexotic maize lines testcrossed to (LH132 × LH51), Mo44 × (LH132 × LH51), and seven commercial hybrids from Set 1 evaluated in 10 North Carolina environments.

Race	Accession	Family	Inbred line ID	Grain yield	Grain moisture	Erect plants	Days to anthesis†	Days to silk†	Ear height	Plant height
				Mg ha <sup>-1</sup>	g kg <sup>-1</sup>	%	d		m	
Tusón	BAI III	c	3	7.5*	179	85	73	73	1.0*	2.2*
Tusón	BAI III	d	2	7.5*	176	83	72	71	1.0*	2.3*
Canilla	VEN 981	a	1	7.7*	189*	83	76*	74	1.1*	2.3*
Tuxpeño	VEN 767	a	1	7.3	179	83	73	74	1.1*	2.3*
Tuxpeño	VEN 767	a	3	7.2	178	86	72	73	1.0*	2.2*
Puya	SAN 349	a	1	7.4*	181	84	73	75	1.1*	2.3*
Cubano Amarillo Duro	ECU 653	b	1	7.3	176	87	73	73	1.1*	2.3*
Cubano Amarillo Duro	ECU 770	a	1	7.4*	183*	90	73	75	1.0*	2.3*
Cubano Amarillo Duro	ECU 770	b	2	7.7*	179	86	72	74	1.1*	2.4*
Cubano Amarillo Duro	BOV 585	a	1	7.2	180	87	71*	73	1.0*	2.3*
Perla	LIM 13	b	1	7.3	184*	87	72	73	1.1*	2.4*
Mean of selected semiexotic line testcrosses				7.4a‡	180a	86ab	73a	73a	1.0a	2.3a
Mo44 × (LH132 × LH51)				6.8b	176b	88b	73a	72a	0.9a	2.1b
LH132 × LH51				7.7c	174b	88b	72a	72a	1.0a	2.2ab
Mean of 7 commercial hybrids				8.4d	185c	85a	73a	73a	1.0a	2.3a
LSD <sub>1</sub> §				0.5	6	5	2	1	0.1	0.1
LSD <sub>2</sub> ¶				0.6	7	6	2	2	0.1	0.1
LSD <sub>3</sub> #				0.4	5	4	1	1	0.1	0.1

\* Significantly different from the mean of Mo44 × (LH132 × LH51) at  $P = 0.05$ .

† Days to anthesis and days to silk recorded at Clayton only.

‡ Means followed by the same letter are not significantly different at  $P = 0.05$ .

§ LSD<sub>1</sub> is appropriate to compare means of two semiexotic line testcrosses, two commercial hybrids, or a semiexotic line testcross to a commercial hybrid at  $\alpha = 0.05$ .

¶ LSD<sub>2</sub> is appropriate to compare means of one semiexotic line testcross or a commercial hybrid to Mo44 × (LH132 × LH51) at  $\alpha = 0.05$ .

# LSD<sub>3</sub> is appropriate to compare mean of one semiexotic line testcross to mean of all seven commercial hybrids at  $\alpha = 0.05$ .

### Advanced Yield Trials

The mean testcross grain yield across 10 environments of the 33 selected semiexotic lines was greater than the Mo44 testcross; however, their percent grain moisture also was greater. Twelve of the 33 lines had individually significantly greater grain yield than Mo44 × (LH132 × LH51) (Tables 2 and 3). Eight of these 12 superior lines were derived from the race Tusón (Tables 2 and 3).

Among the 33 selected semiexotic line testcrosses that were included in the advanced yield trials, all had greater plant height and all but one had greater ear height than Mo44 × (LH132 × LH51), but the differences were no greater than 0.2 m (Tables 2 and 3). Most semiexotic line testcrosses exhibited significantly fewer days to anthesis, but six of them had significantly more days to silk emergence than Mo44 × (LH132 × LH51). None of the differences in days to flowering was greater than 3 d, however (Tables 2 and 3). The percentage of erect plants in six of the superior semiexotic line testcrosses was reduced compared with the Mo44 testcross, indicating a reduced resistance to lodging.

The mean grain yield of the selected semiexotic line testcrosses was significantly lower than the mean of seven commercial hybrids in both sets (Tables 2 and 3). However, the selected semiexotic lines performed well compared with commercial hybrids for other important agronomic traits. The mean semiexotic line testcross grain moisture was significantly lower than the mean of seven commercial checks in both sets. The semiexotic testcrosses of set one had significantly better lodging resistance than the commercial hybrids and exhibited no other significant differences (Table 2). In addition to a reduction in grain moisture, the selected semiexotic line testcrosses in set two also had fewer days to both anthesis and silk than the commercial hybrids (Table 3).

### Relationships among Superior Latin American Accessions

A rational method for choosing better germplasm sources among landrace accessions in the absence of yield trial data would be useful to maize breeders. Identification of common geographic or ecological origins among superior landrace accessions could provide guidance for designing optimal germplasm sampling strategies. The most striking feature in common among many of the superior accessions evaluated in this study was that they represent relatively recent introductions (since the 1920s) into the regions where they were collected. Twelve accessions in the set of semiexotic lines evaluated in this experiment were introduced races (Table 1). All of the accessions from Ecuador that were represented in the final set of semiexotic inbred lines were introduced there, probably from Cuba or Mexico (Timothy et al., 1963). The accessions from Brazil, Bolivia, Peru, and Venezuela represented in our study also were introduced, but their original countries of origins are unknown (Grant et al., 1963; Paterniani and Goodman, 1977; Ramírez et al., 1960; R. Sevilla, personal communication). We suggest that the superior semiexotic lines disproportionately represent introduced races because those races that flourished sufficiently in their introduced ranges have broader adaptability and superior productivity. Introduced accessions with broad adaptability and outstanding productivity may have out-competed local landraces and spread beyond their introduced range. For example, races such as Cubano Amarillo Duro, Cubano Cateto, Cubano Dentado, and Cubano Tusón, which were collected at relatively high frequency outside of Cuba, likely represent highly competitive germplasm. In contrast, introduced races that lacked outstanding adaptability would not have com-

**Table 3.** Least square means of best performing semiexotic maize lines testcrossed to (LH132 × LH51), Mo44 × (LH132 × LH51), and seven commercial hybrids from Set 2 evaluated in 10 North Carolina environments.

Race	Accession	Family	Inbred line ID	Grain yield	Grain moisture	Erect plants	Days to anthesis†	Days to silk†	Ear height	Plant height
				Mg ha <sup>-1</sup>	g kg <sup>-1</sup>	%	d		m	
Cubano Amarillo Duro	ECU 653	b	2	7.0	176	82	74	72	1.1*	2.2*
Cubano Amarillo Duro	ECU 904	c	1	7.4	182*	86	72*	73	1.1*	2.3*
Tusón	BAI III	b	2	7.3	181*	83	71*	73	1.1*	2.3*
Tusón	BAI III	b	3	7.5*	180*	81*	72*	73	1.1*	2.3*
Tusón	BAI III	b	4	7.2	180*	84	71*	72	1.1*	2.3*
Tusón	BAI III	b	5	7.1	174	80*	70*	71	1.0*	2.2*
Tusón	BAI III	b	1	7.4	178	86	71*	71	1.0*	2.2*
Tusón	BAI III	b	6	7.7*	175	80*	72*	73	1.1*	2.3*
Costeño	ATL 329	a	1	7.2	180*	87	72*	73	1.0*	2.1
Costeño	ATL 329	a	2	7.1	187*	88	71*	74*	1.0*	2.3*
Tusón	CUB 57	c	1	7.9*	182*	86	73	74*	1.1*	2.4*
Tusón	CUB 57	c	2	7.8*	179*	87	72*	74*	1.1*	2.3*
Tusón	CUB 57	c	3	7.8*	179*	86	72*	72	1.1*	2.3*
Tusón	CUB 57	c	5	7.6*	178	85	72*	74*	1.1*	2.3*
Tusón	CUB 57	c	6	7.3	179*	88	72*	73	1.1*	2.4*
Perla	LIM 13	d	5	7.1	179*	86	72*	73	1.2*	2.4*
Perla	LIM 13	d	3	7.3	188*	76*	73	75*	1.1*	2.3*
Perla	LIM 13	d	4	7.2	189*	81*	73	75*	1.1*	2.4*
Canilla	VEN 981	c	2	6.8	178	85	70*	71	1.0*	2.2*
Cubano Amarillo Duro	ECU 904	b	8	7.2	181*	88	71*	72	1.1*	2.3*
Cubano Amarillo Duro	ECU 904	b	7	7.2	178	92	71*	72	1.1*	2.3*
Cubano Amarillo Duro	ECU 904	b	9	7.1	180*	91	73	72	1.0*	2.2*
Mean of selected semiexotic line testcrosses				7.3a‡	180a	85ab	72a	73ab	1.1a	2.3a
Mo44 × (LH132 × LH51)				6.9c	173c	87ab	74b	72b	0.9b	2.1b
LH132 × LH51				7.5ac	175c	89b	73ab	72b	1.0ab	2.2ab
Mean of 7 commercial hybrids				8.5b	186b	85ab	73ab	74a	1.1a	2.3a
LSD <sub>1</sub> §				0.5	5	5	2	1	0.1	0.1
LSD <sub>2</sub> ¶				0.6	6	6	2	2	0.1	0.1
LSD <sub>3</sub> #				0.4	4	4	2	1	0.1	0.1

\* Significantly different from the mean of Mo44 × (LH132 × LH51) at  $P = 0.05$ .

† Days to anthesis and days to silk recorded at Clayton only.

‡ Means followed by the same letter are not significantly different at  $P=0.05$ .§ LSD<sub>1</sub> is appropriate to compare means of two semiexotic line testcrosses, two commercial hybrids, or a semiexotic line testcross to a commercial hybrid at  $\alpha = 0.05$ .¶ LSD<sub>2</sub> is appropriate to compare means of one semiexotic line testcross or a commercial hybrid to Mo44 × (LH132 × LH51) at  $\alpha = 0.05$ .# LSD<sub>3</sub> is appropriate to compare mean of one semiexotic line testcross to the mean of all seven commercial hybrids at  $\alpha = 0.05$ .

peted adequately with local landraces and would have been extinct or approaching extinction by the time of large-scale maize germplasm collections in the 1940s to 1960s.

## CONCLUSIONS

The recovery of semiexotic lines with superior combining abilities compared with their temperate-adapted parent, Mo44, supports our hypothesis that superior exotic alleles can be maintained through the inbreeding process even in the absence of selection for testcross performance during line development. The performance of these semiexotic lines indicates that these lines inherited alleles from their tropical accession parents that contribute to enhanced productivity compared with Mo44 alleles. Although none of the semiexotic line testcrosses was competitive with current commercial hybrids for grain yield, neither was their temperate parent testcross, Mo44 × (LH132 × LH51), nor their single-cross tester, LH132 × LH51 (Tables 2 and 3). Furthermore, the commercial cultivars are single-cross hybrids, whereas the semiexotic line testcrosses were three-way crosses, with less potential for heterosis. We hypothesize that semiexotic hybrids competitive with commercial cultivars could be developed by transferring the favorable exotic-derived alleles recovered in these semiexotic lines

to superior genetic backgrounds and crossing the resulting lines to elite inbred testers.

The semiexotic lines we evaluated were less homozygous ( $F = 0.87$ ) than inbreds typically used to produce commercial hybrids. Several more generations of self-fertilization would be required to produce highly inbred lines, and some of the exotic alleles maintained in the semiexotic lines tested in this study could be lost during additional generations of inbreeding. However, it is likely that exotic alleles with strongly deleterious effects were already eliminated in the early generations of inbreeding and selection, so that additional inbreeding and selection would cause only relatively minor changes in allele frequencies. Therefore, it should be possible to develop highly inbred semiexotic lines similar to the lines evaluated in this study in terms of their proportions of exotic germplasm and testcross performances.

Because the semiexotic lines have distinct genetic backgrounds compared with the commercial maize of the USA, it is likely that some of the favorable yield alleles they inherited from their tropical accession parents are not represented in the elite maize breeding germplasm of the USA. Furthermore, Holland and Goodman (1995) reported that the parental semiexotic populations of these inbred lines exhibited similar levels of heterosis when combined with either Reid Yellow Dent or Lancaster Sure Crop testers. This result suggests that

the tropical landraces contain alleles for productivity absent from both of the major heterotic groups used in the USA and that lines from most tropical accessions can be considered a third heterotic group with respect to Reid Yellow Dent and Lancaster Sure Crop temperate germplasm. This alternative heterotic group provides maize breeders with a new source of parental breeding lines that can contribute to broadening the genetic base of modern U.S. inbred lines without sacrificing productivity.

## REFERENCES

- Brown, W.L. 1953. A summary of maize breeding techniques. *Trop. Agric.* 30:1–12.
- Brown, W.L. 1975. A broader germplasm base in corn and sorghum. p. 81–89. *In* H.D. Loden and D.B. Wilkinson (ed.) *Proc. 30th Annu. Corn and Sorghum Industry Res. Conf.*, Chicago, IL. 9–11 Dec. 1975. Am. Seed Trade Assoc., Washington, DC.
- Brown, W.L. 1988. Plant genetic resources: A view from the seed industry. p. 218–230. *In* J. R. Kloppenburg (ed.) *Seeds and Sovereignty*. Duke Univ. Press, Durham, NC.
- Brownie, C., D.T. Bowman, and J.W. Burton. 1993. Estimating spatial variation in analysis of data from yield trials: A comparison of methods. *Agron. J.* 85:1244–1253.
- Castillo-Gonzalez, F., and M.M. Goodman. 1989. Agronomic evaluation of Latin American maize accessions. *Crop Sci.* 29:853–861.
- Committee on Preservation of Indigenous Strains of Corn. 1954. Collections of original strains of corn, I. Division of Biol. and Agric., Nat. Acad. Sci., Nat. Res. Council, Washington, DC.
- Committee on Preservation of Indigenous Strains of Corn. 1955. Collections of original strains of corn, II. Division of Biol. and Agric., Natl. Acad. Sci., Natl. Res. Council, Washington, DC.
- Crossa, J., and C.O. Gardner. 1987. Introgression of exotic germplasm for improving an adapted maize population. *Crop Sci.* 27:187–190.
- Darrah, L.L., and M.S. Zuber. 1986. 1985 United States farm maize germplasm base and commercial breeding strategies. *Crop Sci.* 26:1109–1113.
- del-Blanco, I.A., S. Rajaram, and W.E. Kronstad. 2001. Agronomic potential of synthetic hexaploid wheat-derived populations. *Crop Sci.* 41:671–676.
- Gerdes, J.T., and W.F. Tracy. 1993. Pedigree diversity within Lancaster Sure Crop heterotic group of maize. *Crop Sci.* 33:334–337.
- Goodman, M.M. 1983. Racial diversity in maize. p. 29–40. *In* D.T. Gordon et al. (ed.) *Proc. Int. Maize Virus Disease Colloq. and Workshop*, Wooster, OH. 2–6 Aug. 1982. Ohio State Univ., Ohio Agric. Res. and Dev. Center, Wooster, OH.
- Goodman, M.M. 1985. Exotic maize germplasm: Status, prospects, and remedies. *Iowa State J. Res.* 59:497–527.
- Goodman, M.M. 1990. Genetic and germ plasm stocks worth conserving. *J. Hered.* 81:11–16.
- Goodman, M.M. 1999. Broadening the genetic diversity in maize breeding by use of exotic germplasm. p. 139–148. *In* J.G. Coors and S. Pandey (ed.) *Genetics and exploitation of heterosis in crops*. ASA, Madison, WI.
- Goodman, M.M., J. Moreno, F. Castillo, R.N. Holley, and M.L. Carson. 2000. Using tropical maize germplasm for temperate breeding. *Maydica* 45:221–234.
- Grant, U.J., W.H. Hatheway, and D.H. Timothy. C. Cassalet D., and L.M. Roberts. 1963. Races of maize in Venezuela. National Academy of Sciences. Washington, DC.
- Hawbaker, M.S., W.H. Hill, and M.M. Goodman. 1997. Application of recurrent selection for low grain moisture content at harvest in tropical maize. *Crop Sci.* 37:1650–1655.
- Holland, J.B., and M.M. Goodman. 1995. Combining ability of tropical maize accessions with U.S. germplasm. *Crop Sci.* 35:767–773.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. SAS System for mixed models. SAS Institute Inc., Cary, NC.
- Lynch, M., and B. Walsh. 1997. Genetics and analysis of quantitative traits. Sinauer Associates, Inc., Sunderland, MA.
- Paterniani, E., and M.M. Goodman. 1977. Races of maize in Brazil and adjacent areas. Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico.
- Pollak, L.M., and W. Salhuana. 1998. Lines for improved yield and value-added traits results from GEM. p. 143–158. *In* *Proc. 53rd Annu. Corn and Sorghum Industry Res. Conf.*, Chicago, IL. 9–10 Dec. 1998. Am. Seed Trade Assoc., Washington, DC.
- Ramírez, R.E., D.H. Timothy, E. Díaz B., and U.J. Grant. 1960. Races of maize in Bolivia. Natl. Acad. Sci., Washington, DC.
- Salhuana, W., Q. Jones, and R. Sevilla. 1991. The Latin American Maize Project: Model for rescue and use of irreplaceable germplasm. *Diversity* 7:40–42.
- SAS Institute. 2000. SAS user's guide version 8: Statistics. SAS Inst., Cary, NC.
- Self, S.G., and K. Liang. 1987. Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. *J. Am. Statist. Assoc.* 82:605–610.
- Smith, J.S.C. 1988. Diversity of United States hybrid maize germplasm: Isozymic and chromatographic evidence. *Crop Sci.* 28:63–69.
- Smith, J.S.C., D.N. Duvik, O.S. Smith, A. Grunst, and S.J. Wall. 1999. Effect of hybrid breeding on genetic diversity in maize. *In* J.G. Coors and S. Pandey (ed.) *Genetics and exploitation of heterosis in crops*. ASA, Madison, WI.
- Stuber, C.W. 1978. Exotic sources for broadening genetic diversity in corn breeding programs. p. 34–47. *In* H.D. Lodgen and D. Wilkinson (ed.) *Proc. 33rd Annu. Corn and Sorghum Industry Res. Conf.*, Chicago, IL. 12–14 Dec. 1978. Am. Seed Trade Assoc., Washington, DC.
- Timothy, D.H., W.H. Hatheway, and U.J. Grant, M. Torregroza C., D. Sarria V., and D. Varla A. 1963. Races of maize in Ecuador. Natl. Acad. Sci., Washington, DC.
- Thompson, J.A., and R.L. Nelson. 1998. Utilization of diverse germplasm for soybean yield development. *Crop Sci.* 38:1362–1368.
- Troyer, A.F. 1999. Background of U.S. hybrid corn. *Crop Sci.* 39:601–626.