

Combining Ability of Tropical Maize Accessions with U.S. Germplasm

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ABSTRACT

To supplement minimal information regarding the utility of tropical maize (*Zea mays* L.) germplasm to temperate maize breeding programs, agronomic evaluations of typical accessions of the Latin American races were made. Based on data from previous evaluation stages, 40 accessions exhibiting superior agronomic performance in tropical environments were chosen for photoperiod conversion and combining-ability evaluations with U.S. germplasm in temperate environments. Accessions were converted to photoperiod insensitive semiexotic populations by crossing each to Mo44, a temperate-adapted inbred unrelated to either of two major U.S. heterotic groups. Four families from each semiexotic population were crossed to two U.S. testers. Testcrosses were evaluated in three North Carolina locations for 2 yr. Based on these results, 29 agronomically superior semiexotic testcrosses were tested a third year. The variation for combining ability for yield was estimated to be two times greater among vs. within accessions, suggesting that sampling among accessions be given priority compared with sampling within to maximize genetic diversity for combining ability. Family yields were highly correlated across testers ($r = 0.78$), suggesting that a single temperate tester would be sufficient for evaluating large samples of Latin American accessions. Grain yields, resistance to gray leaf spot disease (incited by *Cercospora zea-maydis* Tehon & E.Y. Daniels), and other agronomic traits of superior semiexotic testcrosses were competitive with the public U.S. hybrid Mo17 × B73. The best accessions should be a promising source of useful genes for commercial U.S. maize breeding programs.

APPROXIMATELY 20 000 ACCESSIONS of Latin American maize have been collected, most of which have been classified into about 250 races (Goodman, 1983; Goodman and Brown, 1988). In contrast to the genetic diversity represented by these accessions, the germplasm base of commercial U.S. maize is narrow. United States hybrids are derived almost exclusively from a few open-pollinated cultivars of a single race, Corn Belt Dent (Baker, 1986; Goodman and Brown, 1988). Furthermore, pedigrees are extensively duplicated (Darrah and Zuber, 1986; Goodman, 1990) and genetic uniformity can be detected by isozyme and RFLP marker studies (Smith, 1988; Smith et al., 1992) of modern U.S. hybrids. Among the potential consequences of this narrow genetic base are increased susceptibility to genetic shifts in pathogen populations and reduced chances for long-term genetic improvement.

Use of exotic maize to broaden the germplasm base of U.S. maize has been advocated by many breeders (e.g., Brown, 1953; Geadelmann, 1984; Hallauer, 1978). The minor use of exotic germplasm by U.S. commercial maize breeders results, at least in part, from problems in adapting tropical maize to temperate environments (Goodman, 1985; Smith et al., 1992). In temperate regions, many tropical maize cultivars exhibit weak roots

and stalks, late maturity due to photoperiod sensitivity, and susceptibility to smut [*Ustilago maydis* (DC.) Cda.; Goodman, 1985]. Another obstacle to the incorporation of tropical maize into U.S. breeding programs is that, until recently, little information was available regarding the agronomic utility of these accessions (Goodman, 1992).

The Latin American Maize Project currently is identifying tropical racial accessions with superior agronomic and breeding qualities (Salhuana et al., 1991; Pollak, 1993). A similar, smaller-scale project was conducted by Goodman (1983) and Castillo-Gonzalez and Goodman (1989). Goodman (1983) collected agronomic information on ≈ 1300 typical Latin American racial accessions in a short-day environment in southern Florida. About 400 of the better racial accessions were chosen for additional evaluation in replicated yield trials in short-day environments in Florida and Texas (Castillo-Gonzalez and Goodman, 1989). Based on the results of Castillo-Gonzalez and Goodman (1989), we chose 40 accessions to convert to photoperiod insensitivity and to evaluate combining ability involving temperate germplasm. One objective of our study was to identify tropical germplasm accessions that showed promising breeding values for important agronomic traits in temperate areas, such as grain yield and moisture, standability, flowering date, and resistance to gray leaf spot (GLS), incited by *Cercospora zea-maydis* (Tehon and Daniels, 1925).

A second objective was to obtain information on the heterotic patterns of racial accessions in combination with temperate germplasm. Pollak et al. (1991) and Geadelmann (1984) reported that some tropical maize germplasm exhibits important population by tester interactions when combined with the predominant U.S. heterotic groups, Lancaster Sure Crop and Reid Yellow Dent. Gerrish (1983), in contrast, found no significant specific combining ability effects for yield in a diallel study involving three tropical and three Corn Belt populations. The heterotic patterns of tropical accessions by U.S. maize should be understood to effectively integrate tropical maize into temperate breeding programs.

A third objective was to assess the relative amounts of genetic variation within and among accessions for combining ability. A racial accession generally represents a collection of an open-pollinated, farmer cultivar of a single land race. High levels of genetic variability within accessions have been reported (Doebly et al., 1985). To devise efficient sampling procedures for future evaluation of tropical accessions, it is necessary to determine whether sampling within or among accessions should be emphasized.

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MATERIALS AND METHODS

All 40 tropical racial accessions chosen for evaluation (Table 1) represented single farmer collections, except Cateto DES I, Cateto MG II, Cateto Nortista GIN I (Paterniani and Goodman, 1977), and Amarillo Salvadoreño Comp. (Wellhausen et al., 1957). These are regional composites of phenotypically similar collections. Accessions considered to be related to U.S. Corn Belt germplasm were excluded from the present study.

Photoperiod Conversion

To effectively evaluate combining ability in a temperate environment, photoperiod sensitivity must be overcome. Hallauer and Sears (1972) and Spencer (1978) reduced photoperiod sensitivity by selecting within genetically broad-based tropical compos-

ite populations directly. However, each individual racial accession included in our study represented a much narrower base of germplasm. Recovery of photoperiod insensitive individuals from within-accession crosses may not readily be possible.

Maunder (1992) described a successful photoperiod conversion program for tropical sorghum [*Sorghum bicolor* (L.) Moench] in which accessions were crossed to a photoperiod-insensitive inbred and the less photoperiod-sensitive progeny in the segregating populations were selected for backcrossing to the accessions. Each racial accession was crossed to a temperate-adapted, photoperiod-insensitive inbred line, Mo44, to produce *semiexotic populations*. The Mo44 line was derived from a cross of Mo22 and Pioneer Mexican Synthetic 17 (Gerdes and Tracy, 1993) and is largely unrelated to either Reid Yellow Dent or Lancaster Sure Crop heterotic groups.

Table 1. Means† of semiexotic populations derived from 40 Latin American accessions averaged across four families, two testers, 2 yr, and three locations.

Race	Accession	Grain yield	Grain moisture	Erect plants	Ear height	DTP‡
		t ha ⁻¹	g kg ⁻¹	%	m	d
Data from 1991-1992						
Canilla	VEN 981	7.97	162	92	1.12	74
Tusón	BAI III	7.79	158	92	1.15	73
Puya	SAN 349	7.73	157	94	1.11	73
Tuxpeño	VEN 598	7.72	164	94	1.16	74
Tuxpeño	VEN 767	7.72	161	89	1.17	75
Cubano Amarillo Duro	ECU 904	7.69	165	92	1.16	73
Tuxpeño	ECU 942	7.69	162	92	1.19	74
Tusón	CUB 57	7.64	159	94	1.10	74
Costeño	ATL 329	7.63	161	92	1.08	73
Puya	MAG 322	7.63	165	94	1.13	74
Olotón	GUA 383	7.61	162	92	1.14	75
Perla	LIM 13	7.58	168	93	1.16	75
Cubano Dentado	BOV 585	7.56	159	88	1.13	73
Cateto Nortista	GIN I	7.53	162	90	1.15	75
Chandelle	VEN 352	7.53	160	95	1.18	75
Cubano Tusón	ECU 660	7.53	160	92	1.12	74
Costeño	MAG 350	7.49	158	92	1.16	75
Cateto	MG II	7.48	168	93	1.17	74
Cubano Amarillo Duro	ECU 653	7.45	156	91	1.11	74
Cateto	CE I	7.40	166	93	1.12	74
Cubano Amarillo Duro	ECU 770	7.40	164	94	1.14	74
Cubano Tusón	ECU 542	7.39	161	93	1.11	73
Chandelle	CUB 68	7.36	164	93	1.08	72
Cubano Amarillo Duro	ECU 326	7.36	159	90	1.15	73
Cubano Cateto	ECU 339	7.36	160	93	1.13	74
Cubano Amarillo Duro	ECU 327	7.33	160	93	1.23	74
Costeño	ATL 314	7.32	159	91	1.06	71
Amarillo Salvadoreño	Composite	7.28	164	95	1.15	73
Costeño	ATL 328	7.28	156	95	1.04	72
Early Caribbean	MAR 9	7.28	161	92	1.06	73
Tusón	CUB 62	7.28	165	95	1.13	74
Cuban Flint	CUB 63	7.27	157	92	1.16	73
Tepecintle	GUA 597	7.26	156	90	1.09	72
Morado	BOV 402	7.22	159	94	1.08	73
Cateto	DES I	6.95	163	94	1.08	73
Dzit Bacal	GUA 131	6.92	153	91	1.10	74
Nal-Tel	GUA 110	6.83	153	94	1.03	71
Coroico Blanco	BOV 582	6.72	160	93	1.09	74
Mean of exotic testcrosses		7.42	161	93	1.12	73
Mean of 3 commercial checks		9.09	174	97	1.10	77
LSD (0.05, exotic vs. exotic)		0.24	3	2	0.04	1
LSD (0.05, exotic vs. checks)		0.21	2	2	0.03	1
CV, %		3	1	4	4	1
Data from 1992-1993						
Cariaco	VEN 408	6.51	163	89	1.22	77
Negrilo	MAG 321	6.32	156	82	1.16	74
Mean of exotic testcrosses		6.42	159	85	1.19	75
Mean of 3 commercial checks		8.21	182	91	1.14	79
LSD (0.05, exotic vs. exotic)		0.51	4	7	0.06	1
LSD (0.05, exotic vs. check)		0.81	7	12	0.09	1
CV, %		8	3	9	6	1

† Means not adjusted for lattice effects.

‡ Days from planting to 50% pollen shed; measured at Clayton, NC, only.

Four plants per accession were mated as females to Mo44 in southern Florida during the winter of 1985-1986 to produce four full-sib, semiexotic families. The following summer in Clayton, NC, the earliest maturing plants were intermated among full-sib families within each population to produce four more full-sib families per population. This procedure was repeated for two more generations in Clayton, NC, during the summers of 1987 and 1988. The four full-sib families harvested per population in 1988 represented photoperiod-insensitive versions of the original semiexotic populations. Each full-sib family was then crossed to two testers: A632*Ht* × B73*Ht* (referred to as TR, representing the Reid Yellow Dent heterotic group) and Mo17*Ht* × Oh43E (referred to as TL, representing the Lancaster Sure Crop heterotic group). Crosses were made reciprocally between testers and semiexotic full-sib families (generally using 25 plants per family), and seed was bulked for yield trials.

Yield Trials

For 38 of the 40 semiexotic populations, each representative family was randomly assigned to one of four sets. Each set contained one full-sib family from each of 38 semiexotic populations, each crossed to two testers. In addition, (i) the public hybrid, B73*Ht* × Mo17*Ht*, (ii) the three-way cross of B73*Ht* × Mo17*Ht* to the temperate-adapted, 100% tropical public inbred line, NC296, and (iii) three commercial hybrid checks, Pioneer brand 3165, Northrup King brand N8727, and DEKALB brand 689, were included, for a total of 81 entries in each set. A replications-within-sets field design was used, with three replications of each set grown at three environments (Clayton, Lewiston, and Plymouth, NC) for 2 yr (1991 and 1992). Each set was analyzed as a nine by nine triple lattice design, and adjusted lattice means within sets are presented where noted. Each set was also analyzed as a randomized complete-block design for the purposes of combining analyses across sets (see later).

The other two semiexotic populations, representing the races Cariaco and Negrito, were tested in a separate experiment. Four full-sib families of each population crossed to the two testers and four check hybrids were grown in three replications at each of the three North Carolina locations in 1992 and 1993. This test was analyzed as a triple rectangular lattice design of five blocks of four entries per block.

In all experiments, each test plot was two 4.86-m rows, including a 1-m alley at the end of each plot. Interrow spacing was 0.97 m at Clayton and Plymouth and 0.91 m at Lewiston.

Plots were planted with 44 kernels per plot. Average plant densities were 43 200 plants ha⁻¹ in Clayton and Plymouth and 45 600 plants ha⁻¹ in Lewiston. Grain yield adjusted to 155 g kg⁻¹ moisture, weight of moisture per mass of grain, height of uppermost ear, and percentage erect plants were recorded for each plot. Days from planting to 50% pollen shed were recorded on every plot at Clayton only.

Advanced Yield Trials

Based on performance within sets, the 29 highest yielding full-sib family topcrosses were chosen for the advanced yield trial experiments. No entries were chosen from the Cariaco/Negrito experiment due to their poor performances relative to the checks. The same five check entries used in the 1991 to 1992 trials and the three-way crosses of Mo44 to A632*Ht* × B73*Ht* and Mo17*Ht* × Oh43E were included. A six by six triple lattice design was used, with three replications planted at the three North Carolina locations in 1993. Because 320 testcrosses were evaluated initially, we present individual testcross data only for the entries tested for 3 yr.

Gray Leaf Spot Resistance Evaluation

The GLS disease does not occur in the coastal plain environments where the yield trials were conducted. Therefore, two replications of the advanced yield trial experiment also were planted at Laurel Springs, NC, a mountain environment (elevation 995 m), to evaluate resistance to GLS. Plot length and seeding rates were the same as for yield trials, except 1-row plots were used. The experiment was artificially inoculated ≈ 60 d after planting by placing sorghum grains infected with the fungus in the whorl of each plant. Each plot was visually rated on a scale of 1 (susceptible, dead plants) to 9 (resistant, no lesions). The experiment was scored on four dates after flowering: 10 Aug., 20 Aug., 10 Sept., and 19 Sept. 1993. Mean scores across the four dates were analyzed.

Analysis of Variance and Variance Component Estimation

An analysis of variance across sets was performed on the data from the original yield trial experiments (except for the Cariaco/Negrito trial) to estimate the amount of variability for grain yield due to different sources of variation (Table 2). Data from the check entries were eliminated prior to analysis. Each year × location combination was considered an environment, and entry means from each environment (not adjusted for

Table 2. Analysis of variance for grain yield, not including check entries, for entry means obtained from randomized complete-block analyses for each environment.

Source	df	Mean square	Expected mean square
Environment [E]	5	189.127***	$\sigma_e^2 + 2\sigma_{ESA}^2 + 8\sigma_{EA}^2 + 76\sigma_{ES}^2 + 304\sigma_E^2$
Set [S]	3	4.481	$\sigma_e^2 + 2\sigma_{ESA}^2 + 12\sigma_{SA}^2 + 76\sigma_{ES}^2 + 456\sigma_S^2$
E × S	15	6.061***	$\sigma_e^2 + 2\sigma_{ESA}^2 + 76\sigma_{ES}^2$
Tester [T]	1	14.874	$\sigma_e^2 + 6\sigma_{TAS}^2 + 4\sigma_{TAE}^2 + 38\sigma_{EST}^2 + 24\sigma_{TA}^2 + 228\sigma_{ST}^2 + 152\sigma_{ET}^2 + 912\sigma_T^2$
E × T	5	4.114***	$\sigma_e^2 + 4\sigma_{TAE}^2 + 38\sigma_{EST}^2 + 152\sigma_{ET}^2$
S × T	3	0.051	$\sigma_e^2 + 6\sigma_{TAS}^2 + 38\sigma_{EST}^2 + 228\sigma_{ST}^2$
E × S × T	15	0.113	$\sigma_e^2 + 38\sigma_{EST}^2$
Accession [A]	37	3.405***	$\sigma_e^2 + 2\sigma_{ESA}^2 + 12\sigma_{SA}^2 + 8\sigma_{EA}^2 + 48\sigma_A^2$
T × A	37	0.602***	$\sigma_e^2 + 6\sigma_{TAS}^2 + 4\sigma_{TAE}^2 + 24\sigma_{TA}^2$
E × A	185	0.230***	$\sigma_e^2 + 2\sigma_{ESA}^2 + 8\sigma_{EA}^2$
S × A	111	0.510***	$\sigma_e^2 + 2\sigma_{ESA}^2 + 12\sigma_{SA}^2$
E × S × A	555	0.140	$\sigma_e^2 + 2\sigma_{ESA}^2$
T × A × E	185	0.135	$\sigma_e^2 + 4\sigma_{TAE}^2$
T × A × S	111	0.215***	$\sigma_e^2 + 6\sigma_{TAS}^2$
Error	555	0.133	σ_e^2
Corrected total	1823		

*** Significant at the 0.001 probability level.

Table 3. Means† of best semiexotic topcross entries in Set 1 averaged across three locations and 3 yr.

Entry‡	Grain yield	Grain moisture	Erect plants	Ear height	DTP§	GLS¶
	t ha ⁻¹	g kg ⁻¹	%	m	d	score
Canilla VEN 981-a × TR	7.86	162	92	1.16	74	5.8
Canilla VEN 981-a × TL	8.11	161	94	1.07	74	8.0
Costeño ATL 329-a × TL	7.76	164	96	0.99	72	7.4
Cub. A.D. ECU 770-a × TL	7.75	162	94	1.05	73	6.9
Cub. Den. BOV 585-a × TL	7.81	158	96	1.10	73	6.3
Puya SAN 349-a × TL	7.77	157	96	1.05	71	7.0
Tepec. GUA 597-a × TL	7.52	155	96	1.02	71	7.0
Tusón BAI III-a × TR	7.72	157	95	1.15	73	6.1
Tusón BAI III-a × TL	7.79	156	97	1.09	72	7.0
Tuxpeño VEN 767-a × TL	7.70	163	94	1.06	73	7.8
DEKALB 689	9.04	170	97	1.08	75	7.4
Mo17Ht × B73Ht	7.86	146	96	1.05	72	5.4
(Mo17Ht × B73Ht) × NC296	8.56	169	96	1.20	74	7.3
Northrup King N8727	8.86	176	97	0.97	74	5.5
Pioneer 3165	8.83	189	97	1.11	77	4.9
Mean	8.06	163	96	1.08	73	6.7
LSD (0.05)	0.39	5	3	0.05	1	0.8
CV, %	5	3	3	5	1	6

† Means adjusted for lattice effects.

‡ Letter following accession name designates family within accession; TR = A632Ht × B73Ht, TL = Mo17Ht × Oh43E.

§ Days from planting to 50% pollen shed; measured at Clayton, NC, only.

¶ Gray leaf spot (GLS) score (1 = susceptible, 9 = resistant); data from 1993 only.

lattice block effects) were analyzed. Environments, accessions (represented by semiexotic populations), and sets were considered random effects, whereas testers were considered a fixed effect. Expected mean squares were derived following Schultz (1955). Quasi *F* ratios were used to approximate *F* tests where appropriate (Satterthwaite, 1946). Families within accessions were confounded with sets, so variation among families within accessions included variation due to field block effects. Thus, the interaction of sets and accessions was considered an estimate of the effect of families within accessions, corrected for mean set effects, and possibly biased upward by genotype × environment interaction variance.

Variance components were estimated by equating the expected mean squares with the observed mean squares and solving for the individual variance components. Variances of estimated variance components were calculated following the method of Anderson and Bancroft (1952).

The entry means from each set in each environment also served to identify accessions that exhibited significant interactions with testers. The mean yield at each environment of each entry crossed to TR was defined as a new variable, TR-Yield. Similarly, the mean yield of each entry crossed to TL was termed TL-Yield. The difference between these two variables

was termed Yield-Diff. Analyses of variance for each of the three variables were performed, and appropriate estimates of the error variance for comparisons among accession means were constructed based on the expectations of the mean squares. Degrees of freedom for these error variances were estimated following Satterthwaite (1946). The coefficient of linear correlation between entry yields on the two testers was calculated from unadjusted entry means to remove bias due to lattice effects.

RESULTS AND DISCUSSION

Mean values for important agronomic traits of each semiexotic population averaged across all other factors are presented in Table 1. Data from the advanced yield trials are shown in Tables 3 to 6. The following entries from these advanced trials had yields equal to or greater than Mo17Ht × B73Ht: Canilla VEN 981-a × TR and Canilla VEN-a 981 × TL (Table 3); Cubano Amarillo Duro ECU 904-c × TL, and Puya MAG 322-c × TL (Table 5); Costeño ATL 329-d × TL, Perla LIM 13-d × TL, and Tuxpeño VEN 598-d × TR (Table 6). The

Table 4. Means† of best semiexotic topcross entries in Set 2 averaged across three locations and 3 yr.

Entry‡	Grain yield	Grain moisture	Erect plants	Ear height	DTP§	GLS¶
	t ha ⁻¹	g kg ⁻¹	%	m	d	score
Canilla VEN 981-b × TR	7.82	163	95	1.16	74	5.6
Canilla VEN 981-b × TL	7.96	161	96	1.02	73	6.8
Chandelle VEN 352-b × TL	7.72	164	96	1.12	74	8.4
Perla LIM 13-b × TL	7.61	171	96	1.05	73	6.8
Puya SAN 349-b × TL	7.73	155	95	1.06	72	5.9
Tusón BAI III-b × TL	7.75	159	92	1.10	72	7.9
DEKALB 689	8.91	171	97	1.08	76	7.4
Mo17Ht × B73Ht	8.00	148	95	1.05	73	5.4
(Mo17Ht × B73Ht) × NC296	8.79	169	96	1.21	75	7.3
Northrup King N8727	8.86	177	98	0.98	75	5.5
Pioneer 3165	8.65	189	95	1.09	77	4.9
Mean	8.16	166	95	1.08	74	6.5
LSD (0.05)	0.39	6	3	0.05	1	0.8
CV, %	5	4	3	5	1	6

† Means adjusted for lattice effects.

‡ Letter following accession name designates family within accession; TR = A632Ht × B73Ht, TL = Mo17Ht × Oh43E.

§ Days from planting to 50% pollen shed; measured at Clayton, NC, only.

¶ Gray leaf spot (GLS) score (1 = susceptible, 9 = resistant); data from 1993 only.

Table 5. Means† of best semiexotic topcross entries in Set 3 averaged across three locations and 3 yr.

Entry‡	Grain yield	Grain moisture	Erect plants	Ear height	DTP§	GLS¶
	t ha ⁻¹	g kg ⁻¹	%	m	d	score
Cub A.D. ECU 904-c × TL	7.84	170	93	1.10	73	6.5
Cub Tus ECU 660-c × TL	7.80	158	94	1.10	73	8.0
Olotón GUA 383-c × TR	7.59	170	96	1.09	74	6.3
Puya MAG 322-c × TR	7.71	162	95	1.18	74	6.1
Puya MAG 322-c × TL	7.94	161	97	1.12	74	7.0
Puya SAN 349-c × TL	7.68	153	96	1.04	73	7.3
Tusón CUB 57-c × TR	7.65	157	96	1.13	73	5.8
Tuxpeño VEN 598-c × TL	7.70	166	95	1.13	73	7.6
Tuxpeño VEN 767-c × TL	7.80	167	92	1.08	75	7.5
DEKALB 689	8.76	169	98	1.06	76	7.4
Mo17Ht × B73Ht	7.82	147	93	1.03	72	5.4
(Mo17Ht × B73Ht) × NC296	8.52	169	96	1.18	75	7.3
Northrup King N8727	8.86	176	98	0.99	74	5.5
Pioneer 3165	8.83	188	97	1.10	77	4.9
Mean	8.04	165	95	1.10	74	6.6
LSD (0.05)	0.37	5	4	0.05	1	0.8
CV, %	5	3	4	5	1	6

† Means adjusted for lattice effects.

‡ Letter following accession name designates family within accession; TR = A632Ht × B73Ht, TL = Mo17Ht × Oh43E.

§ Days from planting to 50% pollen shed; measured at Clayton, NC, only.

¶ Gray leaf spot (GLS) score (1 = susceptible, 9 = resistant); data from 1993 only.

yield advantage of none of these entries over B73Ht × Mo17Ht, however, was significant at $P = 0.05$. Also, the semiexotic testcrosses did not perform competitively with the current commercial hybrid checks. On the other hand, none of the semiexotic testcrosses chosen for advanced yield trials yielded significantly less than Mo17Ht × B73Ht. Smith (1988) reported that commercial U.S. maize breeding programs were heavily dependent on usage of B73 and Mo17 (along with A632 and Oh43) or closely related lines. Therefore, the performance of these semiexotic topcrosses (which have not yet been fully developed by intensive plant breeding) relative to that of Mo17Ht × B73Ht indicated that the superior racial accessions identified in this study are a useful source of unique germplasm for improving yield in temperate environments.

In addition to yield, all semiexotic testcrosses in the advanced trials performed at least reasonably well for the other agronomic traits measured. No semiexotic entries flowered later or had greater grain moisture than Pioneer 3165. Some semiexotic entries had significantly poorer standability than the commercial checks, but the lowest mean percentage erect plants was only 92% (Tables 3–6).

None of the semiexotic testcrosses had ear heights that were more than 0.1 m greater than Pioneer 3165 (Tables 3–6).

Comparisons among semiexotic testcrosses and Mo44 testcrosses were available only from the advanced yield trial data (1993 data; not shown). Twenty-four of the 29 testcrosses evaluated in 1993 yielded more than Mo44 × TR, and all 29 testcrosses yielded more than Mo44 × TL. These results suggested that favorable alleles for yield in the exotic accessions were maintained in the photoperiod-converted populations and that the better accessions contained germplasm that was superior to Mo44 for combining ability with Corn Belt maize for yield.

The overall effect of testers on yield was not significant (Table 2). The coefficient of correlation for full-sib family yields across testers was $r = 0.78$ ($P < 0.0001$). This suggested that an initial testing of tropical accessions on a single temperate tester would be appropriate. The high yields of several families on both testers (e.g., Canilla VEN 981-a, Table 3, and Puya MAG 322-c, Table 5) suggested that some accessions could have broad utility in U.S. breeding programs. Five of 38 accessions tested in the main experiments showed significant differences

Table 6. Means† of best semiexotic topcross entries in Set 4 averaged across three locations and 3 yr.

Entry‡	Grain yield	Grain moisture	Erect plants	Ear height	DTP§	GLS¶
	t ha ⁻¹	g kg ⁻¹	%	m	d	score
Costeño ATL 329-d × TL	7.64	163	96	1.04	71	7.0
Perla LIM 13-d × TL	7.64	170	95	1.12	74	7.0
Tuxpeño VEN 598-d × TR	7.69	162	94	1.20	73	5.4
Tuxpeño VEN 598-d × TL	7.59	168	95	1.07	73	7.3
DEKALB 689	8.79	169	98	1.12	76	7.4
Mo17Ht × B73Ht	7.62	147	97	1.04	72	5.4
(Mo17Ht × B73Ht) × NC296	8.58	167	95	1.19	74	7.3
Northrup King N8727	8.80	173	99	0.98	75	5.5
Pioneer 3165	8.68	186	97	1.10	77	4.9
Mean	8.11	167	96	1.09	74	6.4
LSD (0.05)	0.47	6	3	0.05	2	0.8
CV, %	6	4	3	5	1	6

† Means adjusted for lattice effects.

‡ Letter following accession name designates family within accession; TR = A632Ht × B73Ht, TL = Mo17H5 × Oh43E.

§ Days from planting to 50% pollen shed; measured at Clayton, NC, only.

¶ Gray leaf spot (GLS) score (1 = susceptible, 9 = resistant); data from 1993 only.

Table 7. Mean grain yields† of semiexotic populations yielding significantly differently ($P = 0.05$) on two testers, averaged across four families, three locations, and 2 yr.

Population		Tester‡		Difference (TR - TL)
Race	Accession	Reid (TR)	Lancaster (TL)	
t ha ⁻¹				
Coroico Blanco	BOV 582	7.03	6.42	+ 0.61
Cuban Dent	BOV 585	7.33	7.79	- 0.46
Nal-Tel	GUA 110	6.47	7.19	- 0.73
Puya	SAN 349	7.49	7.97	- 0.48
Tepecintle	GUA 597	6.93	7.60	- 0.67
Mean of all accessions		7.34	7.52	- 0.18
LSD (0.05)		0.34	0.38	0.38

† Mean grain yields not adjusted for lattice effects.

‡ TR = A632Ht × B73Ht, TL = Mo17Ht × Oh43E.

between their yields on Reid Yellow Dent vs. Lancaster Sure Crop testers (Table 7). No geographic or phylogenetic relationships were obvious among accessions that interacted with the testers.

The fact that most of the semiexotic populations exhibited opposite heterotic responses to those of Mo44 with the Reid Yellow Dent and Lancaster Sure Crop testers provided further evidence that exotic germplasm was maintained in the semiexotic populations during selection for photoperiod insensitivity. The mean yield of the 38 semiexotic populations crossed to the Reid Yellow Dent tester in the main experiments was 0.18 t ha⁻¹ less than the mean Lancaster Sure Crop testcross yield. The Reid Yellow Dent testcrosses ranked higher for yield than did the Lancaster Sure Crop testcross for only 5 of 38 populations. In contrast, in the 1993 experiment, Mo44 × TR yielded 0.60 t ha⁻¹ greater than Mo44 × TL.

The set by accession interaction component of variance included genetic variation among families within accessions. Although substantial variation for combining ability existed within accessions (estimate of $\sigma_{SA}^2 = 0.031 \pm 0.006$), variance among accessions was estimated to be 0.058 ± 0.016 , approximately two times greater. In an evaluation of tropical accessions, sampling among accessions should be assigned priority compared with sampling within accessions. Fifteen accessions were represented among the 29 entries in the advanced yield trials. All 15 were represented in three (Sets 1-3) of four random sets. Therefore, to identify superior accessions at this level of selection intensity (29/320), samples of four families per accession was adequate. An alternative scheme would be to initially ignore family structure within semiexotic populations and to testcross bulked samples of each accession. After identifying the best accessions, individual families from these accessions could be sampled for further testing and selection.

The results of the disease trial indicated that many of the tropical accessions with good combining ability for yield also possessed resistance to GLS (Tables 3-6). Twenty-six of 29 semiexotic testcrosses were more resistant to GLS than was their respective Mo44 testcross check, with 10 of these differences being significant ($P = 0.05$). One semiexotic testcross, Chandelle VEN 352-b × TL, was significantly more resistant than was DEKALB 689 (Table 4), the most widely grown GLS

resistant hybrid in North Carolina. The sources of GLS resistance discovered in this experiment may be useful for improving levels of GLS resistance in commercial hybrids because this trait is apparently conditioned by multiple genes (Bubeck et al., 1993).

Our results suggested that superior tropical maize accessions are a useful source of germplasm for commercial U.S. maize breeding programs. Previous experience with open-pollinated tropical maize populations indicated that inbreeding depression for yield may be severe in semiexotic populations (Goodman, 1992). This will limit their immediate utility in temperate hybrid breeding programs. Use of slow rates of inbreeding via sib-mating has proven an effective method for extracting inbreds from tropical maize germplasm (Holley and Goodman, 1988; Uhr, 1991). The increased chances for recombination during sib-mating compared with during selfing was the probable explanation for this observation. We have chosen 69 semiexotic families, representing 29 accessions, based on the data in this experiment, for inbred line development through sib-mating. Our goal is to develop a diverse set of 50% tropical inbred lines, each representing a well-defined racial background and possessing good combining ability with U.S. Corn Belt germplasm.

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