

DEVELOPING TEMPERATE INBREDS USING TROPICAL MAIZE GERMPLASM: RATIONALE, RESULTS, CONCLUSIONS¹

M.M. Goodman*

Department of Crop Science, North Carolina State University, Raleigh, NC 27695, U.S.A.

Received December 23, 2003

ABSTRACT - Use of exotic germplasm in U.S. maize (*Zea mays* L.) hybrids increased almost 3-fold from 1984 to 1996, but use of tropical exotic germplasm still reached only 0.3% in 1996. The focus of this paper is intensive use of tropical germplasm in temperate areas, rather than the more commonly used backcross or introgression procedure that introduces small segments of tropical germplasm into a mostly temperate background. More specifically, can largely-tropical germplasm lead to improvement in polygenic traits such as yield, in addition to being a source of disease- and insect-resistance? Yield-trial data demonstrate that at least a few largely-tropical or completely-tropical inbreds can be crossed with domestic materials to produce topcross hybrids that are competitive with commercial hybrids. Similarly, a few GEM (Germplasm Enhancement of Maize) F₂S₂, 50%-tropical families have topcross yields at least equivalent to those of commercial hybrids. Development of temperate-adapted, largely-tropical inbreds usually requires a slower approach to homozygosity (STRINGFIELD, 1974) than conventional ear-to-row selfing. Early selection within a variable exotic source is not necessary for developing partly-exotic inbreds, but variance component distributions among and within lines under development suggest that selection within the variable F₁ would be helpful if only a small portion of the exotic variation is desirable.

KEY WORDS: Tropical germplasm; Maize breeding; Germplasm base; Corn breeding; *Zea mays*.

INTRODUCTION AND RATIONALE

The rationale for use of exotic germplasm in maize breeding increases generation by generation

as elite-line recycling proceeds, especially when the recycling is concentrated on a very narrow germplasm base (SMITH, 1988). Further impetus is provided by the current emphasis on backcrossing transgenes into existing or newly-developed, elite lines, sometimes at the expense of progress available from breeding (HOLLAND and GOODMAN, 2003). For the past 50 years, maize breeders have relied on a very small set of elite inbreds, Stiff Stalk females and 'anything that works' males. The most prevalent of the recycled female families have been B14, B37 and B73. The most dominant male families used in these recycling efforts have been C103, Mo17, and Oh43 (BAKER, 1984; SMITH, 1988).

Other U.S. germplasm sources of consequence trace their ancestry to Iodent and Minnesota 13 (TROYER, 1999), often directly or indirectly from reworked Pioneer materials. Surveys of exotic germplasm use covering the 1984 and 1996 (the latter is summarized in Table 1) planting seasons (GOODMAN, 1985, 1998) indicate that the use of tropical germplasm in U.S. hybrids is minuscule (0.1% in 1983, 0.3% in 1996).

The 1996 survey covered both conventional seed companies (Pioneer, DeKalb, etc.; Table 2) and foundation seed companies (Holden's, Illinois Foundation Seeds, etc.; Table 3), and thus probably covered more than 90% of the corn seed sold in the United States. Only two non-U.S. sources contributed greatly to U.S. maize inbreds and hybrids. One was the pair of related French lines, F2 and F7, from the open-pollinated variety Lacaune. This source of germplasm was limited to use in the far North. The other source came from the Argentine variety Maíz Amargo via B64 and B68. This source has contributed small (1% to 5%) doses of germplasm to numerous hybrids throughout all maize growing regions of the United States. Note that the percentages of inbred exotic germplasm

¹ This paper is dedicated in behalf of G.H. Stringfield, a pioneering breeder whose influence continues today.

* For correspondence (fax +1 919 515 7959; e-mail: maize_resources@ncsu.edu).

TABLE 1 - Use of exotic germplasm in U.S. hybrids in 1996 (adapted from GOODMAN, 1998).

Use of temperate exotic germplasm in U.S. hybrids.				
Source	No. of Companies	No. of Hybrids	Average % Exotic	Total No. of Units Sold*
Argentina	5	75	5.6	8,887,100
Australia	2	5	5.5	138,000
Europe	5	34	7.8	1,488,800
South Africa	1	5	6.0	338,700
"Temperate"	1	1	25.0	unreported

* Golden Harvest reported sale of 3 hybrids with an average of 10% exotic germplasm from Argentine sources for which sales figures were not available. Ciba reported one hybrid with temperate exotic germplasm, but did not report either the source or the sales figure.

The overall average % of temperate exotic germplasm is 5.91% of 10,852,600 units and represents about 2.57% of the total U.S. hybrid maize seed market.

Use of tropical exotic germplasm in U.S. hybrids.

Source	No. of Companies	No. of Hybrids	Average % Exotic	Total No. of Units Sold*
Caribbean	1	19	2.1	2,834,400
Mexico	6	24	6.2	270,500
"Tropical"	2	13	26.7	1,000*

* This figure excludes a set of 12 Ciba hybrids which averaged 24.7% exotic, but for which no sales figures were provided.

The overall average % of tropical exotic germplasm is 2.47% of 3,105,900 units and represents about 0.31% of the total U.S. hybrid maize seed market.

Jointly, temperate plus tropical exotic germplasm represent about 2.88% of the U.S. market, but tropical maize germplasm represents about a ninth of the total exotic germplasm use.

that are listed in Tables 2 and 3 are not reflected in the (even lower) percentages of exotic germplasm in use in hybrids (Table 1). The main reason for this is that inbreds with exotic germplasm tend to be used more in the South or, in the case of F2/F7 germplasm, on the northern fringes of maize growing, where seed maize sales are much lower than in the Midwest.

Virtually all commercial maize breeding efforts involve the same heterotic groups: Stiff Stalk Synthetic, Lancaster Sure Crop, Iodent, and Minnesota 13 (*SLIM*). To this short list, a fifth group must be added, which will herein simply be called Pioneer.

TABLE 2 - 1994 maize seed market share by company¹ in the U.S. and the approximate percentage² of exotic germplasm in their inbreds in commercial use in 1996 (adapted from GOODMAN, 1998).

Company	1994 Market %	Inbred % Exotic ²	
		Temperate	Tropical
Pioneer Hi-Bred	44	6	6
DeKalb	9	1	4
Northrup King	4	4	0
Cargill	3	2	5
Garst	3	1	0
Golden Harvest	3	0	1
Ciba	3	3	5
Mycogen [†]	2	4	1
Asgrow	2	0	1
Limagrain	1	1	0
Agripro/Hyperformer	1	0	0
Crows	1	0	0
NC+	1	0	0
KWS	1	0	0

¹ Taken from NEWLIN (1995), LLOYD-EVANS and BARFOOT (1996) and Farm Progress Companies 1994 Nationwide Brand Study. All of these companies responded to the survey reported in Table 1. Note that Ciba has merged with Northrup King (Novartis), Mycogen now owns DowElanco's United Agriseeds, and Monsanto owns Asgrow and DeKalb. Golden Harvest (a group of 5 independent companies for which group figures may be inexact) suggests that the figures above underestimate their market share, they suggest 4% market share.

² These figures are based solely on numbers of inbreds in production use in 1996, not on hybrid sales.

[†] Percentage data for Mycogen inbreds includes both Mycogen and DowElanco.

TABLE 3 - Foundation seed companies and the approximate percentage* of exotic germplasm in their inbreds in use in 1996 (adapted from GOODMAN, 1998).

Approximate Ranking	Company	Approximate % Exotic	
		Temperate	Tropical
1	Holden's Foundation Seeds	1	1
2	Illinois Foundation Seeds	0	0
3	SGI	0	1
4	Thurston Genetics	2	2
5	MBS	†	†
6	Downing Foundation Seeds	0	0
7	FFR	0	0
8	Stine Seed	0	1
9	MGR	†	†

* These figures are based solely on numbers of inbreds in production use in 1996, not on seed sales.

[†] Data not available.

TABLE 4 - Means for Latin American maize hybrids compared to U.S. hybrids, grown in daylength-neutral conditions. Weslaco, Tx., 1984 and 1985 autumn seasons. (8 reps in 1984; 6 reps in 1985; grain moisture had 4 reps in 1984; 3 reps in 1985; adapted from CASTILLO and GOODMAN, 1988).

HYBRID	GRAIN YIELD t/ha	GRAIN MOIST %	ERCT PLTS %	EAR QLT*	SO. LF. BLT*	SO. RUST*	MALE FLW. gdu
<i>Tropical:</i>							
Pioneer 507	9.16	32.0	91	8.9	6.2	6.5	1382
Pioneer 3214	8.69	30.4	78	8.7	7.9	6.8	1402
Pioneer X304C	9.33	29.8	89	8.8	8.1	6.4	1355
<i>Domestic:</i>							
Pioneer 3055	7.50	23.1	89	8.5	5.2	3.1	1324
Pioneer 3165	6.85	22.3	89	8.0	3.3	2.9	1344
B73 x Mo17	6.35	20.3	78	7.7	3.7	3.9	1292
C.V.(%)	4.20	8.3	9	4.6	8.4	5.4	1.8
LSD(.05)	0.63	2.6	9	0.5	0.9	0.5	29

* 9 = best or no disease; 1 = worst or dead.

TABLE 5 - Comparisons of NC296A¹ topcrosses and commercial hybrids for 1992-1994 trials at Clayton, Lewiston (not 1993), and Plymouth, NC.

	Commercial Hybrid				NC296A ¹ x Hybrid			
	YIELD t/ha	% H ₂ O ²	% EP ²	GLS ³	YIELD t/ha	% H ₂ O ²	% EP ²	GLS ³
B73HtxMo17Ht	7.5	16.1	92	3.0	9.5	18.0	83	6.9
Dekalb 689	8.8	18.0	91	4.9	8.2	19.3	82	7.3
LH132 x LH82	7.1	16.8	97	5.1	9.1	18.0	89	6.7
NK N8727	9.1	18.7	95	4.0	9.8	19.8	90	6.4
Pioneer 3140	8.8	18.0	97	4.7	8.4	19.8	89	6.7
Pioneer 3162	8.8	18.8	97	3.3	9.2	20.0	89	6.7
Pioneer 3165	8.9	19.8	89	5.5	9.1	20.8	83	6.5
Pioneer 3379	7.8	15.8	97	3.5	9.2	18.0	89	6.8
Pioneer 3394	8.6	16.4	98	2.7	9.7	17.8	90	6.9
<i>Average</i>	8.2	17.5	95	3.9	9.2	19.1	87	6.8
LSD.05 (EntxEnv)	0.7	0.7	8	1.5	0.7	0.7	8	0.7
C.V.% (EntxEnv)	8	4	9	10	8	4	9	8

¹ NC296A is a temperate-adapted line that was derived from a cross of two tropical hybrids, Pioneer X105A from Jamaica and H5 from CENTA (Centro Nacional de Tecnologia Agricola) in El Salvador. Three of the lines in H5 were developed by Jesus Merino of CENTA; the fourth was from the Rockefeller program in Central America.

² % H₂O = percent moisture; % EP = percent erect plants at harvest.

³ Gray leaf spot rated only in 1992 at two locations, scored on a 9 = no disease, 1 = dead basis.

This source is notably heterogeneous, including each of the other four, plus various others (including Midland, Northwestern Dent, and several other open-pollinated varieties, see SMITH *et al.*, 1990;

TROYER, 1999) from this longest-running, major commercial breeding program. It was initiated in the 1920s by Henry Wallace and Raymond Baker; Baker provided much of the information summarized

TABLE 6 - NC296¹ and NC346¹ topcrosses vs. commercial hybrids². 1995-96: Clayton, Lewiston, Plymouth (not '96), NC.

HYBRID	Commercial			x NC296			x NC346		
	YIELD t/ha	% H ₂ O	% EP	YIELD t/ha	% H ₂ O	% EP	YIELD t/ha	% H ₂ O	% EP
B73Ht.Mo17Ht	6.8	16.6	68	8.2	18.4	81	8.2	18.1	80
DeKalb 743	7.9	19.5	78	8.3	19.6	80	8.5	19.4	83
NK N8727	8.4	19.1	86	8.8	19.4	87	8.4	19.5	84
Pioneer 3245	8.6	17.8	84	9.3	18.8	86	9.1	18.9	83
Pioneer 3394	8.1	16.5	92	8.5	17.7	82	8.8	18.2	84
Pioneer 3283W	7.3	17.5	86	7.9	18.1	84	8.0	18.5	84
Pioneer 3287W	7.1	18.3	81	8.0	18.8	77	7.6	18.7	81
<i>Average:</i>	<i>7.7</i>	<i>17.9</i>	<i>82</i>	<i>8.4</i>	<i>18.7</i>	<i>82</i>	<i>8.4</i>	<i>18.8</i>	<i>83</i>
LSD .05	0.8	0.7	11						(Entry x Env.)
C. V. %	8	3.	11						(Entry x Env.)

¹ NC296 and NC346 are temperate-adapted lines that were derived from a cross of two tropical hybrids, Pioneer X105A from Jamaica and H5 from CENTA (Centro Nacional de Tecnologia Agricola) in El Salvador. Three of the lines in H5 were developed by Jesus Merino of CENTA; the fourth was from the Rockefeller program in Central America.

² % H₂O = percent moisture; % EP = percent erect plants at harvest.

above, in his paper (BAKER, 1984) and in other, informal correspondence and discussion. More information about this set of germplasm may become available in potential legal transcripts, *a la* O'BRIEN (1987). SMITH (1988) provided additional information about the limited germplasm base of U.S. hybrids.

Since the 1970s, there has been only one publicly released line of 'new' parentage that has made a major contribution to U.S. maize breeding. B97 from the Corn Borer Synthetic was released in 1995. There is no indication that privately developed lines of notable consequence have been developed from sources outside the Lancaster, Iodent, Minnesota 13, Pioneer, Stiff Stalk (*LIMPS*) group of germplasm.

That substantial progress has been, and continues to be, made both within and between members of the *LIMPS* sources cannot be denied (DUVICK, 1990). Still, by scanning trade pedigree lists, such as those published by MBS (2002), and foundation seed company promotion brochures, the suspicion arises that much of the progress made by recycling pedigrees throughout much of the industry may have come from incorporating Pioneer germplasm. In any case, there is every indication that the U.S. maize germplasm base is dangerously narrow despite high productivity levels (GOODMAN, 1998).

In the late 1970s and early 1980s, it became ap-

parent that the initial flurry of interest in broadening the U.S. maize germplasm base that accompanied the Southern Leaf Blight (*Bipolaris maydis*, then called *Helminthosporium maydis*) scare of 1970 (SPRAGUE, 1971) had greatly diminished. Furthermore, most U.S. maize breeders held (and still hold) a well-earned prejudice against exotic germplasm (TROYER, 1994). Finally, it had been demonstrated, particularly at Funks/Ciba in the 1980s, that short term (less than 15 years) breeding work with even elite, semi-exotic sources was unlikely to be successful.

At that time, there appeared to be no long-term, serious commitment to the development of usable inbred lines from alternative germplasm sources, although excellent population improvement efforts were underway at several public and private institutions. There is often no problem in developing inbred lines from domestic, recurrent-selection programs, but inbreeding within largely exotic or exotic x domestic populations is often sabotaged by the high frequency of deleterious recessive genes carried by unadapted, non-inbred germplasm. This may be a case where S₁ or S₂ recurrent selection might have a chance of ultimate success (as measured by the actual production of useful inbred lines, instead of the usual rate-of-gain-per-cycle-of-selection basis).

TABLE 7 - *TROPHY* low-moisture selections x NC268, a Stiff-Stalk tester: 1996 - 1998, Clayton, Lewiston, and Plymouth (not 1996), N.C.

PEDIGREE	YIELD t/ha	% H ₂ O	% EP	HT. ER.	(cm) PLT.	DAYS to TASSEL
NC356 x NC268	7.6	19.5	83	116	293	77
NC358 x NC268	7.6	19.0	77	104	271	73
NC390 x NC268	7.8	19.4	79	118	296	77
NC392 x NC268	8.2	18.1	73	116	274	75
NC394 x NC268	7.9	18.6	78	101	270	74
DeKalb 689	7.9	17.8	68	105	271	75
LH132 x LH51	7.5	16.2	84	98	269	73
Pioneer 3165	8.0	20.0	58	104	276	77
LSD .05 (EntxEnv)	0.6	.7	10	6	8	1
C. V. % (EntxEnv)	8	4.	13	6	3	1

TABLE 8 - NC258.NC296 inbred derivatives crossed to FR992.FR1064 as tester: 1996 - 1998, Clayton, Lewiston, and Plymouth (not 1996), N.C.

PEDIGREE	YIELD t/ha	% H ₂ O	% EP	HT. ER.	(cm) PLT.	DAYS to TASSEL
NC302 985-1	7.5	17.9	73	97	266	75
NC386 992-1	7.4	18.2	85	93	253	74
NC404 1013-3	7.8	18.3	74	101	274	73
NC436 1013-2	7.8	18.2	77	104	271	73
8075-e/5524-1	7.4	18.0	80	91	253	73
8076-a/ 992-3	7.5	17.6	77	97	253	74
DeKalb 689	7.5	16.7	64	104	265	75
LH132 x LH51	6.9	15.6	80	98	260	74
Pioneer 3165	7.4	19.3	59	106	267	77
LSD .05 (EntxEnv)	0.6	.5	7	6	7	1
C. V. % (EntxEnv)	7	3.	10	6	3	1

Thus, when the maize breeding program at North Carolina State University needed a niche while educating graduate maize breeders, heavy emphasis on inbred development from mostly tropical germplasm almost guaranteed a monopoly position, simply due to the low likelihood of short-term success (indeed there was high probability of long-term failure, if conventional wisdom were correct). The development of the first generation of temperate-adapted, all-tropical inbreds (including NC296, NC296A, NC336, NC346, NC352, and NC458) relied exclusively on the slow-inbreeding technique suggested by Stringfield (1974). Basically, 5 to 6 generations of bulk ear-to-row sib-mating preceded selfing. The first yield trials were usually conducted after two ear-to-row selfing generations, following,

most typically, six generations of either ear-to-row or bulked ear-to-row sibbing, where the number of bulked ears was usually small (less than 5). Similarly, NC302, NC338, and NC354, second-generation, temperate-adapted, all-tropical (TAAT) inbreds were developed by 5 to 6 generations of ear-to-row sib mating, prior to selfing, starting with crosses among essentially unselected first-generation TAAT inbreds.

The data in Table 4 first demonstrated that U.S. hybrids had no monopoly on high yield, when comparisons were made in a daylength neutral environment, although the presence of southern rust (*Puccinia polysora*) may have been a factor in one of the two years. Both Pioneer 3214 and X304C were purely tropical hybrids, while 507 is partially temperate. In its day (the last bags of seed were

TABLE 9 - *P105.A155 x NC262 inbred derivatives crossed to LH195 as tester*. 1993 - 1995, Clayton, Lewiston (not 1993), and Plymouth, N.C.

PEDIGREE	YIELD t/ha	% H ₂ O	% EP	HT. ER.	(cm) PLT.	DAYS to TASSEL	SO. RUST ¹
NC360	8.6	18.0	100	107	257	76	5.4
NC362	8.4	16.8	99	117	266	76	4.3
NC364	8.6	17.5	99	112	258	74	5.3
NC380	8.4	17.7	98	124	264	76	8.0
DeKalb 689	8.6	17.5	97	115	256	75	4.4
LH132 x LH51	7.8	16.8	99	106	251	72	3.8
NC258 x LH195	8.2	19.3	98	105	248	76	4.3
NC262 x LH195	8.2	17.6	97	99	245	73	4.4
Pioneer 3165	8.4	19.1	94	112	260	77	3.5
LSD .05 (EntxEnv)	0.5	.4	2	5	6	1	1.1
C. V. % (EntxEnv)	5	3.	2	4	2	1	11

¹ Southern rust scored only at Clayton in 1995; 9 = no disease; 1 = dead.

TABLE 10 - *P105.A155 x NC262 inbred derivatives crossed to FR992.FR1064 as tester*. 1996 - 1998, Clayton, Lewiston, and Plymouth (not 1996), N.C.

PEDIGREE	YIELD t/ha	% H ₂ O	% EP	HT. ER.	(cm) PLT.	DAYS to TASSEL
NC360 921-1	7.9	17.0	81	91	271	72
NC382 914-4	7.3	16.4	93	101	255	73
NC384 925-1	7.6	16.6	88	85	254	71
NC418 914-1	7.4	16.6	91	99	253	73
NC420 918-1	7.4	17.2	86	94	265	72
192-1 911-3	7.3	16.5	87	102	271	73
194-1 914-2	7.5	16.6	91	103	261	74
DeKalb 689	7.3	17.6	83	100	260	74
LH132 x LH51	7.0	16.1	92	94	259	72
Pioneer 3165	7.3	19.8	68	103	259	76
LSD .05 (EntxEnv)	0.5	.5	8	7	11	2
C. V. % (EntxEnv)	7	3.	9	7	4	1

probably sold in 1998), Pioneer 3165 was the leading southern hybrid and 3055 was the latest-maturing, high-yielding hybrid sold in North Carolina. However, there is a long and bumpy road between showing yield potential in exotic germplasm and obtaining useful inbreds from such a source. Nevertheless, one of the biggest restrictions to the U.S. use of tropical inbreds and hybrids for breeding is the lack of, or lack of public access to, useful uniform trial data from the tropics. The number of tropical lines and hybrids available, despite various phytosanitary and bureaucratic restrictions, greatly

exceeds the available, published comparative yield-trial data.

RESULTS

By the early 1990s, it was possible to demonstrate rather convincingly that three factors were consequential for the operation of a largely-exotic, inbred breeding program (GOODMAN, 1992):

1. All-tropical materials could be intercrossed and pedigree-selected for adaptation to U.S. condi-

tions, basically following procedures suggested by STRINGFIELD (1974).

2. With all-tropical materials, a single tester of B73/Mo17-type is adequate for screening purposes.
3. Use of tropical material from inbred/hybrid programs is vastly more successful than use of materials of similar quality from recurrent selection programs (such as those of CIMMYT before the mid-1980s) that did not practice inbreeding.

Randy Holley (HOLLEY and GOODMAN, 1988) demonstrated points 1 and 2 above. Holley's dissertation led directly to the release of NC296 and NC296A (and indirectly to a third sister-line, NC346), both of which are all-tropical lines that have been used for the production of white hybrids in the United States and abroad. As an extension project for maize breeders, two studies were conducted to demonstrate their potential contribution to increased yields. Tables 5 and 6 demonstrate that these lines can increase the yields of even elite U.S. hybrids by as much as 1 metric ton per hectare. Although gray leaf spot scores are presented in Table 5, they were obtained from a separate non-yield-trial experiment grown in parts of North Carolina where the disease is endemic, and neither gray leaf spot or any other consequential disease limited the yield trials of Table 5 or subsequent tables. Later studies by Jose Moreno (GOODMAN *et al.*, 2000) led to the release of NC298, NC300, and NC304 (and eventually to NC348, NC350, and NC396), each of which is all tropical. NC298 has been used for breeding and at least pilot production in the U.S and for much breeding work in Argentina, as it carries resistance to the Rio Cuarto virus. NC300 has been promoted for hybrid production by CIMMYT in Central America, India, and China (Hugo Cordoba, personal communication), while NC304 (a very unattractive germplasm release) has the best gray leaf spot resistance of any U.S. line yet tested in North Carolina, and, despite its appearance, does produce hybrids with good yield potential.

A selection program for faster drydown (HAWBAKER *et al.*, 1997) among both all-tropical and late-maturing temperate materials led to a set of better-adapted, all-tropical materials, including NC356, NC358, NC388, NC390, NC392, and NC394, released in 1999 and 2001 (Table 7). More recently, we have begun development of 50% tropical-50% temperate materials, on the basis of crosses to NC258 and NC262A (Tables 8, 9, and 10). These were all de-

rived following the STRINGFIELD (1974) protocol with 5 to 6 generations of sibbing preceding selfing. Longer term, the GEM (Germplasm Enhancement of Maize) project has identified a set of promising families (some of which are listed in Tables 11 through 14) of 50% temperate, 50% tropical origin that should eventually lead to line development at N.C. State and at public and private collaborating institutions as well. The GEM project is a public/private cooperative effort to move exotic germplasm more quickly into U.S. breeding programs. Elite materials identified in LAMP (Latin America Maize Project, see SALHUANA *et al.*, 1991), tropical hybrids, and tropical inbreds are crossed to elite, private lines; families are derived by ear-to-row selfing, and topcross yield trials are conducted to identify superior families.

Data in Tables 5 through 10 are based on 3 replications per location, while Tables 11 through 14 are mostly based upon single replication per location data, much of which came from collaborators outside North Carolina (Delaware, Georgia, Kentucky, Indiana, Iowa, Maryland, Missouri, Nebraska, Tennessee, and Texas). The data in Tables 5 through 10 are averages over environments (using standard randomized complete blocks analyses) of lattice designs used in each individual environment. The means in Tables 11 through 14 are Least Squares means from SAS procedure GLM as there were occasional datapoints missing and additional checks were often included in second-year trials. Much more data can be found at http://www.public.iastate.edu/~usda-gem/Yield_Trial_Data/GEM_YT_Data.html

Theory was developed to demonstrate that if a variable population (such as a germplasm accession or double-cross hybrid) is to be effectively sampled via a pedigree breeding program (such as crossing to an existing, adapted, elite line), then very early generation testing (of actual F_1 individuals or of F_1S_1 progeny) must be done. Otherwise, the variation present in the source to be sampled will be swamped by the inter-varietal or inter-racial variation arising in the F_2 (GOODMAN, 2002).

CONCLUSIONS

What has been emphasized here are the successes that we have had. The failures outnumber the successes by a ratio of well over 100:1, as in most plant breeding programs.

TABLE 11 - 50%-Tropical GEM E₂S₃ Topcrosses - Four Testers¹
Means Across Testers Source.

ENTRY	YIELD t/ha	% H ₂ O	% EP	PEDIGREE ²
B2011-01	11.2	18.6	97.4	SE32 x S17
B2120-01	12.0	20.6	96.5	DK888 x S11
B2121-04	11.1	20.6	98.3	DK888 x S11
B2143-02	11.3	19.3	98.3	DK888 x S11
B2226-02	11.2	18.1	93.5	XL370A x S11
B2283-01	11.6	19.1	97.9	XL380 S11
Check mean	11.1	18.7	97.7	
DK687	11.3	18.7	99.8	
LH132.51	10.7	17.8	93.0	
LH200.262	12.2	19.1	99.8	
P3165	10.8	21.0	99.4	
P32K61	11.2	18.0	99.8	
31 Env. CV:	4.6	2.2	2.6	

¹ Testers: NC258 x OH43E; FR697 x FR615; LH287; LH185Bt

² SE32 is a composite population from Brazil; XL370A and XL380 are hybrids from Brazil; DK888 is a hybrid from Thailand. S11 and S17 are company codes for Stiff-Stalk lines.

What has been learned?

- I. While photoperiod response is a major block for evaluating tropical materials (in yield and disease trials), it is not a major hindrance to breeding work, particularly if inbreeding proceeds slowly (as in STRINGFIELD, 1974).
- II. By using all-tropical sources, we can do preliminary screening using a single tester (currently LH132 x LH51).
- III. Resistance to most major diseases is common among most all-tropical materials.
- IV. New, or at least additional, heterosis can be found by crossing the best of the temperate-adapted, all-tropical inbreds with the best U.S. single-cross hybrids.
- V. Attention must be paid to smut (*Ustilago maydis*) and anthracnose (*Colletotrichum graminiicola*) resistance.
- VI. Perhaps the most difficult problem encountered is poor seedling vigor under unfavorable planting conditions.
- VII. Another major problem is choosing among the many possible tropical breeding sources available.

Germplasm sources

The LAMP [Latin American Maize Project (SALHUANA *et al.*, 1991)] has identified some 200 to 300 germplasm accessions that are promising, and over 50% of these are tropical. [The non-tropical ones are basically of less interest as a group for two reasons - (1) many are from high elevations and have such specific, quantitatively-inherited, ecological adaptation that they are not very amenable to migration to a different climate and (2) others are from areas that have been heavily sampled (such as Argentina) in the past by public and private breeding programs]. Although much of this data is effectively locked up on a user-unfriendly CD-ROM, a published, hard copy is available from the National Seed Storage Laboratory at Fort Collins (SALHUANA *et al.*, 1997). Much of our work was facilitated by trials of public and private tropical hybrids conducted by CIMMYT (1972, 1974), but these sorts of trials are no longer published. At present, choices among available tropical inbreds and hybrids remain largely on a personal-recommendation basis. Alternatively, it is possible to identify commercially-successful, tropical hybrids and utilize them for U.S. breeding.

Because we have invested about 30 years of effort in developing temperate-adapted inbreds from all-tropical sources, while virtually all other temperate breeding programs emphasized (probably more wisely) standard midwestern U.S. sources, the germplasm base at N.C. State is rather distinct and is undergoing cyclic line selection (essentially recurrent selection on the basis of inbred lines). We also constantly introduce new tropical hybrids and lines into the program as successful ones are identified and obtained. It takes about eight growing seasons, most of which must be in Raleigh, to adapt a new tropical hybrid x temperate-adapted, all-tropical inbred cross. The success rate is fairly low, and progress is painfully slow. Why did we start this sort of work and why do we persist in doing it? In part, because no one else was/is doing so, and, for insurance purposes, someone should. In part, because it was, and is, a challenge.

We have been somewhat surprised that more breeders have not used NC296, NC296A or NC346 in intensive breeding programs, as they have consistently performed well (TALLURY and GOODMAN, 1999). At the insistence of several former graduate students [notably Randy Holley and David Uhr, whose thesis work (UHR and GOODMAN, 1995), led to the release of NC302, NC338, and NC354, tem-

TABLE 12 - 50%-Tropical GEM F_2S_2 Topcrossed onto LH132 x LH195.

ENTRY	YIELD t/ha	% H ₂ O	% EP	PEDIGREE ¹
1778-001	9.7	20.0	96.6	DK888 x N11
Check mean	9.2	19.2	97.0	
AS897	8.5	18.1	96.7	
DK687	9.4	18.8	98.4	
DK697	10.3	19.8	95.8	
LH132.51	8.3	18.1	96.4	
LH200.262	9.7	19.2	96.4	
N8811	9.0	21.7	98.0	
P3165	8.4	21.1	96.7	
P3223	10.1	17.8	97.5	
P32K61	9.6	18.4	96.7	
P33G26	9.0	17.3	96.5	

21 Env. CV: 11.5 6.5 4.0

ENTRY	YIELD t/ha	% H ₂ O	% EP	PEDIGREE ¹
9527-1/97	9.0	19.6	96.1	XL380 x N11
9531-2/97	9.3	19.4	97.0	XL380 x N11
Check mean	9.0	18.9	95.3	
DK683	9.8	18.4	95.3	
DK689	9.2	18.8	95.8	
DK714	9.0	19.6	95.1	
DK743	10.1	20.1	92.8	
LH132.51	8.0	17.9	95.3	
P3165	8.4	20.5	95.0	
P32K61	9.3	17.6	96.9	

1 N11 is a company code for a non-Stiff-Stalk line.

perate-adapted, all-tropical lines], we are now doing more 50% temperate - 50% tropical line development. Three sets of materials are now in advanced yield trials or are awaiting release decisions. One set is from NC258 x NC296 (partial results shown in Table 8); a second is from NC268 x NC300; a third involves NC262A with several all-tropical lines, including NC296, NC298, and NC300 (LEWIS and GOODMAN, 2003). These all have been more successful than our purely domestic line recycling efforts, such as NC258 x NC262 or NC258 x Va59.

TABLE 13 - 50%-Tropical GEM F_2S_2S Topcrossed onto FR615 x FR697.

ENTRY	YIELD t/ha	% H ₂ O	% EP	PEDIGREE ¹
1415-1/97	9.3	19.2	94.4	DK888 x S11
1415-6/97	9.4	21.4	94.7	DK888 x S11
Check mean	9.3	17.9	93.5	
DK683	9.5	17.4	92.8	
DK714	9.6	18.6	94.5	
LH132.51	8.3	16.9	92.9	
P3165	9.2	19.6	92.6	
P32K61	10.7	16.6	97.5	

13 Env. CV: 10.2 7.5 7.9

¹ S11 is a company code for a Stiff-Stalk line.TABLE 14 - 50%-Tropical GEM F_2S_2S Topcrossed onto FR992 x FR1064.

ENTRY	YIELD t/ha	% H ₂ O	% EP	PEDIGREE ¹
1881-002	9.2	18.2	95.6	XL370A x N11
1883-001	9.3	19.0	95.7	XL370A x N11
1883-002	9.2	19.1	96.1	XL370A x N11
Check mean	8.9	19.5	96.6	
DK687	9.1	19.3	97.8	
DK697	9.7	19.4	95.3	
LH132.51	8.4	18.3	96.4	
LH200.262	9.4	19.6	95.0	
P3165	8.3	21.8	96.4	
P32K61	9.1	18.6	98.0	

19 Env. CV: 12.4 7.4 4.2

¹ N11 is a company code for a non-Stiff-Stalk line.

At the same time second-cycle TROPHY (*Tropical Hybrid* derived) lines were developed, a similar effort was made with two domestic, southern hybrids and with their cross: Funks G-5820, Pioneer 3055, and 5820 x 3055. Not a single line from these three sources was good enough to pass first-year yield trials (although, for academic reasons, several of the "least bad" were tested a second year). While the midwestern tester was undoubtedly more closely related to the southern hybrids (note, however, that the Funks hybrid was chosen specifically because of its lack of relationship to B73 x Mo17) than

to tropical ones, and these two hybrids may not have been the cream of the southern crop (but they were certainly good, but late, hybrids), the performance of the lines derived from them was notably disappointing. Several all-tropical derivatives, developed at the same time, not only passed several cycles of yield trials, but were eventually released (NC302, NC304, NC338, NC348, NC350, NC354, NC396). While this was not a formal experiment, it did suggest that the successes we have had were probably more a result of the germplasm used rather than plant breeding techniques *per se*.

While it would not be prudent for a new assistant professor or a marginally-profitable seed company to devote a major portion of breeding effort to the sorts of work described here, certainly those organizations sporting 15%+ profit margins and those USDA scientists with real budgets (university professors of most any rank rarely have any budgets other than grants or contracts and there are few, if any, grants available for plant breeding) should be able to at least duplicate these results or use lines or families described here profitably as a part of their own programs. These materials are all essentially unrelated to most advanced breeding materials from other U.S. programs.

While tropical materials can be an excellent source of disease and insect resistance, and while we do screen heavily for disease tolerance, none of the yield trials reported here that were conducted in North Carolina had consequential disease incidence and insect damage was minimal. Gray leaf spot and fusarium resistance is common among the tropical materials we have used, while anthracnose resistance and common smut resistance are much rarer, but easily selected for in segregating progenies.

ACKNOWLEDGEMENTS - Special thanks go to those who have helped with the GEM experiments. Jim Hawk, Randy Holley, Dennis West, and Neil Widstrom helped screen numerous first year materials. Asgrow (Maryland), DeKalb (Georgia, North Carolina, Tennessee), Garst (Missouri, Kentucky), Hoegemeyer (Nebraska), Mycogen (Iowa, Indiana), Pau (Missouri, Indiana), and Pioneer (Georgia, North Carolina, Tennessee) have grown first and second year trials. Bill Hill has overall responsibility for all our yield trials, and Joseph Hudyncia coordinates the GEM trials. Mike Hawbaker and David Uhr were supported by Pioneer Fellowships. Data in Tables 5 and 6 were adapted from a presentation at the 1997 Heterosis Symposium sponsored by CIMMYT and held in Mexico City. Special thanks are due to Agrocere, whose hybrid 155 contributed substantially to our first-generation TAAT inbreds, the Rockefeller Program in Central America, which provided H5, and Pioneer Overseas Corporation, which provided X105A; together these three tropical hybrids account for a very high percentage of the pedigrees of TAAT inbreds.

REFERENCES

- BAKER R.J., 1984 Some of the open-pollinated varieties that contributed most to modern hybrid corn. Illinois Corn Breeders School Proc. **20**: 1-19.
- CASTILLO-GONZALEZ F., M.M. GOODMAN, 1988 Agronomic evaluation of Latin American maize accessions. Crop Sci. **29**: 853-861.
- CIMMYT, 1972 Results of the first international maize adaptation nursery (IMAN) 1970-71. CIMMYT Information Bull. No. 7. Mexico City. 51 p.
- CIMMYT, 1974 Results of the second and third international maize adaptation nursery (IMAN) 1971-72a, 1972-73b). CIMMYT Information Bull. No. 11. Mexico City. 118 p.
- DUVICK D.N., 1990 The romance of plant breeding and other myths. pp. 39-54. *In*: J.P. Gustafson (Ed.), Gene Manipulation in Plant Improvement. Plenum Press, New York.
- GOODMAN M.M., 1985 Exotic maize germplasm: Status, prospects and remedies. Iowa State Journal of Research **59**: 497-527.
- GOODMAN M.M., 1992 Choosing and using tropical corn germplasm. Ann. Corn Sorghum Ind. Res. Conf. Proc. **47**: 47-64.
- GOODMAN M.M., 1998 Research policies thwart potential payoff of exotic germplasm. Maize diversity and maize breeding. Diversity **14**: 30-35.
- GOODMAN M.M., 2004 Incorporation of exotic germplasm into elite maize lines: Maximizing favorable effects of the exotic source. Theor. Pop. Biol. (in press).
- GOODMAN M.M., J. MORENO, F. CASTILLO, R.N. HOLLEY, M.L. CARSON, 2000 Using tropical maize germplasm for temperate breeding. Maydica **45**: 221-234.
- HAWBAKER M.S., W.H. HILL, M.M. GOODMAN, 1997 Application of recurrent selection for low moisture content in tropical maize (*Zea mays* L.). I. Testcross yield trials. Crop Sci. **37**: 1650-1655
- HOLLAND J.B., M.M. GOODMAN, 2003 Combining ability of a tropical-derived maize population with isogenic Bt and conventional testers. Maydica **48**: 1-8.
- HOLLEY R.N., M.M. GOODMAN, 1988 Yield potential of tropical hybrid corn derivatives. Crop Sci. **28**: 213-217.
- LEWIS R.S., M.M. GOODMAN, 2003 Incorporation of tropical maize germplasm into inbred lines derived from temperate x temperate-adapted tropical line crosses: agronomic and molecular assessment. Theor. Appl. Genet. **107**: 798-805.
- LLOYD-EVANS L.P.M., P. BARFOOT, 1996 EU boasts good science base and economic prospects for crop biotechnology. Genetic Engineering News **16**: 16.
- MBS, 2002 Genetic Handbook. MBS, Inc., Story City, Iowa. 57 p.
- NEWLIN O.J., 1995 Looking back to see ahead: Reflections of a retired seedsman. Ann. Corn Sorghum Industry Research Conf. Proc. **50**: 33-55.
- O'BRIEN D.E., 1987 Pioneer Hi-Bred International vs. Holden Foundation Seeds. U.S. District Court, Southern District of

- Iowa, Central Division, Civil Case No. 81-60-E, Des Moines, Iowa. 108 p.
- SALHUANA W., Q. JONES, R. SEVILLA, 1991 The Latin American Maize Project: Model for rescue and use of irreplaceable germplasm. *Diversity* **7**: 40-42.
- SALHUANA W., R. SEVILLA, S.A. EBERHART, 1997 Final Report, Latin American Maize Project. Pioneer Hi-Bred International, Johnston, IA.
- SMITH J.S.C., 1988 Diversity of United States hybrid maize germplasm; isozymic and chromatographic evidence. *Crop Sci.* **28**: 63-69.
- SMITH O.S., J.S.C. SMITH, S.L. BOWEN, R.A. TENBORG, S.J. WALL, 1990 Similarities among a group of elite maize inbreds as measured by pedigree, F₁ grain yield, heterosis and RFLPs. *Theor. Appl. Genet.* **80**: 833-839.
- SPRAGUE G.F., 1971 Genetic vulnerability in corn and sorghum. *Ann. Hybrid Corn Ind. Res. Conf. Proc.* **26**: 96-104.
- SPRINGFIELD G.H., 1974 Developing heterozygous parent stocks for maize hybrids. DeKalb AgResearch, Inc. DeKalb, Illinois. 41 p.
- TALLURY S.P., M.M. GOODMAN, 1999 Experimental evaluation of the potential of tropical germplasm for temperate maize improvement. *Theor. Appl. Genet.* **98**: 54-61.
- TROYER A.F., 1994 Breeding early corn. pp. 341-396. *In*: A. Hallauer (Ed.), *Specialty Corns*. CRC Press, Boca Raton, FL.
- TROYER A.F., 1999 Background of U.S. hybrid corn. *Crop Sci.* **39**: 601-626.
- UHR D.V., M.M. GOODMAN, 1995 Temperate maize inbreds from tropical germplasm. I. Testcross yield trials. *Crop Sci.* **35**: 779-784.