

## BROADENING THE U.S. MAIZE GERMPLASM BASE

M.M. Goodman\*

*Department of Crop Science, North Carolina State University, Raleigh, NC 27695-7620, USA*

Received January 30, 2005

**ABSTRACT** - In U.S. maize breeding, exotic germplasm is considered high-risk and usually is introduced by back-crossing specific traits into elite lines. The U.S. maize germplasm base is narrow; only a few open-pollinated varieties are well represented in current programs. In other areas of the world, germplasm bases can also occur be narrow. Today, the barrier to use of exotic germplasm in the U.S. is less formidable than in the 1980s. A major reason is that U.S. materials are now used in tropical breeding to add earlier maturity and lodging resistance. These exotic materials, developed with U.S. germplasm, are being introduced back into the U.S. Although use of exotic germplasm in U.S. maize breeding is limited, a 3-fold increase occurred from 1% in 1984 to 3% in 1996. Primary sources of exotic germplasm are Maíz Amargo from Argentina and the French lines, F2 and F7. While there is little evidence that breeding gains have been restricted by the narrow U.S. germplasm base, it continues to be a concern, as demonstrated by the GEM (Germplasm Enhancement of Maize) project, promoted by ASTA (American Seed Trade Association). GEM is a cooperative public/private effort aimed at injecting exotic germplasm into U.S. commercial breeding. Although most exotic germplasm being used in U.S. maize breeding is from temperate regions, inbreds and hybrids from the tropics have great potential for improving U.S. maize yields. GEM has already identified about fifty, 50%-tropical, 50%-temperate families tracing primarily to tropical hybrids that are competitive with commercial checks. In our program, we have examined the potential of tropical inbreds and hybrids for U.S. breeding by crossing temperate-adapted, 100%-tropical lines to U.S. hybrids. That higher yields can be acquired from elite exotic sources was demonstrated, mostly by NC346, but such events are rare. Of the GEM breeding crosses evaluated, DeKalb's tropical hybrids and largely tropical synthetics from Brazil and Florida show the most immediate promise.

**KEY WORDS:** Maize breeding; Tropical inbreds; Germplasm; Incorporation.

---

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

## INTRODUCTION

Conventional wisdom says that in U.S. maize (*Zea mays* L.) breeding, exotic germplasm is beneficial only through slow integration into mature breeding programs that are, in turn, grounded on historic heterotic patterns (TROYER, 1994). Elsewhere in the world, however, exotic germplasm is a commonplace feature of maize breeding. A prime example is the fact that elite U.S. lines and hybrids constitute important exotic sources in most countries. U.S. public breeding lines are readily available for international breeding activities (typically at no cost to other public programs, foreign or domestic), while various devices such as restrictive contracts, trade secrets, patents and licenses (MORRISSEY, 1995; ROTH, 1995) limit the use of private lines (especially in the U.S. and Europe). Hybrid seed and field-run ( $F_2$ ) seed are often available without restriction for conventional (non-transgenic) hybrids. Even  $F_2$  seed from transgenic hybrids can sometimes be used indirectly for breeding if the transgenes can be selectively eliminated from descendants of field-run seed. Thus, for practical purposes, most U.S. maize germplasm is available for international breeding.

### *Genetic base of maize breeding in the U.S.*

There were thousands of open-pollinated varieties of maize in use in the U.S. in the late 1800s and early 1900s. Today, however, only a few of these are well-represented in current U.S. programs (BAKER, 1984; GOODMAN, 1990). The maize germplasm base for the U.S. (and hence for most of the temperate world) has recently been reviewed by several authors. Briefly summarized, many U.S. lines currently used as female parents trace their parentage to A632, B14, B37 and B73 (TROYER, 1996; GOODMAN, 2004), all derived from the Stiff Stalk Synthetic of largely Reid Yellow Dent origin. Many U.S. lines used as

male parents have ancestry from C103, Mo17 and Oh43, lines derived from Lancaster. LU and BERNARDO (1999) and TALLER and BERNARDO (2004) suggest adding B84 and H99, respectively, to these two lists. Iodent lines (derived from I159, I198, I205, MBS847, etc.) and Minnesota 13 (TROYER, 1994, 1996) lines have added early dry-down, allowing earlier harvesting with less artificial drying, and permitting hybrid corn to be grown further north. Midland, Krug, Leaming, Northwestern Dent, Pride of Saline, and Jarvis are varieties that also have contributed to current breeding programs, but at a much lower level than Reid, Lancaster, Iodent and Minnesota 13. The Iodent lines originated (1930s) from Iowa State (WALLACE, 1923), but were much improved over a long period of time, largely under the guidance of the late Raymond Baker of Pioneer (BAKER, 1984; GOODMAN, 2004; SMITH *et al.*, 2004; TROYER, 2004). In some northern areas, the French lines, F2 and F7, made maize-growing really feasible.

In recent years, the Iodent and Minnesota 13 materials have largely been restricted to private line development, while U.S. public breeders have concentrated on Stiff Stalk x Lancaster combinations. In addition, many private (and perhaps a few public) breeders have made use of Pioneer's domestic lines and hybrids. Today, in private breeding circles, Pioneer sources probably rank second only to Stiff Stalk derivatives. TROYER (1996, 2004), DUVICK *et al.* (2004) and SMITH *et al.* (2004) have described these sources, inferring the overall extent of their use from SMITH *et al.* (1990, 1999). While much overlap exists with other programs, Pioneer alone seems to have made a continual effort from the 1930s to the 1990s to acquire and evaluate virtually all available maize germplasm sources.

#### ***Genetic base of maize breeding outside the U.S.***

In other areas of the world, important heterotic patterns differ widely from region to region, but the tale of a restricted germplasm base is all-too-similar to that in the U.S. In the tropics, several races dominate these patterns. Various Tuxpeños form the basis for dent breeding efforts (especially for the white dents) in the tropics, while Cuban Flint and Suwan 1 are the predominant yellow flints. ETO and Tusón are semidentals of major importance. Coastal Tropical Flint (called Costeño in many regions) is a semi-flint that has been widely used. These six groups are crossed in virtually all permutations for hybrid development. Consider Tuxpeño x ETO as an example of how U.S. germplasm can

be employed: B73- or Mo17-type lines can be used on either side of the Tuxpeño-ETO heterotic combination, but B73-types are often used to cross with Tuxpeño-type materials, while Mo17-type lines are often used with ETO materials (Glenn Robison, retired from DeKalb, personal communication). The usual goals are to increase stalk and root strength, lower plant height, decrease maturity and add yield potential from U.S. sources, while maintaining the disease and insect resistance and wide adaptation of the tropical sources. Usually U.S. materials contribute 25% to 50% of the germplasm of the resulting breeding lines. In some cases, southern U.S. lines can be used directly, to form as much as 1/4 to 1/2 of the parentage of tropical hybrids. Lines developed in the tropics, but containing some U.S. germplasm, are occasionally crossed with U.S. breeding stocks by multinational breeding companies. Jerry Arnold, now retired from Asgrow, was a strong proponent of such procedures, and Don Bockelmann successfully used such tropical lines at Asgrow; that practice may increase as U.S. materials have a larger impact overseas.

#### ***Attempts/strategies to broaden the genetic base of maize in the U.S.***

The narrow genetic base of U.S. maize is recognized widely; however, there was a 3-fold increase in the use (defined here as percentage of parentage of all inbreds used in production of hybrid seed) of exotic germplasm between 1984 and 1996, from slightly less than 1% in 1984 (GOODMAN, 1985) to 2.9% in 1996 (GOODMAN, 1998). This increase was both for exotic germplasm from temperate regions, which increased from 0.8% in 1984 to 2.6% in 1996, and for germplasm from tropical areas, which increased from a minuscule 0.1% in 1984 to a still tiny 0.3% in 1996. Among the available examples of use of exotic germplasm for hybrid production, there seem to be two extremes in the actual deployment of tropical germplasm in U.S. hybrids. The most widely-sold U.S. hybrids containing tropical germplasm have relatively small amounts of exotic germplasm that has been introduced by slow introgression, mostly from backcrossing, of experimental lines over time. On the other hand, there are a few hybrids with 25% or more tropical parentage, where, for example, a 50%-temperate/50%-tropical line was adapted well enough to the U.S. to enable its use as a parent of a U.S. hybrid.

The bulk of exotic maize germplasm currently employed in the U.S. is temperate in origin, and

most of that traces to two specific sources. Maíz Amargo was discovered in Argentina in the late 1930s (MARCHIONI, 1939) and has been used in the U.S. as a source of insect and disease resistance, mostly via B64 and B68 from Iowa State. Derivatives of B68 are represented in most breeding programs in the Midwest, East and South, although B68 itself was never a dominant inbred. The second major source of temperate exotic germplasm in the U.S. is the pair of French lines, F2 and F7, both derived from the open-pollinated population Lacaune. These lines have excellent capability to germinate well under adverse conditions and are widely used for breeding and seed production across the northern parts of both the Old and New Worlds.

While broadening the germplasm base of temperate maize breeding has frequently been advocated (WELHAUSEN, 1956, 1965; BROWN, 1975; STUBER, 1978; GEADELMANN, 1984; GOODMAN, 1999, 2004; GOODMAN *et al.*, 2000; HALLAUER, 1978, 2003; BETRÁN *et al.*, 2004, 2005), there is little evidence to show that breeding gains have been restricted by the narrow U.S. germplasm base (DUVICK, 1984, 1990; DUVICK *et al.*, 2004). Indeed, bringing in exotic germplasm sources generally results in yield losses, despite general increases in disease and insect resistance. There are exceptions (GOODMAN, 1999, 2004; GOODMAN *et al.*, 2000), but they are rare. To paraphrase Arnel Hallauer: most genetic variation is not favorable.

Nonetheless, the narrowing of the U.S. maize germplasm base continues to be a widespread concern, as evidenced by the GEM (Germplasm Enhancement of Maize) project, that was established as a result of the concerns of ASTA (American Seed Trade Association) an organization that represents the interests of commercial seedsmen. GEM (SALHUANA *et al.*, 1994; POLLAK and SALHUANA, 1998) is a cooperative public/private effort to quickly inject exotic germplasm into U.S. commercial breeding. Briefly summarized, the GEM program uses F<sub>1</sub> crosses between private lines and tropical sources to derive partially inbred families that are then topcrossed to foundation-seed-company testers. These topcrosses are tested collaboratively, the best performing families are distributed to cooperators and a year later released to the public through the North Central Regional Plant Introduction Station (NCRPIS) at Ames. This part of GEM is coordinated at NC State. At Ames, a similar program is carried out with temperate materials and with 25%-tropical crosses.

A major problem confronting anyone wanting to incorporate exotic germplasm into a breeding program is what exotic germplasm to use. DUDLEY (1984, 1987, 1988) and some of his students (for example, BERNARDO, 1990) and GERLOFF and SMITH (1988) have tried to address this issue in terms of improving specific lines and hybrids, but the number of potential lines and hybrids to be improved is very large and constantly changing. In addition, the number of potential exotic sources is large and many are very unadapted to the central Corn Belt of the U.S., and thus not amenable to the Dudley estimation procedures.

If the goal is overall improvement of U.S. maize breeding stocks (incorporation, in the sense of SIMMONDS, 1993), then several generalizations can be made on the basis of extensive experimentation by both public and private sources. Much of this work was ultimately unproductive and therefore unpublished, yet it is widely known. First, virtually all readily-available, temperate-adapted, Argentine, Uruguayan and Chilean sources (accessions, lines and hybrids) have been tested repeatedly by public and private organizations and have generally been found not to be widely useful [Maíz Amargo has been a notable exception and the GEM website (<http://www.public.iastate.edu/~usda-gem/>) lists other materials with promise]. This broad generalization is based on personal conversations with many people, but Raymond Baker and William Brown, both now deceased but formerly research leaders at Pioneer, were primary sources. Second, synthetics and accessions from the tropics often carry recessive alleles adaptational to that region but which hamper U.S. inbreeding efforts (GOODMAN, 1992). Third, highland materials, whether from Mexico, Peru or elsewhere (and southwestern U.S. ones as well), also often carry ecologically-specific, adaptive alleles that make them recalcitrant sources for general breeding (this generalization comes from personal experience, along with that of several Latin American colleagues with whom I have worked, especially Fernando Castillo and Jesus Sanchez of Mexico and Wilfredo Salhuana and Ricardo Sevilla of Peru). Fourth, inbreds and successful hybrids from the tropics (often carrying some small amount of U.S. germplasm) are by far the easiest tropical sources to use for general improvement of U.S. maize (GOODMAN, 1993). Fifth, although largely-exotic lines with slightly better per se performance can be driven by several generations of sib mating before selfing (UHR and GOODMAN, 1995), the time-costs of this line im-

provement (which does not generally carry-over to hybrids) are usually not worthwhile unless both parental-source materials are unadapted. Sixth, it is probably far more sensible to build on existing efforts than to 'go it alone'. Today, adapted exotic synthetics and inbreds are available from HALLAUER (2003), BETRÁN *et al.* (2004) and GOODMAN (2004), while partially-inbred families of widely-tested, high-yielding, 50%-exotic and 25%-exotics are available from the GEM program through NCRPIS at Ames, IA (<http://www.public.iastate.edu/~usda-gem/>).

If one is instead searching for unique traits, not readily encountered in any commercial maize, then working with less-adapted highland or other specialized accessions or even teosinte (WILSON *et al.*, 2004) might be advisable, but, if so, the goals need to be clear. Useful alleles can probably be found in any line, race, accession or species, but the tools for extracting them are expensive and the time involved is lengthy. Such endeavors, some of which are novel and exciting, are now largely limited to single, major genes (CASTLE *et al.*, 2004) rather than the polygenic traits that form the basis for almost all successful maize breeding.

Use of public lines developed in the tropics for commercial breeding in the U.S. is largely undocumented (a Pioneer breeder who must remain anonymous says that one parental line of one commercial hybrid was derived partly from a CML [CIMMYT] line) or barely-existent, although the old Cuban line A6, a line that was still being used in tropical hybrids 40+ years after its development by DEVALLE (1952), may have had some use. A major reason for the lack of attention paid to public tropical lines is the sparse amount of yield-trial data. Although many such lines are available (largely from CIMMYT, IITA, NCRPIS or from Jim Brewbaker in Hawaii) and substantial amounts of disease and insect resistance data exist (BREWBAKER *et al.*, 1989), very little yield data have been published in a form that allows line-choices to be made. Since such data cannot readily be collected in temperate locations, interest of temperate breeders in such lines has been minimal.

For the past 30 years, genetic resource programs for maize have generally been under-staffed and under-funded (GOODMAN, 1984). This is unlikely to change until more successful uses of such resources are demonstrated. Somehow, the widespread use of Maíz Amargo, first evaluated in the early 1940s, is not considered adequate justification for further evaluation of accessions and sometimes not even

for maintenance of exotic maize accessions. GEM, LAMP (Latin American Maize Program; see SALHUANA *et al.*, 1995) and regeneration programs coordinated by CIMMYT and NC State have been exceptionally successful, but fewer than half of the Latin American accessions have been evaluated; many still desperately need immediate regeneration. Proposals for maize photoperiod conversion have been submitted from the U.S. Maize Crop Advisory/Germplasm Committee; all have been turned down by the US-DA-ARS for lack of available funds. LAMP was completely funded by a major international seed company (Pioneer), and GEM was funded solely because of a successful Congressional lobbying effort by ASTA (an influential Senator and a senior House member, both from Iowa, served on the Agriculture Conference Committee that funded GEM at the last moment in the 1994 Congress – it had not been in either of the original House or Senate budget proposals). Once material has been evaluated, as has happened with LAMP, years of breeding and testing must follow to convert potentially promising, but agronomically inferior, germplasm accessions into useful breeding lines. In the U.S., widespread use of Maíz Amargo germplasm in successful hybrids did not occur until the 1980s, after 40 years of breeding and selection, and Maíz Amargo itself is more temperate than tropical in its adaptation.

Three types of experiments will be reported here. The first involves a set of temperate-adapted, all-tropical (TAAT) inbreds crossed to a currently important set of maize hybrids to determine whether TAAT germplasm can add to the performance of currently elite hybrids. The second is a comparison of 50%-tropical F<sub>1</sub> breeding crosses involving elite Latin American accessions and hybrids crossed to elite, private lines to determine which of these F<sub>1</sub> hybrids are most promising for future breeding work. The third compares topcrosses of partially inbred families derived from such breeding crosses to commercial checks to determine whether some families show immediate promise for general use in breeding.

## MATERIALS AND METHODS

NC336, NC346, NC352, NC400 and NC458, used in the first experiment, are temperate-adapted, all-tropical (TAAT) lines developed from tropical hybrids that were elite in the early 1970s. Their pedigrees are listed in Table 1; the important point is that they were derived from materials that themselves belonged to the era (though not the pedigree) of B73 x Mo17 hybrids in the

U.S.; tropical breeding has made much progress since then, so that much better materials are available today. The TAAT inbreds were crossed to DeKalb 697, FR1064.LH185, HC33.TR7322, LH132.LH51, LH200.LH262, Pioneer 31G98 and Pioneer 33P66, all currently, or very recently, important hybrids.

In the second set of experiments, F<sub>1</sub> hybrids between tropical accessions (or tropical hybrids or tropical inbreds, together called 'accessions' here) and proprietary lines were compared to commercial checks. The hybrids were made by commercial companies, coded from 1 to 27, with codes known only to the GEM coordinators at Iowa State, and the F<sub>1</sub>s are labelled as S, N or D for Stiff Stalk, non-Stiff Stalk or Argentine Dent crosses, respectively.

The third set of experiments reported here compares families (slightly inbred lines) derived from such F<sub>1</sub> crosses to commercial checks.

Experimental procedures used included lattice designs, with three replications, for individual NC environments, with randomized complete blocks analysis across environments. For GEM trials involving topcrosses of partially inbred families conducted across multiple states, single-replication trials were analyzed using the GLM Procedure in SAS and LS Means are reported here (SAS INSTITUTE, 1988).

TABLE 1 - Pedigrees of TAAT lines.

LINE	PEDIGREE <sup>1</sup>
NC336	Pioneer X105A x H5
NC346	Pioneer X105A x H5
NC352	Pioneer X105A x H5
NC400	NC300 x NC348
NC458	KU2301 x PM703

<sup>1</sup> Pioneer X105A was from Jamaica, H5 was from the Rockefeller Program in Nicaragua, KU2301 was a Suwan 1 hybrid from Thailand and PM703 was a Peruvian hybrid of Cuban origin. NC300 and NC348 are second-generation TAAT inbreds.

TABLE 2 - Mean grain yield, grain moisture and percent erect plants (EP) at maturity of TAAT line crosses to DK 697, FR1064.LH185, HC33.TR7322, LH132.LH51, LH200.LH262, P31G98, and P33P66 across 9 North Carolina environments (2003-2004).

LINE	YIELD t/ha	% H <sub>2</sub> O	% EP
NC336	7.54	15.7	59
NC346	7.91	15.4	64
NC352	7.28	15.4	61
NC400	7.54	15.5	57
NC458	7.47	17.0	57
Tester mean	7.41	14.5	66
Trop. line mean	7.54	15.8	60
LSD (.05)*	0.25	0.3	3

\* For comparing individual line means to the mean of all testers.

TABLE 3 - Better performing hybrids and all checks for experiment summarized in Table 2.

ENTRY	YIELD t/ha	% H <sub>2</sub> O	% EP	Southern Rust <sup>1</sup>
DK697 x NC346	8.11	16.0	53	6.6
DeKalb 697	8.34	15.3	63	4.2
FR1064.LH185 x NC346	7.90	15.1	66	7.1
FR1064 x LH185	6.86	13.8	75	5.2
HC33.TR7322 x NC346	8.14	14.6	68	7.1
HC33 x TR7322	7.07	13.9	66	4.6
LH132.LH51 x NC336	8.02	15.7	62	6.7
LH132.LH51 x NC346	8.04	15.7	67	6.6
LH132 x LH51	7.17	14.6	69	5.0
LH200.LH262 x NC346	8.13	16.4	61	6.9
LH200 x LH262	8.04	15.3	59	5.8
P31G98 x NC346	8.49	15.6	64	6.4
P31G98 x NC400	8.38	16.1	58	8.7
P31G98 x NC458	8.19	17.3	58	6.3
Pioneer 31G98	9.04	14.9	64	4.1
P33P66 x NC336	8.17	16.0	61	5.8
P33P66 x NC346	8.21	15.4	66	6.4
P33P66 x NC352	8.01	15.6	53	5.6
Pioneer P33P66	7.67	14.8	66	5.2
Garst 8288	7.89	15.0	75	5.4
LSD .05 (ENTRY x ENV)	0.62	0.8	9	1.0
C. V. % (ENTRY x ENV)	8.01	5.2	15	11.9

<sup>1</sup> Rust severity, rated on a nine-point scale, where 9 = immune to 1 = plant death due to severe disease, was collected only in 2003 (at all locations).

## RESULTS

Tables 2 and 3 summarize the results of the crosses of TAAT inbred lines with commercial hybrids. The data in Table 2 suggest that NC346 might have potential to contribute to the U.S. germplasm base, despite its TAAT origin. That said, no NC346 cross equalled the highest-yielding domestic hybrid, Pioneer 31G98, as can be seen in Table 3, that lists all NC346 crosses, all domestic hybrids and all other crosses in the set that exceeded 8 tons/ha.

There are a large number of GEM breeding crosses (F<sub>1</sub>s between private lines and tropical accessions, lines and hybrids; some of which are listed in Tables 4 and 5) that have yet to receive serious attention, but the range in potential general productivity is large. Tables 4 and 5 include examples of breeding crosses currently under consideration for use in GEM. Even some F<sub>1</sub>s with the

TABLE 4 - Yield, moisture and percent erect plants (EP) at harvest for 50%-tropical GEM Breeding Crosses ( $F_1$ s), Year 2003: Clayton, Lewiston, Plymouth, Sandhills and Kinston, NC.

ENTRY	YIELD t/ha	% H <sub>2</sub> O	% EP	ENTRY	YIELD t/ha	% H <sub>2</sub> O	% EP
Pioneer 31G98	8.77	14.3	68	CHIS462:N08d	5.84	18.4	76
FS8B(S):S03	7.22	15.4	74	BVIR155:S20	5.75	16.7	62
RN07:S20 (BR51721)	7.03	15.7	74	FS8B(S):S17a	5.67	16.7	69
FS8B(T):N11a	6.88	15.4	77	DREP269:S06	5.63	14.7	65
PE27:D27 (BR51675)	6.88	18.4	73	DREP150:N20	5.62	15.2	61
CUBA84:D27	6.71	18.5	67	GUAT209:N19	5.55	15.5	64
PE1:S02 (BR51403)	6.67	17.5	71	BA38:N15 (BR51039)	5.50	17.1	74
SANM126:N12	6.63	16.3	74	DKXL370:S08b	5.49	15.6	64
RN07:N20 (BR51721)	6.59	15.9	64	MDIO22:S21	5.13	17.2	74
BG070404:D27	6.56	17.6	62	DKXL380:S08a	4.88	17.9	69
CUBA164:D27	6.46	18.4	67	FS8B(S):S17b	4.88	15.9	78
FS8B(T):N18	6.23	16.1	68	DK888:S08a	4.75	18.8	73
MDIO22:N21	6.07	17.7	71	SANM126:S12	4.57	15.3	66
SCROGP3:N20	6.02	16.0	64	LSD.05 (ENTRY x ENV)	.98	1.3	13
PE27:N06 (BR51675)	5.85	14.3	73	CV % (ENTRY x ENV)	12.63	6.2	15

TABLE 5 - Yield, moisture and percent erect plants (EP) at harvest for 50%-tropical GEM Breeding Crosses ( $F_1$ s), 2004: Clayton, Lewiston and Plymouth, NC.

ENTRY	YIELD t/ha	% H <sub>2</sub> O	% EP	ENTRY	YIELD t/ha	% H <sub>2</sub> O	% EP
Pioneer 32D99	8.73	17.4	76	PASCO14:N11b	5.53	16.4	55
DeKalb 697	7.90	16.2	82	PE1:N16 (BR51403)	5.31	16.6	72
LH200 x LH262	7.89	15.9	61	GUAT209:S13	5.10	16.3	65
Garst 8288	7.65	16.9	84	SANM126:N12	4.96	17.0	84
Pioneer 31G98	7.53	15.2	85	CML325:S18	4.88	15.6	64
PE11:S11a (BR51501)	7.21	16.5	53	GUAD05:N06	4.84	17.7	17
DKB830:S19	7.06	16.8	81	NEI9004:N08	4.78	17.0	68
PE27:D27 (BR51675)	6.90	18.0	51	GUAT209:N19	4.70	16.9	69
FS8B(S):S03	6.86	16.5	67	MBRC10:S17	4.58	15.8	55
BG070404:D27	6.69	18.1	37	DK888:S08b	4.58	18.0	57
FS8B(T):N11a	6.62	17.1	74	FS8A(S):S09	4.36	15.9	80
BR105:S16	6.67	17.8	75	DKXL370:S08c	4.22	16.0	78
CL-00331:N18	6.57	17.9	82	CL-G1501:S17b	4.00	15.7	65
SE32:N11c (BR52051)	6.53	16.6	65	CML287:N13	3.99	17.2	46
PASCO14:S11a	6.38	17.0	53	NEI9008:N08	3.92	17.5	53
CML329:N18	6.36	16.5	85	NEI9008:S17c	3.89	16.5	58
BR105:N16	6.34	17.2	67	NEI9008:S17b	3.64	17.7	74
GUAT209:N11c	6.21	16.7	64	CML323:S17b	3.59	17.1	67
CUBA84:D27	6.16	19.2	40	CHIS740:S14	3.61	17.3	58
CL-G1607:S18	6.18	16.6	91	CML323:S17a	3.48	16.8	76
PASCO14:N24	6.20	18.5	37	NEI9008:S17a	3.34	17.5	73
BA38:S15 (BR51039)	6.00	18.2	77	CML247:N17b	3.15	17.0	67
CHIS462:N24	5.86	18.0	67	SANM126:S12	3.09	17.3	51
DK212T:S06	5.70	17.0	63	CML247:N17c	2.90	18.4	55
PASCO14:S01	5.68	17.3	58	CML247:N17a	2.68	16.6	70
NS1:S08	5.63	17.6	65	CHIS462:N08a	2.59	17.4	58
MD1022:N21	5.62	18.4	56	LSD .05 (ENTRYxENV)	1.14	1.5	26
RN07:S20 (BR51721)	5.51	16.7	59	CV % (ENTRY x ENV)	13.74	5.6	25

TABLE 6 - Publicly released 50%-tropical GEM families competitive with check hybrids.

FAMILY	SOURCE			FAMILY	SOURCE		
B2011-01	SE32	S17	F <sub>2</sub> S <sub>3</sub>	B2253-01	XL370A	S11	F <sub>2</sub> S <sub>3</sub>
B2084-02	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	B2258-03	XL380	S11	F <sub>2</sub> S <sub>3</sub>
B2086-01	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	B2282-01	XL380	S11	F <sub>2</sub> S <sub>3</sub>
B2088-01	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	B2283-01	XL380	S11	F <sub>2</sub> S <sub>3</sub>
B2089-01	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	BCr1-044	PE 1	N16	F <sub>2</sub> S <sub>3</sub>
B2109-01	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	BCr1-181	PE 1	N16	F <sub>2</sub> S <sub>3</sub>
B2111-01	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	BCr1-239	PE 1	N16	F <sub>2</sub> S <sub>3</sub>
B2112-02	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	BCr1-705	PE 1	N16	F <sub>2</sub> S <sub>3</sub>
B2116-02	DK212T	S11	F <sub>2</sub> S <sub>3</sub>	1937-2/96	DK844	S16	F <sub>1</sub> S <sub>2</sub>
B2120-01	DK888	S11	F <sub>2</sub> S <sub>2</sub>	1357-007/97	DK212T	S11b	F <sub>1</sub> S <sub>1</sub>
B2121-04	DK888	S11	F <sub>2</sub> S <sub>3</sub>	1367-001/97	DK888	S11b	F <sub>1</sub> S <sub>1</sub>
B2127-01	DK888	S11	F <sub>2</sub> S <sub>3</sub>	1776-001/98	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2131-01	DK888	S11	F <sub>2</sub> S <sub>3</sub>	1778-001/98	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2132-03	DK888	S11	F <sub>2</sub> S <sub>3</sub>	1780-001/98	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2142-01	DK888	S11	F <sub>2</sub> S <sub>3</sub>	9366-001/97	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2143-02	DK888	S11	F <sub>2</sub> S <sub>3</sub>	9366-005/97	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2146-01	DK888	S11	F <sub>2</sub> S <sub>3</sub>	9367-001/97	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2150-01	DK888	S11	F <sub>2</sub> S <sub>3</sub>	9375-001/97	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2152-02	DK888	S11	F <sub>2</sub> S <sub>3</sub>	9376-001/97	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2152-03	DK888	S11	F <sub>2</sub> S <sub>3</sub>	161-7/W97	CHIS740	S14	F <sub>2</sub> S <sub>1</sub>
B2156-02	DK888	S11	F <sub>2</sub> S <sub>3</sub>	1937-002/98	XL380	N11	F <sub>2</sub> S <sub>2</sub>
B2201-01	DKB830	S11	F <sub>2</sub> S <sub>3</sub>	3050-003/00*	DK212T	N11	F <sub>2</sub> S <sub>2</sub>
B2226-02	XL370A	S11	F <sub>2</sub> S <sub>3</sub>	3291-001/00*	DK888	N11	F <sub>2</sub> S <sub>2</sub>
B2228-03	XL370A	S11	F <sub>2</sub> S <sub>3</sub>	3315-003/00*	DK212T	N11	F <sub>2</sub> S <sub>2</sub>
B2250-01	XL370A	S11	F <sub>2</sub> S <sub>3</sub>	3315-022/00*	DK212T	N11	F <sub>2</sub> S <sub>2</sub>
B2250-02	XL370A	S11	F <sub>2</sub> S <sub>3</sub>	3407-003/00*	CHS775	N19	F <sub>1</sub> S <sub>3</sub>

\* Publicly available 4/1/2006 from NCRPIS.

Dekalb tropical hybrids and some with CIMMYT lines that looked good in the nursery yielded less than half as well as a good check hybrid in replicated yield trials. However, other GEM breeding crosses perform reasonably well.

The GEM project has already identified about fifty, 50%-tropical, 50%-temperate, families that are competitive with commercial checks (Table 6). For the most part, these trace back to a set of DeKalb commercial, tropical hybrids (contributed to the project by Bruce Maunder and Glenn Robison) crossed to private inbred lines from other U.S. companies. Table 7 provides examples of recently-tested, 50%-tropical GEM families that were reasonably competitive with commercial checks after two years of testing in a minimum of 19 test environments, with different experiments grown in different sets of environments, that ranged from Delaware to Georgia and as far west as Nebraska.

## DISCUSSION

That high yields can be acquired from elite exotic sources has been demonstrated with 50%-tropical lines such as NC312 to NC316 (LEWIS and GOODMAN, 2003) and by TAAT lines like NC296 and NC346 (TALLURY and GOODMAN, 1999; GOODMAN and CARSON, 2000), but such events are rare. However, such lines and others, like NC298 or NC300 (HOLLAND and GOODMAN, 2003), that perform adequately, offer an important insurance policy against diseases that could affect today's entire elite U.S. germplasm base that carries essentially no resistance to diseases as important as streak virus or *mal de Rio Cuarto* (NC298 and NC348, both TAAT lines, carry resistance to the latter), both spread by leafhoppers. This latter virus (virus is used here in its common sense to describe a broad spectrum of virus and virus-like diseases) has many alternate hosts, including the fes-

cues, unlike common U.S. maize viruses where the alternate host is almost always Johnson grass [*Sorghum halepense* (L.) Pers]. The southern rust data in Table 3 suggest that NC346 and NC400 both offer more resistance than is often found in current hybrids; this is a disease that occurs sporadically in North Carolina, thus far appearing late enough in the growing season so that it does not cause yield losses. Further south, it occurs with sufficient force and regularity that hybrids with resistance are often required. All crosses involving NC400 had rust ratings above 8.0, i.e., near immunity on a 1 to 9 scale.

The results in Tables 4 and 5 were surprising, even to one who has worked with exotic germplasm for several decades. Two things stand out there: (1) the better entries are not necessarily from hybrids or inbreds, but instead are often Florida Synthetic or Brazilian synthetics; (2) the better crosses often originate from the same companies (companies 3, 11, 20, 24 and 27), while companies 8 and 17 have had less success here. There are several possible reasons for these two observations, but two may be most pertinent: few DeKalb tropical hybrids were represented in these two tables, as most of those had already been through the GEM pipeline and were not being evaluated here, and assignment of materials to companies is far from a random process; it depends largely on which company has winter nursery space available at the appropriate time. Nevertheless, the data do suggest that the choice of what U.S. line to use in these crosses is critical: certain GEM collaborators have had far greater experience with tropical germplasm than others, and that experience may be responsible for some differences seen here. The range in yield was extreme, with some breeding crosses yielding less than half of the commercial checks. It is theoretically possible to obtain a superior line from a population with low mean performance if the genetic variation is high enough. However, even the widest range of genetic variation for maize yield ever encountered would not compensate for mean yields that are as different as observed in Tables 4 and 5. Perhaps the closest corresponding estimates of genetic variance relative to these studies are from W.L. Brown's West Indian Composite, a 50%-adapted, 50%-tropical population (GOODMAN, 1965). The range of estimates there were from 0.07 (additive genetic) to 0.22 (total genetic, including some gxe, from NC only), thus providing a range of genetic standard deviations from 0.27 to 0.48 t/ha. As a rule of thumb, if yields are normally distributed, to over-

come a difference of two standard deviations would require a minimum of 100 families; three standard deviations would require about 1,000 families (and of course this also assumes, among other things, that the yield distributions are symmetrical and that yield is the only trait of consequence!). In the case at hand, the range between the commercial checks and several  $F_1$  breeding crosses was on the order of ten genetic standard deviations. Admittedly, these comparisons are only approximate, but deriving families competitive with commercial checks when trailing the checks by 10 genetic, or five or more phenotypic, standard deviations (in 2003, the phenotypic standard deviation was 0.78 t/ha; in 2004, it was 0.71) would be a serious challenge. Perhaps marker-assisted selection might be of some help, but switching to more promising sources among GEM breeding crosses, trying to make a better breeding cross or switching to alternate exotic sources, would probably be more economical.

Furthermore, simple nursery observation without replicated, measured yield trials (at least in NC) often fails to identify the most productive breeding crosses, and some of the poorer ones haven't a chance of producing competitive families. This was not immediately apparent, as when the GEM project started,  $F_1$  seed was scarce, and it seemed reasonable to evaluate the various breeding crosses available by topcrossing them to standard testers and comparing the resulting hybrids in yield trials. This minimized the large differences among the breeding crosses (basically reducing the variation among entries by at least one-half), as the testers were generally uniformly good, while the breeding crosses ranged from quite good to very low yielding.

The other feature that GEM yield trials quickly demonstrated was that the numbers of outstanding GEM families were inversely correlated with the numbers of test environments and the ages of checks used to identify those families. The outlier families that looked good at six or eight environments with older checks often looked ordinary or worse with 15 to 20 environments compared to checks like DeKalb 697 and Pioneer 31G98, introduced within the past few years. In addition, even the best of the GEM families are generally less stable across environments than commercial, domestic hybrids that have had generations of selection for stable, high yields. However, results obtained thus far have exceeded all reasonable initial expectations with several GEM families identified with outstanding yields and acceptable agronomic performance

TABLE 7 - Yield, moisture and percent erect plants (EP) at harvest for 50%-tropical GEM trials; two year averages, selected experiments, 2003-2004; best families.

EX87 ENTRY	t/ha YIELD	% H <sub>2</sub> O	%EP
<i>DK212T N11 F<sub>2</sub>S<sub>2</sub> x FR992.FR1064</i>			
3315-003/00	11.0	19.5	86.3
Check mean	11.3	18.6	91.0
DK697	11.5	19.7	89.7
DK743	10.9	21.1	90.0
HC33.TR7322	9.8	16.5	94.4
LH200.LH262	11.3	19.2	85.7
P31G98	12.5	18.3	89.6
P32K61	11.0	17.9	95.5
LSD (.05)	0.7	0.6	10.4
23 Env. CV:	10.8	5.1	15.4
EX89 ENTRY	YIELD	H <sub>2</sub> O	%EP
<i>DK888 N11 F<sub>1</sub>S<sub>2</sub> x FR992.FR1064</i>			
3607-034/00	10.4	19.3	85.0
Check mean	10.8	18.4	87.8
DK687	10.5	18.5	89.5
DK697	11.2	19.7	84.6
DK743	10.8	20.4	81.5
FR1064.LH185	9.7	17.7	87.2
HC33.TR7322	9.4	16.3	90.8
LH200.LH262	10.3	18.8	84.5
P31G98	12.2	18.1	87.7
P32K61	10.8	18.0	93.2
LSD (.05)	0.6	0.7	6.2
24 Env. CV:	10.1	6.5	12.1
EXF2 ENTRY	YIELD	H <sub>2</sub> O	%EP
<i>DK888 S11 F<sub>2</sub>S<sub>4</sub> x FR615.FR697</i>			
4018-001/00	10.4	21.3	81.3
Check mean	11.0	19.1	85.3
DK697	11.6	19.6	82.7
G8288	11.1	19.6	85.4
HC33.TR7322	9.8	16.8	83.0
LH195.LH256	9.9	20.5	89.7
LH200.LH262	10.3	19.5	80.7
NK91-R9	11.2	21.2	88.0
P31G98	11.8	18.3	89.8
P32D99	12.4	20.4	82.5
P32K61	10.5	18.3	89.8
P32R25	10.5	18.4	82.7
P32W86	12.3	18.8	89.0
LSD (.05)	0.9	0.9	7.4
21 Env. CV:	13.1	7.8	14.7
EXF6 ENTRY	t/ha YIELD	% H <sub>2</sub> O	%EP
<i>DK888 S11 F<sub>2</sub>S<sub>4</sub> x FR615.FR697</i>			
4064-001/00	10.5	20.9	77.9
Check mean	11.2	19.2	86.1
DK697	12.1	20.0	83.6
G8288	11.5	19.5	86.7
HC33.TR7322	9.5	16.9	85.1
LH195.LH256	10.0	20.3	89.4
LH200.LH262	10.6	19.6	80.3
NK91-R9	11.5	21.1	89.4
P31G98	12.1	18.5	89.5
P32D99	12.5	20.1	84.5
P32K61	10.8	18.1	91.2
P32R25	10.9	18.4	82.3
P32W86	12.7	18.6	90.5
LSD (.05)	1.0	0.8	8.3
20 Env. CV:	12.0	6.7	16.5
EXG2 ENTRY	YIELD	H <sub>2</sub> O	%EP
<i>DKXL380 N11 F<sub>2</sub>S<sub>3</sub> x R992.FR1064</i>			
B9527-01/97	10.6	19.2	88.1
Check mean	10.7	18.7	89.5
DK697	11.1	19.3	89.8
G8288	11.1	19.9	88.0
HC33.TR7322	9.1	16.6	90.5
LH200.LH262	10.6	19.2	89.0
P31G98	11.8	18.8	90.4
LSD (.05)	0.7	0.9	7.4
19 Env. CV:	11.1	8.0	13.7
EXG4 ENTRY	YIELD	H <sub>2</sub> O	%EP
<i>DK888 N11 F<sub>2</sub>S<sub>3</sub> x FR992.FR1064</i>			
3439-001/00	10.3	20.4	76.9
<i>DKXL380 N11 F<sub>2</sub>S<sub>3</sub> x FR992.FR1064</i>			
3483-005/00	10.2	20.8	79.3
Check mean	10.7	19.3	85.5
DK697	11.3	19.9	85.0
G8288	10.7	19.6	84.4
HC33.TR7322	9.1	16.7	84.3
LH195.LH256	9.6	20.5	88.5
LH200.LH262	10.2	19.3	81.0
NK91-R9	10.9	21.2	87.1
P31G98	11.4	19.0	88.9
P32D99	11.8	20.5	83.1
P32K61	10.2	18.2	89.0
P32R25	10.5	18.4	82.9
P32W86	11.8	19.0	87.9
LSD (.05)	0.8	0.8	7.0
19 Env. CV:	11.2	6.6	13.3

across 19 or more environments (recent examples are found in Table 7). Most of these lines will be increased in 2005 for distribution in 2006.

The number of companies actively breeding maize in the U.S. has greatly decreased, and universities as renowned for their breeding as Purdue no longer have any maize breeding. It is very unlikely that industry will depart from the elite x elite crosses that have carried us to higher and higher yields, despite the interest in GEM. In the 1980s, almost every major maize seed company (Asgrow, Cargill, DeKalb, NK, Pioneer, etc.) had at least one person working full-time on incorporation of exotic germplasm into their overall breeding efforts. Today, among all the major companies, no one person is so employed and the grand total now adds to less than 0.5 scientist.

The last survey of maize germplasm use organized by ASTA collapsed due to industrial secrecy concerns (David Smith, then of DeKalb, personal communication), so the most recent report on the use of maize germplasm in the U.S. was that of GOODMAN (1998), who showed that only 0.3% of the U.S. maize germplasm base was represented by tropical germplasm. The use of U.S. germplasm in the tropics appears to have been much more successful than the use of tropical germplasm in the U.S. This is a phenomenon that has occurred since the early 1980s, as until then, it was widely believed that U.S. germplasm was useless in the tropics (personal communications, William Brown and Surinder Sehgal).

Despite the dominance of organizations that have invested in long-term maize germplasm improvement (Pioneer in the private sector; Iowa State in the public sector), in most of the world, today's breeding focuses on what can be achieved in 5 to 10 years. In addition, with few exceptions, there is usually the equivalent of a firewall between genetic resources programs and plant breeding programs. Until such barriers are breached (and GEM is one such fissure), there is little hope for efficient use of maize genetic resources, for adequate funding of maize germplasm collections or for their integration into active breeding programs.

Although the potential impact of tropical germplasm on yield in U.S. maize breeding is obvious, U.S. industry has been unable to capitalize greatly upon this opportunity. Much breeding effort that once focused on line development now is directed at backcrossing the latest transgene into existing lines. Budgets that once supported a half-dozen field breeders for a year now often support a

month or two of genomics research for a single scientist (GOODMAN and CARSON, 2000). Overall field breeding for maize has declined precipitously over the last decade, even within persisting companies or public programs (GOODMAN, 2002).

Utilization of exotic germplasm via GEM or other routes is a long-term breeding program; but with current emphases (public and private) on how quickly and how profitably lines can be developed (although no examples of "profitable" U.S. public maize lines exist), few long-term breeding projects may survive. Repeated studies have shown that very high returns on investment are available from expenditures on breeding and germplasm utilization (RUTTAN and SUNDQUIST, 1983), but the returns are not the instantaneous sort favored by the 5-year funding plans currently used almost universally by industry, universities and the USDA. No granting agency exists to support such long-term work in the public sector, even on a short-term basis. At present, the only viable, long-term public U.S. maize breeding programs appear to be those conducted by the USDA-ARS and the program at Iowa State University that is largely funded by a portion of the earnings of a large bequest by Raymond Baker, an Iowa State alumnus and one of the founders of Pioneer.

Regardless of whether there are grain surpluses or shortages, there is always a demand for higher productivity, quicker drydown and resistance to lodging. These traits govern competitiveness and efficiency; they ultimately protect the environment by insuring that marginal lands are not used for production. Each is a polygenic trait that can readily be addressed only by field breeding. While better statistical procedures and molecular marker data may assist, there is no substitute for quality, well-replicated field trials. Applied public breeding programs continue to be essential for educating future plant breeders, demonstrating nursery and yield-trial selection procedures and teaching the many parts of plant breeding that depend more on field experience than academic achievement. Public programs are also essential for high risk research that private companies cannot justify to shareholders who are often interested in fairly short term gains; in plant breeding "short term" usually means about ten years whether the approach is field- or laboratory-oriented. The largely-tropical maize breeding program at NC State, mainly intended to serve as an insurance policy for U.S. maize breeding's narrow germplasm base, would probably not be tolerated at a private company, despite its minimal out-of-pocket costs, averaging

about \$50,000/yr over the past two decades, roughly equal to the cost of one postdoc in a laboratory (with minimal supplies). Typically, 5,000 nursery rows, 11,000+ yield trial plots, 2,000 isolation plots, 2,000 disease plots and 1,500 winter nursery have been grown on an annual basis, with an average of at least three line releases per year. At least a dozen of these lines have been used in commercial hybrids, including at least one TAAT line. The productivity of the better public maize breeding programs compare well to the better private programs. Certainly, the relative return on investment to the public for maize breeding at Iowa State - effectively responsible for most female inbred lines - compares favorably to the much larger investments made at Pioneer's home station at Johnston, IA, less than 50 km distant.

A major argument for investment in plant molecular biology is that advances in that field would speed up plant breeding. In fact, plant molecular biology is sufficiently important in its own right that it doesn't need excuses to exist, but comparative analyses (GOODMAN and CARSON, 2000) demonstrate that the time frame for moving a new transgene into a commercial hybrid is roughly the same as the time required to develop and deploy a new inbred from a largely-exotic germplasm source, but the costs are vastly higher for transgenic approaches to plant breeding. While the economic returns for any type of plant breeding are uncertain, the returns from maize breeding have been very favorable in the past. How important TAAT lines like NC346 will ultimately be also cannot be foreseen at the moment, but they do represent an entirely new heterotic pattern for U.S. maize breeding, the first identified since the Iodents emerged from obscurity in the 1970s.

ACKNOWLEDGEMENTS - J.B. Holland and T.E. Carter made many suggestions for improvement of this paper, and their advice is gratefully acknowledged. Many GEM collaborators contributed to the results in Tables 6 and 7, but Randy Holley of Syngenta played a primary role in family development as well as testing.

## 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.
- BERNARDO R., 1990 Identifying populations useful for improving parents of a single cross based on net transfer of alleles. *Theor. Appl. Genet.* **80**: 349-352.
- BETRÁN F.J., K. MAYFIELD, T. ISAKEIT, M. MENZ, 2005 Breeding maize exotic germplasm. *International Plant Breeding Sym.*, Mexico City, August 16-23, 2003 (in press).
- BETRÁN E.J., M. MENZ, M. BÄNZIGER, 2004 Corn breeding. pp. 305-398. *In*: C.W. Smith, J. Betrán, E.C.A. Runge (Eds.), *Corn. Origin, History, and Production*. John Wiley, Hoboken, N.J.
- BREWBAKER J.L., M.L. LOGRONO, S.K. KIM, 1989 The MIR (Maize Inbred Resistance) trials: Performance of tropical-adapted maize inbreds. *Univ. of Hawaii (HITAHR) Research Series* **062**: 1-27.
- BROWN W.L., 1975 A broader germplasm base in corn and sorghum. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **30**: 81-89.
- CASTLE L.A., T. YAMAMOTO, J.L. ENGLISH, G. ZHU, 2004 DNA shuffling for improved agricultural traits. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **59**. CD-Rom. ASTA, Alexandria, VA.
- DEVALLE C.G., 1952 La obtención de un híbrido de maíz comercial en Cuba. *Estac. Exp. Agron. Santiago de las Vegas (Cuba)*. *Bol. No.* 69.
- DUDLEY J.W., 1984 Theory for identification and use of exotic germplasm in maize breeding programs. *Maydica* **29**: 391-407.
- DUDLEY J.W., 1987 Modification of methods for identifying populations to be used for improving parents of elite single crosses. *Crop Sci.* **27**: 940-943.
- DUDLEY J.W., 1988 Evaluation of maize populations as sources of favorable alleles. *Crop Sci.* **28**: 486-491.
- DUVICK D.N., 1981 Genetic diversity in corn improvement. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **36**: 48-60.
- DUVICK D.N., 1984 Genetic diversity in major farm crops on the farm and in reserve. *Econ. Bot.* **38**: 61-78.
- 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.
- DUVICK D.N., J.S.C. SMITH, M. COOPER, 2004 Changes in performance, parentage, and genetic diversity of successful corn hybrids, 1930-2000. pp. 65-97. *In*: C.W. Smith, J. Betrán, E.C.A. Runge (Eds.), *Corn. Origin, History, and Production*. John Wiley, Hoboken, N.J.
- GEADELMANN J., 1984 Using exotic germplasm to improve northern corn. *Ann. Hybrid Corn Sorghum Conf. Proc.* **39**: 98-110.
- GERLOFF J.E., O.S. SMITH, 1988 Choice of method for identifying germplasm with superior alleles. *Theor. Appl. Genet.* **76**: 209-216.
- GOODMAN M.M., 1965 Estimates of genetic variance in adapted and exotic populations of maize. *Crop Sci.* **5**: 87-90.
- GOODMAN M.M., 1984 An evaluation and critique of current germplasm programs. pp. 195-249. *In*: Report of the 1983 Plant Breeding Research Forum. Pioneer Hi-Bred International, Des Moines, IA.
- GOODMAN M.M., 1985 Exotic maize germplasm: Status, prospects and remedies. *Iowa State J. Res.* **59**: 497-527.
- GOODMAN M.M., 1992 Choosing and using tropical corn germplasm. *Ann. Hybrid Corn Sorghum Industry Res. Conf. Proc.* **47**: 47-64.
- GOODMAN M.M., 1993 Choosing germplasm for breeding program success. pp. 33-45. *In*: M.B. Callaway, C.A. Francis (Eds.), *Crop Improvement for Sustainable Agriculture*. Univ. Nebr. Press, Lincoln.

- GOODMAN M.M., 1998 Research policies thwart potential payoff of exotic germplasm. Maize diversity and maize breeding. *Diversity* **14**: 30-35.
- GOODMAN M.M., 1999 Broadening the genetic diversity in breeding by use of exotic germplasm. pp. 139-148. *In*: J.G. Coors, S. Pandey (Eds.), *Genetics and Exploitation of Heterosis in Crops*. Crop Sci. Soc. of America, Madison, WI.
- GOODMAN M.M., 2002 New sources of germplasm: Lines, transgenes, and breeders. pp. 28-41. *In*: J.M. Martinez R., F. Rincon S., G. Martinez G. (Eds.), *Mem. Congreso Nacional de Citogenetica*. Univ. Autonoma Agr. Antonio Narro, Saltillo, Coah., Mexico.
- GOODMAN M.M., 2004 Developing temperate inbreds using tropical germplasm: Rationale, results, conclusions. *Maydica* **49**: 209-220.
- GOODMAN M.M., M.L. CARSON, 2000 Myth vs. reality: Corn breeding, exotics, and genetic engineering. *Ann. Hybrid Corn Sorghum Res. Conf. Proc.* **55**: 149-172.
- 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.
- HALLAUER A., 2003 Conversion of tropical maize germplasm for temperate area use. *Ann. Hybrid Corn Sorghum Res. Conf. Proc.* **58**. CD-Rom. ASTA, Alexandria, VA
- 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.
- LU H., R. BERNARDO, 2001 Molecular marker diversity among current and historical maize inbreds. *Theor. Appl. Genet.* **103**: 613-617.
- MARCHIONI A.H., 1939 Small-scale studies of locust resistance in Maíz Amargo. *Anales Inst. Fitotecnico Santa Catalina* **1**: 159-166.
- MORRISSEY B.W., 1995 Protecting an interest in quality seed and quality seed traits: Benefits to all. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **50**: 68-81.
- POLLAK L.M., W. SALHUANA, 1998 Lines for improved yield and value-added traits: Results from GEM. *Ann. Hybrid Corn Sorghum Res. Conf. Proc.* **53**: 143-158.
- ROTH M.J., 1995 Intellectual property policy: Benefits of plant variety protection for seed company customers. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **50**: 17-22.
- RUTTAN V., W.B. SUNDQUIST, 1983 Agricultural research as an investment; past experience and future opportunities. pp. 55-109. *In*: Report of the 1982 Plant Breeding Research Forum. Pioneer Hi-Bred International, Des Moines, IA.
- SALHUANA W., L. POLLAK, D. TIFFANY, 1994 Public/private collaboration proposed to strengthen quality and production of U.S. corn through corn germplasm enhancement. *Diversity* **10**: 77-79.
- SALHUANA W., Q. JONES, R. SEVILLA, 1995 The Latin American corn project. *Diversity* **7**: 40-42.
- SIMMONDS N.W., 1993 Introgression and incorporation. Strategies for the use of crop genetic resources. *Biol. Rev.* **68**: 539-562.
- 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. DUVICK, O.S. SMITH, A. GRUNST, S.J. WALL, 1999 Effect of hybrid breeding on genetic diversity in maize. pp. 119-126. *In*: J.G. Coors, S. Pandey (Eds.), *Genetics and Exploitation of Heterosis in Crops*. Crop Sci. Soc. America, Madison, WI.
- SMITH J.S.C., D.N. DUVICK, O.S. SMITH, M. COOPER, L. FENG, 2004 Changes in pedigree backgrounds of Pioneer brand maize hybrids widely grown from 1930 to 1939. *Crop Sci.* **44**: 1935-1946.
- 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, F<sub>1</sub> grain yield, heterosis and RFLPs. *Theor. Appl. Genet.* **80**: 833-839.
- STUBER C.W., 1978 Exotic sources for broadening genetic diversity in corn breeding programs. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **33**: 34-47.
- SPRAGUE G.F., 1971 Genetic vulnerability in corn and sorghum. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **26**: 96-104.
- 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.
- TALLER J.M., R. BERNARDO, 2004 Diverse adapted populations for improving northern maize inbreds. *Crop Sci.* **44**: 1444-1449.
- TROYER A.F., 1994 Breeding early corn. pp. 341-396. *In*: A. Hallauer (Ed.), *Specialty Corns*. CRC Press, Boca Raton, FL.
- TROYER A.F., 1996 Breeding widely adapted, popular maize hybrids. *Euphytica* **92**: 163-174.
- TROYER A.F., 1999 Background of U.S. hybrid corn. *Crop Sci.* **39**: 601-626.
- TROYER A.F., 2004 Persistent and popular germplasm in seventy centuries of corn evolution. pp. 133-231. *In*: C.W. Smith, J. Betrán, E.C.A. Runge (Eds.), *Corn. Origin, History, and Production*. John Wiley, Hoboken, N.J.
- UHR D.V., M.M. GOODMAN, 1995 Temperate maize inbreds from tropical germplasm. I. Testcross yield trials. *Crop Sci.* **35**: 779-784.
- WALLACE H.A., 1923 Burnett's Iodent. *Wallaces' Farmer* **46**(6) (cited in Troyer, 2004).
- WELHAUSEN E.J., 1956 Improving corn with exotic germplasm. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **11**: 85-96.
- WELHAUSEN E.J., 1965 Exotic germplasm for improvement of corn-belt maize. *Ann. Hybrid Corn Sorghum Ind. Res. Conf. Proc.* **20**: 31-45.
- WILSON L.M., S.R. WHITT, A.M. IBANEZ, T.R. ROCHEFORD, M.M. GOODMAN, E.S. BUCKLER IV, 2004 Dissection of maize kernel composition and starch production by candidate gene association. *Plant Cell* **16**: 2719-2733.