Chapter 13

BROADENING THE GENETIC DIVERSITY IN MAIZE BREEDING BY USE OF EXOTIC GERMPLASM

Major M. Goodman

INTRODUCTION

Maize improvement throughout the world has been accompanied by a narrowing germplasm base, as newer lines and varieties have been derived from intercrosses of existing elite materials. Most other crops have followed the same pattern. For maize, there is no indication that improvement rates have been adversely affected by this narrowing germplasm base (Duvick, 1990), but there is concern that bottlenecks may restrict breeding flexibility and slow response to new opportunities, pests, pathogens, and agronomic practices in the future.

Use of temperate maize germplasm in tropical breeding programs is poorly documented (for an exception see Kim et al., 1987), but clearly increasing. Many newer tropical hybrids contain at least some temperate germplasm, often as a part of only one side of a hybrid pedigree. However, the use of exotic maize germplasm in temperate areas is better documented. Surveys of exotic germplasm in U.S. hybrids suggest that the amount of exotic germplasm used is generally small, but rising (Goodman, 1985; 1998).

Basically, there are three geographic types of maize germplasm exotic to temperate areas. The most widely-used exotic sources are those from other temperate areas, such as Argentine, European, and South African germplasm used in the U.S. (Table 13-1). Conversely U.S. germplasm is used in other temperate regions. The second widely-used source of exotic germplasm is that from the lowland tropics, representing races or varieties such as Cuban Flint, Suwan, Tusón, and Tuxpeño. Thus far these have been used rather sparingly in the U.S., mostly as sources of pest- or disease-resistance. The third potential source of exotic germplasm for temperate areas is from the highland tropics (races like Chalqueño, Cuzco, Sabanero, or San Geronimo); these have had less use in the U.S. due to their low tolerance for heat and other stresses.

Use of exotic germplasm in U.S. maize hybrids has increased almost 3-fold during the past twelve years, with total exotic-germplasm use increasing from about 1% in 1984 (Goodman, 1985) to almost 3% in 1996 (Table 13-1). The largest part of this increase has come from the use of *temperate* exotic germplasm. Use of *tropical* exotic germplasm in U.S. hybrids is much smaller (only about 0.1% in 1984; about 0.3% in 1996). Most widely-sold U.S. hybrids that contain exotic germplasm have small percentages (2 to 6% is typical) of temperate, exotic germplasm from the insect-resistant, Argentine cultivar, Maíz Amargo (mostly via B68). A few have higher percentages, typically 12 to 25%, most often from the related French lines F2 or F7. U.S. hybrids containing tropical germplasm show the same pattern, but at much lower levels of exotic germplasm: widely sold hybrids with tropical maize germplasm usually contain from 1 to 5% tropical germplasm, but a few less-popular hybrids contain 25 to 50% tropical germplasm.

The Genetics and Exploitation of Heterosis in Crops. J. G. Coors and S. Pandey, Editors. 524 p.

Table 13-1. Use of exotic germplasm in U.S. hybrids in 1996 (adapted from Goodman, 1998).

Area	Average % Exotic Germplasm	Area	Average % Exotic Germplasm
Argentina	1.99		
Australia	0.03	Caribbean	0.23
Europe	0.46	Mexico	0.07
South Africa	0.08		
Temperate Total	2.56	Tropical Total 0.30	

Maize breeding throughout the temperate parts of the world is rapidly becoming well-integrated, with phytosanitary restrictions and intellectual property rights being the most important barriers to germplasm, line, and hybrid exchange between organizations. Thus, the focus of this paper is the use of tropical maize germplasm in temperate areas. Five questions are considered:

1. What types of maize germplasm sources are most promising?
2. How can choices be made among the many possibilities within a specific type?
3. How difficult is the problem of photoperiod response?
4. Can tropical maize germplasm lead to yield improvement, in addition to its current role as a last-resort source of disease- and insect-resistance?
5. How can field-based (or molecular-marker-assisted) selection be conducted so as to maximize any positive yield-potential available within a specific, variable, exotic accession or hybrid?

SOURCES OF PROMISING GERMPLASM

While there is little published information comparing selection success with major types of germplasm (from crosses of inbred lines, hybrids, elite families, synthetics, or germplasm accessions), the overwhelming opinion among maize breeders with exotic experience is that inbred lines or hybrids are more promising sources than are populations with no history of inbreeding. Table 13-2 suggests about a 100-fold advantage for improved sources with a history of inbreeding over elite synthetics improved by familial selection. Since initial evaluation of tropical sources must usually be based on yield-trial data from the tropics, germplasm-accession sampling has, until recently, been especially discouraging. The LAMP project (Salhuana, 1995; Salhuana and Sevilla, 1995; Salhuana et al., 1997) has alleviated much of that problem recently. Still, many potentially-available lines, hybrids, and accessions exist for which no performance data are available or accessible.

SELECTING AMONG AVAILABLE POSSIBILITIES

Let us choose tropical hybrids as the category of germplasm for use as base material for a temperate-targeted breeding program. To choose among the available tropical hybrids, it would be helpful to know their pedigrees (often unavailable), and more importantly their agronomic performance, preferably from multiple tropical locations. Once a candidate set of hybrids is identified from such data, they can be grown in short-day winter nurseries alongside elite, domestic breeding stocks to judge their maturities (independent of daylength effects) and agronomic features in comparison to standard, domestic stocks. Late maturity, even under short days, and poor agronomic performance eliminate many candidates either at the initial winter-nursery screening or in subsequent, segregating, breeding nurseries. The better candidates can be crossed with elite lines

Table 13-2. Summary statistics for first-cycle, largely tropical, line development at North Carolina State University (adapted from Goodman, 1992).

Category	Tropical Hybrid derivatives[†]	Tropical Synthetic Derivatives[†]
	------------- no.	-------------
Total Number of Nursery Plots Used for Line Development:	306	7,395
Numbers of Plots for Families with No Testable Lines:	42	247
Numbers of Plots for Families with All Topcrosses Yielding Less than the Check Median:	97	4,060
Numbers of Lines where Topcross Yield Exceeded Check Median:	71	17

[†] Tropical hybrid derivatives were 100% tropical; the tropical synthetic derivatives ranged from 25% to 75% tropical, the remainder being elite U.S. germplasm.

important heterotic groups, tested and subjected to inbreeding (for example, at southern locations in the U.S.).

PHOTOPERIOD

Photoperiod or daylength response is mostly a cosmetic problem. It can be eliminated, even from descendants of 100%-tropical crosses, and is mostly an inconvenience to the uninitiated who try to grow tropical materials for crossing in summer, rather than short-day, winter nurseries. Experimental results at Iowa State University suggest that photoperiod response can readily be eliminated or greatly diminished by mass selection within populations as diverse as ETO, Suwan, Tusón, and Tuxpeño (Hallauer, personal communication). Similar results were reported for derivatives of tropical hybrids handled by pedigree selection at North Carolina State University (Holley and Goodman, 1988).

TROPICAL GERMPLASM FOR YIELD IMPROVEMENT

Tropical germplasm has traditionally been used in the U.S. as a last-resort source of disease- and insect-resistance. Holley and Goodman (1988) reported that topcrosses of derivatives of tropical hybrids were sometimes competitive with commercial hybrids; similar results were reported by Goodman et al. (1990) and by Uhr and Goodman (1995). Cargill and Northrup King provided topcross seed of all recently-released North Carolina (NC) lines crossed with LH132, a short-statured, Stiff-Stalk-Synthetic line, and LH150, a tall, southern, non-Stiff-Stalk-Synthetic line. At the time the yield trials were conducted, all NC lines from NC250 to NC300, representing all NC line releases from 1980 to the early 1990s, were tested in such single-crosses.

Table 13-3. Highest yielding North Carolina (NC) line topcrosses from trials conducted 1991 to 1994 at Clayton, Lewiston, and Plymouth, NC.

	Grain			Ear	Days to	
PEDIGREE[†]	Yield	Moisture	EP[‡]	height	tassel	
	t ha^{-1}	%	%	cm	no.	
NC258 x LH132	8.7	18.9	95	96	74	*NC lines*
NC268 x LH150	9.3	16.6	95	116	76	*less*
NC280 x LH150	8.6	17.0	95	116	75	*than*
NC292 x LH150	8.7	16.7	98	117	74	*10%*
NC294 x LH150	8.7	17.3	94	116	76	*exotic*
NC296 x LH132	9.6	17.1	96	107	75	*NC lines*
NC298 x LH132	8.6	18.0	96	106	76	*100%*
NC300 x LH132	8.4	18.1	97	100	75	*exotic*
Mo17*Ht* x B73*Ht*	7.6	15.2	94	104	72	
Pioneer 3165	8.8	19.0	94	109	77	*Checks*
Dekalb 689	8.9	17.1	97	111	76	
LSD.05(Ent.xEnv.)	0.4	0.4	4	4	1	
C.V.%(Ent.xEnv.)	6	3	5	5	1	

[†] NC lines of largely Lancaster (NC258), B73 (NC268, NC280, NC292, NC294) or tropical (NC296, NC298, NC300) origin were crossed to Holden tester lines (LH132 is a Stiff-Stalk line; LH150 is a non-Stiff-Stalk line).

[‡] EP % = percent erect plants at harvest.

Table 13-4. Comparisons of NC296A topcrosses and commercial hybrids for 1992-1994 trials at Clayton, Lewiston (not 1993), and Plymouth, NC.

	Commercial Hybrid				NC296A Cross[†] with Hybrid			
	Grain				Grain			
	Yield	Mois.[‡]	EP[‡]	GLS	Yield	Mois.[‡]	EP[‡]	GLS[§]
	t ha^{-1}	%	%		t ha^{-1}	%	%	
B73*Ht*xMo17*Ht*	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
Average	*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

[†] 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.

[‡] Mois. % = percent moisture; EP % = percent erect plants at harvest.

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

Three of the 32 NC lines tested were of 100%-tropical origin: NC296, NC298, and NC300. Only better-performing crosses are listed in Table 13-3, which demonstrates that tropical lines can compete with domestic lines in some tropical x domestic combinations. (LH132 x NC258 is sold by several companies and NC296 is used in at least a few commercial hybrids in the U.S. and Mexico). Data indicate that NC296A, another all-tropical inbred, is a source for potentially new factors for yield for U.S. breeding programs; it also has promise for gray leaf spot- and southern rust-resistance (Table 13-4, rust data not shown). All NC296A crosses were essentially immune to southern rust in 1992 (all were rated 9 on a 1 to 9 scale; the most-resistant commercial hybrid, Pioneer 3140 scored 7.5, the others ranged from 2.5 to 5.0). This experiment was conducted as a demonstration to attempt to persuade private breeders that a tropical source could serve to increase yields, even of elite domestic hybrids, which were chosen to represent a range of high-response and stress-resistant, commercial hybrids. The experiment included nine hybrids and the same nine hybrids crossed to NC296A. The NC296A crosses out-yielded the hybrids themselves by an average of about 1 t ha^{-1} at a cost of 1.6% grain moisture and 8% lower standability. A similar experiment was conducted with NC296 and NC346 (two sister lines of NC296A), using a different set of seven hybrids (Table 13-5). The results were similar, although the differences were smaller: a yield gain of 0.7 t ha^{-1} at a cost of 0.85% moisture for the 50%-tropical topcrosses. There was no difference in mean lodging between the commercial hybrids and their topcrosses with these two temperate-adapted, tropical inbreds, despite the effects of a tropical storm (Bertha) and a major hurricane (Fran) in 1996.

The use of tropical germplasm usually introduces more lodging, higher moisture at harvest, taller plants, and susceptibility to smut. However, higher yield and more GLS- and southern rust-resistance suggest that NC296A and its sister lines should not be ignored, despite less-than-perfect appearance and weak roots. Problems related to maturity, standability, and smut-susceptibility are readily improved; NC296 was a first cycle, 100%-tropical, temperate-

Table 13-5. NC296-type topcrosses[†] vs. Commerical Hybrids.
Year 1996: Clayton, N.C.; Lewiston, N.C.;
Year 1995: Clayton, Lewiston, Plymouth, N.C.

Hybrid	Commercial			x NC296			x NC346		
	Grain			Grain			Grain		
	Yield	Mois.[‡]	EP[‡]	Yield	Mois.[‡]	EP[‡]	Yield	Mois.[‡]	EP[‡]
	t ha^{-1}	%	%	t ha^{-1}	%	%	t ha^{-1}	%	%
B73*Ht*.Mo17*Ht*	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
Pioneer3283W	7.3	17.5	86	7.9	18.1	84	8.0	18.5	84
Pioneer3287W	7.1	18.3	81	8.0	18.8	77	7.6	18.7	81
Average:	*7.7*	*17.9*	*82*	*8.4*	*18.7*	*82*	*8.4*	*18.8*	*83*
DeKalb 689	7.6	18.1	78	*Various*					
LH132 x LH51	7.7	17.3	84	*Check*					
Pioneer 3085	8.1	19.7	66	*Hybrids*					
Pioneer 3165	8.1	19.9	74						
LSD .05	0.8	0.7	11	(Entry x Env.)					
C. V. %	8	3	11	(Entry x Env.)					

[†] NC296 and NC346 are sister lines both derived from the cross of the same two tropical hybrids as NC296A (see Table 13-4).

[‡] Mois. % = percent moisture; EP % = percent erect plants at harvest.

adapted inbred derived from two first-cycle tropical hybrids based upon lines that themselves were not fully inbred. We are now testing third cycle inbreds from all-tropical germplasm, and have concluded that two factors restrict our progress with all-tropical derivatives much more than the problems mentioned above:

(1) Poor germination and seedling vigor under adverse (cold, wet, cloudy) spring growing conditions, and

(2) A lack of available high-yielding, early maturing, lowland-tropical inbreds or hybrids. Most all-tropical hybrids are full-season hybrids that are almost as well suited to fence building as grain production, even when grown under short days.

We are attempting to remedy the late-maturity, high moisture problem by selection for earlier dry-down and seem to have had reasonable success (Hawbaker et al., 1997). More cold, wet springs similar to 1997 will probably solve our spring-vigor problem.

SELECTION WITHIN A VARIABLE EXOTIC SOURCE

The Germplasm Enhancement of Maize (GEM) project, a follow-up project to LAMP, is a multi-institutional, public-private, cooperative endeavor to quickly inject elite exotic germplasm into public and private breeding programs (Salhuana et al., 1994). The breeding populations used in GEM include (1) elite germplasm accessions identified by LAMP crossed to elite, domestic, private lines; (2) tropical hybrids crossed to elite, domestic, private lines; and (3) the breeding populations in (1) and (2) crossed to second elite, domestic, private lines from the same heterotic group but from a second company. Nearly all large domestic companies participate, as does one Argentine company, Morgan. Almost every public maize breeding program in the U.S. is included in the project. The companies contribute germplasm, through crosses which they make using their own lines, nursery space and labor for selfing, and yield-trial space. Public programs are involved with disease- and insect-resistance, value-added trait characterization, and breeding work. The effort is led by Linda Pollak of Iowa State University and Martin Carson from North Carolina State University, both USDA-ARS researchers. Wilfredo Salhuana chairs the steering committee, which represents both the private and public sectors.

One immediate question arose concerning which generation of selfing should be used for topcross testing of the (germplasm accession x private line) breeding crosses. These 50%-exotic populations start as variable F_1s, where the F_1 variation represents half the additive genetic variation in the variable germplasm accession. However, once they have been selfed twice, the variation among families is dominated by the newly-generated variance of the racial cross arising as a result of segregation between the elite, domestic Corn Belt inbred and the exotic accession (Table 13-6). Thus, one must test individual F_1 plants or F_1S_1 (F_2) families if efficient selection is to be done within the accession, and many plant breeders familiar with germplasm accessions of maize would want to select within such accessions. This same principle applies to QTL studies with variable exotic populations. If it is important to select *within* such populations, then selection must be done early, before newly generated exotic x elite variation is expressed, or very large sample sizes (not hundreds, but thousands) will be needed to assure that the specific QTL of interest within the variable exotic will be identified (see Beavis, 1994).

RATIONALE AND CONCLUSIONS

The maize breeding program at North Carolina State devotes much of its effort to the development of largely tropical lines adapted to temperate environments. To the best of our knowledge, we are the only organization in the world which emphasizes line development from 50%- to 100%-tropical germplasm for use in temperate areas. There is a strong possibility that day-

Table 13-6. Distribution of readily transmissible genetic variation of a line x accession cross and of subsequent selfed lines (from Goodman, 2000).

	Average genetic variation†	
Generation	Within	Among
(Accession x Line) F_1	0	σ_A^2
(Accession x Line) F_1S_1	σ_B^2	σ_A^2
(Accession x Line) F_1S_2	$\sigma_B^2/2$	$\sigma_A^2 + \sigma_B^2/2$
(Accession x Line) F_1S_3	$\sigma_B^2/4$	$\sigma_A^2 + 3\sigma_B^2/4$
(Accession x Line) F_1S_4	$\sigma_B^2/8$	$\sigma_A^2 + 7\sigma_B^2/8$
.	.	.
.	.	.
.	.	.

† σ_A^2 is the readily heritable variation transmitted from the accession (generally one-half the additive genetic variance within the accession itself plus minor epistatic and usually unknowable dominance effects).

σ_B^2 is the variance arising in the F_2 (F_1S_1) generation from elite x exotic segregation; for simplicity, it is treated here as additive.

F_1S_i is the i^{th} selfed generation derived from the variable F_1 population.

length-neutral, largely-tropical germplasm may also be useful in the tropics and subtropics. Yield trials in Argentina and Brazil (for example, see Goodman et al., 1990), and breeding and production use in India and Mexico support that concept. It is among our all-tropical lines that we have found our highest testcross yields, greatest southern leaf blight resistance, best southern rust resistance, and reliable gray leaf spot resistance, equivalent to that of our best all-temperate line, NC258. We have yet to determine whether we can successfully mine germplasm accessions directly for useful lines, but the initial data look promising (Stuber, 1978; Castillo-Gonzalez and Goodman, 1988; Eberhart et al., 1995; Holland and Goodman, 1995).

Most of the line development work with largely tropical materials that has reached yield-trial stage at North Carolina State has been from either tropical synthetics or tropical hybrids. Work is in progress using lines from CIMMYT, IITA, and Thailand (the latter restricted to Ki3 and Ki11 as Thai inbreds and hybrids are difficult to obtain in the U.S. due to phytosanitary restrictions).

Preliminary data from the GEM project are quite encouraging, but only a single-year's data are complete for individual families, and those are only from a single population, Chis 775. Basically, the topcross of one F_1 family (of the variable accession Chis 775 crossed to a non-Stiff-Stalk inbred) outperformed the checks, while several others were close to the checks. Given the range of variation expected in the F_2 and in subsequent generations, it should be possible to extract superior, 50%-Chis 775 families. Line development will depend upon the prevalence of deleterious recessives. If they are not pervasive, then direct development of 50%-tropical lines should be possible. We will also cross these families with our existing, temperate-adapted, tropical lines and proceed with line development. At Iowa State University, and at cooperating private companies, identified elite families will be crossed to elite Midwestern lines for the development of 25%-tropical, 75%-domestic lines. By the summer of 2001, there should be extensive proprietary and public testing of topcrosses of partially inbred lines tracing to the GEM project. By the year 2005, some of this material could begin to reach farmers fields.

It is very likely that the rate of use of exotic germplasm will continue to increase as data become available to identify the most promising sources of exotic germplasm and as these sources are converted to more readily-used lines and populations, free from daylength restrictions and agronomic flaws. These will be especially useful for QTL (quantitative trait loci) studies such as those of Ragot et al. (1995), where extensive field experimentation is required to accurately estimate genetic effects (and for which pre-adapted materials or several generations of backcrossing are usually needed). There is little doubt that virtually all breeding stocks, germplasm accessions, and wild or weedy crop relatives, no matter how unpromising they may appear phenotypically, contain untapped alleles or allelic-combinations that could be used for plant breeding, with adequate investment in conventional or marker-assisted selection (Tanksley and Nelson, 1996). The more distant the relationship to current elite lines, the greater the probability that there is something unique to discover. Unfortunately, due to the usual amount of backcrossing necessary for most agronomic evaluations of quantitative traits (as opposed to single-gene, qualitative traits) from unadapted sources, there is a low likelihood to find exactly what is sought. For example, to evaluate an unadapted maize accession agronomically, the equivalent of two backcrosses is needed in North Carolina (for Iowa, three are needed). To do the same thing with teosinte would require *at least* an additional backcross. With each backcross, the possibility of loss of the allele of interest increases, and this allele probably is not fixed in the original cross-pollinated accession. Thus, most breeding and applied molecular genetics programs are apt to remain concentrated on elite, improved germplasm as long as genetic advances resulting in improved lines continue at the current rate of 1% to 2% per year.

It is certainly possible to dissect the genetic structure of a second, third, or fourth backcross population of an exotic maize or teosinte accession using a saturating array of molecular markers combined with standard factorial-regression anaysis, bulked-segregant anaysis, or other analytical techniques (Tanksley and Nelson, 1996). The number of distinct families [somewhere between hundreds and thousands (Beavis, 1994)] required to detect differences of the order of 5 to 10% for quantitative traits, such as yield or standability, is particularly daunting in light of the existence of over 250 highly variable races of maize and several species and races of teosinte that are at least equally as geneticly variable as the races of maize. None of the teosintes have been seriously screened for favorable characteristics, and some individual teosinte accessions appear to have genetic variation levels comparable to that found within entire species of some self-pollinated crops (J. Jesus Sanchez, INIFAP, unpublished data). Despite LAMP, lack of preliminary evaluation also is the case for over half of the Latin American accessions - and some entire races - of maize. Under these sorts of circumstances, the use of pre-adapted, elite inbred lines of exotic maize, such as B103, NC296, NC298, or NC300, would be the first choice for molecular-marker work with maize exotics. Elite, proven inbreds from tropical breeding programs, even though they lack U.S. adaptation, would be the second choice because (1) they have passed severe selection for numerous favorable attributes and (2) being commercial-quality inbreds, they have been purged of many, if not most, deleterious recessive alleles that are carried by highly heterogeneous and heterozygous populations of open-pollinated maize and teosinte. A critical advantage of pre-adapted materials is that they can be evaluated as F_2S_1 families, rather than BC_2 (or even BC_4) families. With each backcross, half of the additive variation is lost. Thus, differences of 20% among F_2S_1 families are reduced to only 5% among BC_2 families, and differences of less than 5% are often difficult to detect in many breeding programs.

Clearly, use of exotic germplasm will be needed in the U.S. to provide insurance against certain diseases or pests that are prevalent elsewhere in the world but currently absent in the U.S. In some cases, the U.S. lacks elite lines with resistance. Examples include streak virus from Africa, Rio Quarto virus from Argentina, and African gray leaf spot, a much more aggressive form than the relatively late-developing strains found in the U.S. It would be prudent to spend some of the millions of dollars currently being invested in genetic engineering projects for herbicide resistance on more critical projects to develop adequate safeguards against such readily-identifiable and potent threats to agricultural security as these diseases. Adequate response will require both the use of exotic germplasm (that is where the resistance is), the use of molecular-marker technology (to efficiently transfer the resistance), and international collaboration (because the current disease sites - fortunately for the U.S. - lie outside U.S. borders). At least some of these diseases will reach the U.S.; failure to have an adequate defense could be devastating, since few, if any, elite lines have adequate resistance at present.

While we work on temperate-adapted, tropical line development at North Carolina State and colleagues such as Dudley (1984) and Crossa (1989) develop theory for selecting optimal populations and ideal percentages of exotic germplasm, natural selection itself is apt to provide the ultimate force to encourage the widespread use of genetic resources.

REFERENCES

Beavis, W. D. 1994. The power and deceit of QTL experiments: Lessons from comparative QTL studies. Ann. Corn and Sorghum Research Conf. Proc. 49:250-266.

Castillo-Gonzalez, F., and M. M. Goodman. 1988. Agronomic evaluation of Latin American maize accessions. Crop Sci. 29:853-861.

Crossa, J. 1989. Theoretical considerations for the introgression of exotic germplasm into adapted maize populations. Maydica 34:53-62.

Dudley, J. W. 1984. Theory for the identification and use of exotic germplasm in maize breeding programs. Maydica 29:391-407.

Duvick, D. N. 1990. The romance of plant breeding and other myths. Pp. 39-54 *in* Gustafson, J. P. (ed.), *Gene Manipulation in Plant Improvement*, Plenum Press, New York.

Eberhart, S. A., W. Salhuana, R. Sevilla, and S. Taba. 1995. Principles for tropical maize breeding. Maydica 40:339-355.

Goodman, M. M. 1985. Exotic maize germplasm: Status, prospects and remedies. Iowa State J. of Research 59:497-527.

Goodman, M. M. 1992. Choosing and using tropical corn germplasm. Ann. Corn and Sorghum Research Conf. Proc. 47:47-64.

Goodman, M. M. 1998. Maize diversity and maize breeding. Diversity 14:30-35.

Goodman, M. M. 2000. Incorporation of exotic germplasm into elite maize lines: Maximizing favorable effects of the exotic source. Theor. Pop. Biol. In press.

Goodman, M. M., F. Castillo-Gonzalez, and J. Moreno. 1990. Choosing and using exotic maize germplasm. Illinois Corn Breeders School Proc. 26:148-171. Champaign, IL.

Hawbaker, M. S., W. H. Hill, and 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. and M. M. Goodman. 1995. Combining ability of tropical maize accessions with U.S. germplasm. Crop Sci. 35:767-773.

Holley, R. N. and M. M. Goodman. 1988. Yield potential of tropical hybrid corn derivatives. Crop Sci. 28:213-217.

Kim, S. K., Y. Efron, F. Khadr, J. Fajemisin, and M. H. Lee. 1987. Registration of 16 maize-streak resistant tropical maize parental inbred lines. Crop Sci. 27:824-825.

Ragot, M., P. H. Sisco, D. A. Hoisington, and C. W. Stuber. 1995. Molecular-marker-mediated characterization of favorable exotic alleles at quantitative trait loci in maize. Crop Sci. 35:1306-1315.

Salhuana, W. 1995. Latin American maize project leaves untapped legacy of agricultural riches. Diversity 11(4):6.

Salhuana, W., L. Pollak, and D. Tiffany. 1994. Public/private collaboration proposed to strengthen quality and production of USA corn through germplasm enhancement. Diversity 10(1):77-78.

Salhuana, W., and R. Sevilla. 1995. Latin American Maize Project (LAMP) Stage 4 Results from Homologous Areas 1 and 5. Nat. Seed Storage Lab., Fort Collins, CO.

Salhuana, W., R. Sevilla, and S. A. Eberhart. 1997. Final Report, Latin American Maize Project. Pioneer Hi-Bred International, Johnston, IA

Stuber, C. W. 1978. Exotic sources for broadening genetic diversity in corn breeding programs. Ann. Corn and Sorghum Research Conf. Proc. 33:34-47.

Tanksley, S. W. and J. C. Nelson. 1996. Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite lines. Theor. Appl. Genet. 92:191-203.

Uhr, D. V. and M. M. Goodman. 1995. Temperate maize inbreds from tropical germplasm. I. Testcross yield trials. Crop Sci. 35:779-784.