

Dedication: Major M. Goodman Maize Geneticist and Breeder

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Major M. Goodman is the leading expert on the classification and use of the diverse genetic resources of maize. He pioneered the development and use of mathematical approaches to classification of diverse plant materials; had a primary role in the development of one of the first comprehensive plant genetic marker systems; championed the maintenance, evaluation, and use of gene bank resources for crop improvement; and to this day conducts a very productive applied public maize breeding

programs. His impact on the scientific community has increased as understanding of genetic diversity and its relationship with phenotypic diversity has become a major objective of large-scale plant genomics efforts (Buckler et al. 2006). Maize plays a key role in these efforts thanks in part to the groundwork that Major Goodman developed to elucidate and synthesize the relationships among the bewildering array of diverse maize seed resources. As former students of Dr. Goodman, we dedicate this chapter to an outstanding mentor and a model of scientific vigor and integrity on behalf of all of his colleagues and former students.

I. BIOGRAPHICAL SKETCH

Major Goodman was born in 1938 in Des Moines, Iowa. He was raised in the small town of Johnston in a family of limited means. Fortunately for the plant breeding community, Johnston was and is the headquarters of the Pioneer Hi-Bred seed company, which was the first company to market hybrid maize seed and remains one of the largest seed companies in the world. When Major sought work as a young man, the largest employer in town was Pioneer Hi-Bred, and his brother was a foreman for a field crew. Thus, it was natural for Major to begin working in corn breeding nurseries as a high school student. As a temporary field worker, he quickly attracted the notice of Dr. William Brown, then director of research (later to be president) of Pioneer, who specialized in maize racial diversity, having written or contributed to three of the maize racial collection monographs (Brown 1960; Ramirez et al. 1961; Timothy et al. 1961) as well as coauthoring a history of early maize genetics and breeding with a former Vice President of the United States (Wallace and Brown 1988). Brown (1986) later wrote, "It was clear from my first contact with Dr. Goodman that he was an individual of unusual intellectual capacity and ability."

Supported by a National Merit Scholarship, Dr. Goodman attended Iowa State University, where he majored in mathematics. Major later wrote of his decision to continue studying plant genetics after graduating from college: "Clearly, I would not be here today had I not received the advice of W.L. Brown . . . to attend NC State and enroll in its outstanding quantitative genetics program" (Goodman 1987). Major obtained his M.S. degree in genetics at North Carolina State University (NCSU), studying quantitative genetic variability in an exotic maize population under the supervision of H. F. "Cotton" Robinson, who was well known for his work on the mating designs (North Carolina Designs I, II, and III) to estimate additive and dominant genetic variances in maize populations

(Comstock and Robinson 1952). Following this, according to Cockerham and Weir (1988), Major

worked on cotton for his Ph.D. with S. G. Stephens. His thesis involved a lot of theoretical and experimental work and laid the foundations for another long association. At this time Major developed a deep interest in the evolution of domestic plants, and wrote a monograph on the evolution of maize. The experiment station published the monograph, and it came to the attention of Paul Mangelsdorf at Harvard. At that time Mangelsdorf was the world authority on the evolution of maize, and quite a correspondence and debate started among Major, Stephens, and Mangelsdorf.

Although Major's monograph (Goodman 1965b) did not support Mangelsdorf's "Tripartite Hypothesis" of the evolution of maize from *Tripsacum*, Mangelsdorf appreciated Major's critical assessments of the maize evolution literature, as he later recalled: "I have known Major Goodman and his work since 1968, when I retired to Chapel Hill from Harvard University. His interest and encouragement were very important in helping me to continue my own lifetime research on corn. My book, *Corn, Its Origin, Evolution and Improvement*, published by Harvard University Press in 1974, acknowledges Major Goodman's critical assistance" (Mangelsdorf 1987). Although he never focused primarily on the maize evolution problem, Major's work contributed to this area by helping to define patterns of genetic variability in maize and teosinte, which has direct bearing on some of the evolutionary questions (Doebley 1990; Doebley et al. 1984).

Following the completion of his Ph.D. from NCSU, Major obtained a National Science Foundation Fellowship that supported his research on the races of maize at the Escola Superior de Agricultura in Piracicaba, Sao Paulo, Brazil, in collaboration with Drs. Almiro Blumenschein and Ernesto Paterniani. After two years of this fellowship, he returned to NCSU as a visiting professor in the Department of Statistics. This position was supported by a sizable grant from the National Institutes of Health to a Quantitative Genetics Research Program at NCSU headed by Dr. Clark Cockerham in the Department of Statistics:

Clark realized what an asset Major would be to our quantitative genetics program, and enticed Major back to Raleigh. The Genetics department was up to its ears (!) in quantitative geneticists, but fortunately the statistics department has an open door policy for almost anyone they could attract who didn't cost anything. The arrangement turned out to [be] ideal, and Major made considerable progress in his research in our department. (Cockerham and Weir 1988)

Major recalled of that period in his career:

the strong interdepartmental collaboration exemplified in [the NCSU Quantitative Genetics] program allowed me later, as a faculty member, to work on maize germplasm resources, taxonomy of the races of maize, and isoenzyme genetics, while housed in the Department of Statistics My own research would not even have been possible had it not been encouraged and supported by Dr. C. Clark Cockerham Even so, allowing a faculty member to stray so far afield from the “departmental missions” of the Department of Statistics must have required exceptional tolerance, even for an exceptionally tolerant department. (Goodman 1987)

Dr. Goodman was soon promoted to a permanent faculty position, becoming a full professor in 1976.

In 1983, Dr. Donald Thompson, the United States Department of Agriculture—Agricultural Research Service (USDA-ARS) maize breeder located in the Department of Crop Science at North Carolina State University retired. The USDA planned to refocus this position on genetics, but the university desired to maintain a maize breeding program. Therefore, Dr. Goodman was offered a professorship in the Department of Crop Science in 1983, which he accepted. Although he moved from the Department of Statistics, he maintained a joint appointment with that department, as well as appointments with the Departments of Genetics and Botany. Today, Major Goodman remains the maize breeder in the Department of Crop Science and continues to lead the applied maize inbred line development program.

Major Goodman’s career trajectory has been nontraditional, to say the least, among plant breeders. Yet his unique vision to understand the genetic variability in a crop species and exploit it for practical benefit has resulted in exemplary achievements. He has been rewarded for his outstanding research efforts with honors including election to the National Academy of Sciences in 1986; appointments as William Neal Reynolds Professor (the highest honor in the college of Agriculture and Life Sciences at NCSU) and Distinguished University Professor in 1988; the Frank N. Meyer Medal in 1999 and the Crop Science Research Award in 2005, both from the Crop Science Society of America; and the dedication of an issue of the journal *Maydica* to him in 2006.

II. SCIENTIFIC ACHIEVEMENTS

A. Maize Diversity and Classification

In the 1940s, the Rockefeller Foundation and the Mexican Ministry of Agriculture initiated a program to collect varieties of maize throughout

Mexico in a systematic fashion. The initial collections revealed tremendous phenotypic diversity among farmer-maintained landrace populations. This highlighted the need to collect landraces from other Latin American countries before they were replaced with improved cultivars and lost forever (Wellhausen et al. 1952). Thus, the Rockefeller Foundation promoted the collection of maize landraces throughout the rest of Latin America, which was undertaken in the 1940s and 1950s. Faced with the bewildering variety of maize types in these collections, scientists attempted to classify materials into races in the hope that racial identifications would accurately group related materials. Further, the hope was that classifications would lead to a better understanding of relationships between groups and insights into the historical evolution of maize under natural and artificial selection. The problem was not trivial. As Wellhausen et al. (1952) noted:

Frequently there are no sharp lines of demarcation between the varieties or races which compromise a cultivated species or genus... Since maize not only belongs to a single species but is also largely cross-fertilized, it offers more than the ordinary number of difficulties to the taxonomist. Hence, it is not surprising that the classification of maize, in spite of its importance, should have been so long neglected. Taxonomists who shun cultivated plants as not botanically important may actually be avoiding difficult problems not easily solved by traditional taxonomic methods. The variation in cultivated plants is frequently so bewildering that additional techniques including those of the geneticist, the cytologist, and the agronomist are needed to bring a semblance of order out of apparent chaos.

As a result of this challenge, Wellhausen et al. (1952) developed a plan to classify the races of maize using diverse sources of information on the material:

The classification of maize presented... has made use not only of the morphological characteristics of the ear, the tassel and the plant, but also of genetic, cytological, physiological and agronomic characteristics. Special consideration has been given to geographical distribution.

The collection and classification of the races of maize was a tremendous scientific achievement, resulting in the publication of the *Races of Maize* books for virtually every country or region of Latin America, mostly published by the National Academy of Sciences—National Research Council in Washington, DC. The systematic understanding of maize diversity, however, was hindered by the treatment of maize from each country or region as a separate problem. A different group of scientists worked on each country collection, although some authors

contributed to more than one study, including Dr. Goodman's mentor at Pioneer Hi-Bred, Dr. William Brown, and Dr. Goodman's future North Carolina State University colleague, Dr. David Timothy. Approaching the collections on a country-by-country basis made the undertaking logistically feasible, but hindered the systematic understanding of maize racial diversity across political boundaries, although there were attempts in the later studies to relate new collections to previously defined races. In addition, there was no formalized method to integrate the different traits observed when making the racial assignments. The most detailed example of how racial assignments were made was given by Ramirez et al. (1961) for Bolivian maize:

Ears were laid out on long tables. . . collections which looked similar were placed near each other on the same table, paying attention to color, texture, and size of grain; number of rows and size and shape of ear. It was immediately apparent that several of the races previously described . . . were present in the collections. The remaining races were worked out by distinctive combinations of form and color. . . . Work was continued until a preliminary classification had been worked out using only the appearance of the ears themselves. The notes on location and altitudes of the original collections were then consulted. This on the whole confirmed previous judgments but in one case it demonstrated that two somewhat similar races had been confused and in others that certain classifications made largely on slight color differences had ignored general similarities in form. When the racial composition of the varieties was provisionally worked out, as many selections from each race as possible were planted for study. . . the photographs of the typical ears were then carefully compared with the plants grown from them. . . . In this way it was possible to follow what George Box calls the iterative process of discovery. Hypotheses based on a study of the ears were checked by an examination of the plants. Hypotheses based on plant study could be confirmed by examining the ears. On the basis of these observations new and more inclusive hypotheses could be formed. When a combination of characters which tended to go together was found it could be recognized and used in working out the racial composition of the varieties.

Clearly, the methods used were somewhat subjective. The authors of these reports recognized this fact and viewed the racial assignments as preliminary classifications. The subjective nature of classification, coupled with the highly regionalized focus, hindered not only within-country characterization but also the understanding of racial relationships among countries. As Bird and Goodman (1977) observed: "the systematics of maize have never been convincingly covered above the race level for the simple reason that many variables are needed simultaneously to resolve a significant amount of the variation." Goodman's

contribution to this area was to develop and implement statistical tools to quantify diversity and relationships among the collections. His earlier works on this subject are mostly technical, involving the development of the statistical machinery needed (Goodman 1968, 1972) and identification of those characters most appropriate for maize classification work (Goodman and Paterniani 1969). According to Bruce Weir (1986):

Major's early work was concerned with establishing statistical methodology for determining genetic distance between different populations and species In the Department of Statistics, Major was acknowledged as the local expert in multivariate statistics—no small feat for someone trained as a geneticist.

Based on this groundwork, Goodman then analyzed the higher-order relationships among the races of Latin America, resulting in the identification of groups of related races, termed *racial complexes* (Bird and Goodman 1977; Goodman and Bird 1977; Goodman and Brown 1988). These results clarified evolutionary hypotheses proposed by McClintock et al. (1981), shed light on pre- and post-Columbian migration of maize; and guided germplasm sampling efforts, both for the continued study of maize diversity (Remington et al. 2001; Liu et al. 2003), and for the improvement of U.S. maize hybrids (Goodman and Brown 1988; Holland and Goodman 1995).

B. Isozymes

Goodman, working in close collaboration with Dr. Charles Stuber of USDA-ARS at North Carolina State University, also pioneered the use of isozymes as tools for classifying maize germplasm, understanding relationships among germplasm sources, and laying the groundwork for marker-assisted selection in crops. Schwartz (1960) reported the first example of allelic variation in electrophoretic properties of an enzyme in maize, soon after which, maize became a model plant for isozyme studies. Goodman, Stuber, and coworkers were instrumental in this development by determining inheritance of several complexly inherited isozyme patterns, such as malate dehydrogenase (MDH), which is coded by five loci, forming complex dimerization patterns among multiple alleles at these loci whose electrophoretic properties can also be altered by modifier loci (Goodman et al. 1980a, 1981; Goodman and Stuber 1983). According to Clark Cockerham (1986):

Dr. Goodman was discouraged from working on this system [MDH] by several people because everyone working with plant enzymes had tried

their hand with MDH and most had given up because of the complexity. His persistence and careful analysis, aided by the extreme variation available in his large collection, paid off.... Dr. Goodman's success at identifying and clarifying the genetics of enzymes has received widespread attention.

Further, the maize isozyme group at NCSU localized isozymes on the maize genetic map and determined the variability at these loci across diverse samples of maize germplasm (Goodman et al. 1980b; Goodman and Stuber 1983). In many other plant species, the inheritance of isozyme banding patterns often was not well understood, resulting in complications in the analysis of diversity data. Because of their work on the inheritance of isozymes in maize, Goodman and Stuber were able to appropriately analyze the isozyme diversity data to establish relationships among diverse maize germplasm groups (Goodman 1978; Doebley et al. 1983, 1985, 1986; Goodman and Stuber 1983; Bretting et al. 1987, 1990; Smith 1988; Sanchez et al. 2000, 2006). Conversely, by studying diverse germplasm, they discovered rare isozyme alleles that helped to sort out the allelism patterns of the isozyme bands (Goodman et al. 1980a; Goodman and Stuber 1980, 1983; Stuber and Goodman 1982).

The isozyme surveys of Latin American germplasm were helpful in further refining the understanding of the classification and relationships of maize races. Dr. Goodman is skeptical that isozyme information alone is adequate for classification purposes, in part because of the limited number of loci, but he suggests that isozyme data in conjunction with morphological and ecological data provide reasonable estimates of the genetic relationships among materials (M.M. Goodman, pers. comm.; Bretting et al. 1987; Sanchez et al. 2000, 2006). This work also paved the way for a continuing series of studies on the relationships among maize germplasm collections performed with increasingly powerful genetic marker systems, from simple sequence repeats (Senior et al. 1998; Remington et al. 2001; Matsuoka et al. 2002; Liu et al. 2003; Vigouroux 2008) to single nucleotide polymorphisms (Nelson et al. 2008). In addition, Dr. Stuber, in collaboration with Dr. Goodman, used isozymes for the first studies aimed at developing marker-assisted selection as a breeding methodology for maize (Stuber et al. 1982; Frei et al. 1986). Dr. Stuber continued to emphasize this aspect of genetic markers in his research program, resulting in many of the key studies to establish quantitative trait locus mapping and marker-assisted selection for quantitative traits as important tools for modern plant breeders (Edwards et al. 1987; Stuber 1992).

C. Maize Breeding

Dr. Goodman’s move from the Department of Statistics to the Department of Crop Science to replace Dr. Thompson as maize breeder in 1983 allowed Dr. Goodman to shift the primary focus of his research from classification of maize germplasm to its practical use in plant breeding. This move also provided Dr. Goodman, for the first time in his career, the help of a full-time technical assistant, in this case the dedicated and talented Mr. William Hill. Dr. Goodman attributes much of the success of his program to the assistance provided by Bill Hill. In addition, Dr. Goodman inherited a breeding program with a diverse set of adapted inbred lines and breeding populations from Dr. Thompson. To this solid foundation, Dr. Goodman introduced additional tropical maize germplasm sources to create the most genetically diverse public maize breeding program in the United States. Dr. Goodman has noted the irony that, although he obtained his PhD at North Carolina State University, he took no courses in plant breeding and yet now runs an applied breeding program. Recalling his early years working at Pioneer Hi-Bred as a teenager, however, the past 25 years of his career seem a fitting return to his first interest in maize breeding.

Today, the NCSU maize breeding program is one of the few remaining public maize breeding programs in the United States that is actively releasing inbred lines. Since 1980, 150 NC inbreds have been developed and released on the basis of superior performance for topcross yield or other agronomic traits (Table 1.1). During this time there has also been great emphasis placed on breeding with exotic germplasm, with 86 NC

Table 1.1. Inbred lines released by North Carolina State University maize breeding program, their pedigrees, and year of release.

Line Name	Pedigree ^z	Release Year
Mo44 ^y	Mo22 × Mexican Synthetic 17	1986
NC250	Nigerian Composite ARb × B37 ²	1983
NC250A	Nigerian Composite ARb × B37 ²	1991
NC252	Pa91 × B73 ³	1986
NC254	Pa91 × B73 ³	1986
NC256	Pa91 × B73 ³	1986
NC258	[(NC246 × NC248) × C103] × (McNair 14 × McNair 18) ²	1986
NC258A	[(NC246 × NC248) × C103] × (McNair 14 × McNair 18) ²	1994
NC260	Mo44 ⁴ × Mo17	1988
NC262	McNair 14 × McNair 18	1986
NC262A	McNair 14 × McNair 18	1989

(continued)

Table 1.1. *(Continued)*

Line Name	Pedigree ^z	Release Year
NC262B	McNair 14 × McNair 18	1994
NC264	(SC76 × Gaspé ²) × SC76 ³	1987
NC266	NC250 × B73 ²	1987
NC266A	NC250 × B73 ²	1989
NC266B	NC250 × B73 ²	1991
NC268	NC250 × B73 ²	1987
NC268A	NC250 × B73 ²	1991
NC270	NC250 × B73	1987
NC270A	NC250 × B73	1989
NC272	ETO Blanco × B73-Gaspé ²	1987
NC274	NC250 × B73 ³	1988
NC276	NC244 × B73 ²	1988
NC278	ETO Blanco × B73-Gaspé ²	1988
NC278A	ETO Blanco × B73-Gaspé ²	1989
NC280	Pa91 × B73 ³	1989
NC282	Pa91 × B73 ³	1989
NC284	Pa91 × B73 ³	1989
NC286	[(NC246 × NC248) × C103] × (McNair 14 × McNair 18) ²	1989
NC288	[(NC246 × NC248) × C103] × (McNair 14 × McNair 18)	1989
NC290	McNair 14 × McNair 18	1989
NC290A	McNair 14 × McNair 18	1996
NC292	NC250 × B73 ⁴	1989
NC294	NC250 × B73 ²	1989
NC296	H5 × PHX105A	1990
NC296A	H5 × PHX105A	1991
NC298	AG155 × (H5 × PHX105A)	1991
NC300	(PHX306B × H5) × PHX105A	1991
NC302	H101 × (H5 × PHX105A)	1994
NC304	H101 × (H5 × PHX105A)	1994
NC306	NC250 × B73 ²	1994
NC308	NC250 × B73 ²	1994
NC310	NC250 × B73 ⁴	1997
NC312	NC250 × B73 ²	1994
NC314	NC250 × B73	1994
NC316	NC250 × B73 ⁴	1994
NC318	B52 × SC76 ⁴	1994
NC320	B52 × SC76 ⁴	1994
NC322	B52 × SC76 ⁴	1996
NC324	NC250 × B73	1996
NC326	NC250 × B73 ⁴	1996
NC328	NC250 × B73 ⁴	1996
NC330	NC250 × B73 ⁵	1996
NC332	B52 × SC76 ⁴	1997
NC334	B52 × SC76 ⁴	1997
NC336	H5 × PHX105A	1997

Table 1.1. (*Continued*)

Line Name	Pedigree ^z	Release Year
NC338	(PHX304A × AG504) × (H5 × PHX105A)	1997
NC340	[PHX306B × H5] × PHX105A	1997
NC342	McNair 14 × McNair 18	1997
NC344	[(NC246 × NC248) × C103] × (McNair 14 × McNair 18) ²	1998
NC346	H5 × PHX105A	1998
NC348	AG155 × (H5 × PHX105A)	1998
NC350	H101 × (H5 × PHX105A)	1998
NC352	H5 × PHX105A	1998
NC354	(PHX304A × H101) × (H5 × PHX105A)	1998
NC356	TROPHY Low Moisture C8	1999
NC358	TROPHY Low Moisture C8	1999
NC360	NC262 × (AG155 × PHX105A)	1999
NC362	NC262 × (AG155 × PHX105A)	1999
NC364	NC262 × (AG155 × PHX105A)	1999
NC366	FSHmR	1999
NC368	(NC250 × B73) × (NC250 × B73 ²)	1999
NC370	B52 × SC76 ⁴	1999
NC372	Pa91 × B73 ³	1999
NC374	(NC250 × B73) × (NC250 × B73 ²)	2001
NC376	(NC250 × B73) × (NC250 × B73 ²)	2001
NC378	[(Gaspé × Va35 ²) × (Gaspé × Va35)] FSHmR ³ × [B73 × (PHX306B × PHX105A)]	2001
NC380	NC262 × (AG155 × PHX105A)	2001
NC382	NC262 × (AG155 × PHX105A)	2001
NC384	NC262 × (AG155 × PHX105A)	2001
NC386	NC258 × NC296	2001
NC388	TROPHY Low Moisture C8	2001
NC390	TROPHY Low Moisture C8	2001
NC392	TROPHY Low Moisture C8	2001
NC394	TROPHY Low Moisture C8	2001
NC396	H101 × (H5 × PHX105A)	2001
NC398	[(AG155 × H5 × PHX105A)] × (AG155 × PHX105A)	2002
NC400	[AG155 × (H5 × PHX105A)] × [(PHX306B × H5) × PHX105A]	2002
NC400A	[AG155 × (H5 × PHX105A)] × [(PHX306B × H5) × PHX105A]	unreleased
NC402	NC258 × NC296	2002
NC404	NC258 × NC296	2002
NC406	B52 × SC76 ⁴	2002
NC408	B52 × SC76 ⁴	2002
NC410	NC262A × [AG155 × (H5 × PHX105A)]	2002
NC412	NC262A × [AG155 × (H5 × PHX105A)]	2002
NC414	NC262A × [AG155 × (H5 × PHX105A)]	2002
NC416	NC262A × [(PHX306B × H5) × PHX105A]	2002
NC418	NC262 × (AG155 × PHX105A)	2002

(continued)

Table 1.1. *(Continued)*

Line Name	Pedigree ^z	Release Year
NC420	NC262 \times (AG155 \times PHX105A)	2002
NC422	NC262 \times (AG155 \times PHX105A)	2002
NC424	NC262 \times (AG155 \times PHX105A)	2002
NC426	NC258 ² \times NC296	2002
NC428	NC258 ² \times (H5 \times PHX105A)	2002
NC430	(NC250 \times B73) \times (NC250 \times B73 ³)	2002
NC432	Pa91 \times B73 ³	2002
NC434	B52 \times SC76 ⁴	2002
NC436	NC258 \times NC296	2002
NC438	NC258 \times NC338	2002
NC440	NC296 ⁴ \times B73 Purple	2002
NC442	NC258 \times NC296 ⁴	2002
NC444	NC258 \times NC296 ⁴	2002
NC446	KU2301 \times NC296 ⁴	2002
NC448	H5 \times PHX105A	2002
NC450	NC296 \times (AG155 \times PHX105A)	2002
NC452	NC304 \times NC296	2002
NC454	[AG155 \times (PHX306B \times PHX105A)] \times [AG155 \times (H5 \times PHX105A)]	2002
NC456	PHI100 \times PHX304C	2002
NC458	KU2301 \times PM703	2002
NC460	[AG155 \times (H5 \times PHX105A)] \times NC296	2005
NC462	NC304 \times NC296	2005
NC464	NC348 \times [(PHX306B \times H5) \times PHX105A]	2005
NC466	[AG155 \times (PHX306B \times PHX105A)] \times [AG155 \times (H5 \times PHX105A)]	2005
NC468	TROPHY Low Moisture C8	2005
NC470	NC296 ² \times B73 Purple	2005
NC472	NC268 \times NC300	2005
NC474	NC268 \times [(PHX306B \times H5) \times PHX105A]	2005
NC476	NC262 \times (AG155 \times PHX105A)	2005
NC478	NC262A \times [AG155 \times (H5 \times PHX105A)]	2005
NC480	NC258 \times NC296	2005
NC482	NC258 \times NC296	2005
NC484	NC258 \times NC296	2005
NC486	NC258 \times NC296	2005
NC488	NC258 \times NC296	2005
NC490	NC258 \times NC296	2005
NC492	NC258 \times NC296	2005
NC494	NC258 \times (H5 \times PHX105A)	2005
NC496	NC258 ² \times NC296	2005
NC498	NC258 ² \times (H5 \times PHX105A)	2006
NC500	NC258 \times NC296	2006
NC502	NC258 \times NC296	2006
NC504	NC258 \times NC296	2006
NC506	NC258 \times NC296	2006
NC508	TROPHY Low Moisture C8 \times (H5 \times PHX105A)	2006

Table 1.1. (Continued)

Line Name	Pedigree ^z	Release Year
NC510	TROPHY Low Moisture C8 × (H5 × PHX105A)	2006
NC512	QK37 × (AG155 × PHX105A)	Pending
NC514	NC258 × NC296 ³	Pending
NC516	NC258 × NC296	Pending
NC518	NC258 × NC296	Pending
NC520	NC258 × NC296	Pending
NC522	NC258 × NC296	Pending

^zAbbreviations: Pioneer (PH), Agroceres (AG), Gaspé Flint (Gaspé), Florida Synthetic (FSHmR). The order of parents in pedigree does not necessarily reflect their use as male or female parent unless one parent is known to carry a gametophyte factor, in which case the first parent listed was the female parent.

³Mo44 was a joint release between North Carolina and Missouri.

inbreds having at least 50% exotic parentage and 40 of those having all-tropical parentage. The NCSU maize breeding germplasm represents a potentially useful resource for maize improvement and diversity in the United States. Although detailed pedigree records for all of the NC lines have been kept, they have never been described systematically. We believe that part of Dr. Goodman’s legacy will be this set of lines developed from his program (and in some cases derived directly from Dr. Thompson’s program). Therefore, we include here a description of the NCSU maize breeding line releases to promote their evaluation and use by other breeding and genetics programs.

Breeding efforts in the NCSU maize breeding program are focused primarily on five general germplasm pools (Fig. 1.1): (1) Lancaster, (2) Temperate-Adapted All Tropical (TAAT), (3) Lancaster × Tropical, (4) Stiff Stalk, and (5) Southern Non-Stiff Stalk. The Lancaster germplasm pool was initiated by Dr. D.L. Thompson, although most of the line releases from this pool came after his retirement. This material is heavily influenced by C103, primarily through the single-cross McNair 14 × McNair 18. While the exact pedigrees of McNair 14 and 18 are not known, they are believed to be at least 50% C103. One of the key lines in this group, NC258, is arguably the last public inbred to be widely used in commercial seed production in the southern United States.

The TAAT germplasm pool (Fig. 1.1) primarily traces to these seven double-cross tropical hybrids: Agroceres 155; Agroceres 504, H5, H101; and Pioneer X105A, X304A, X306B (Table 1.1). These hybrids were used in various combinations and are present in the pedigrees of 86 NC lines. Holley and Goodman (1989) reported the development from these crosses of the first inbred lines of pure tropical origin adapted to temperate U.S.

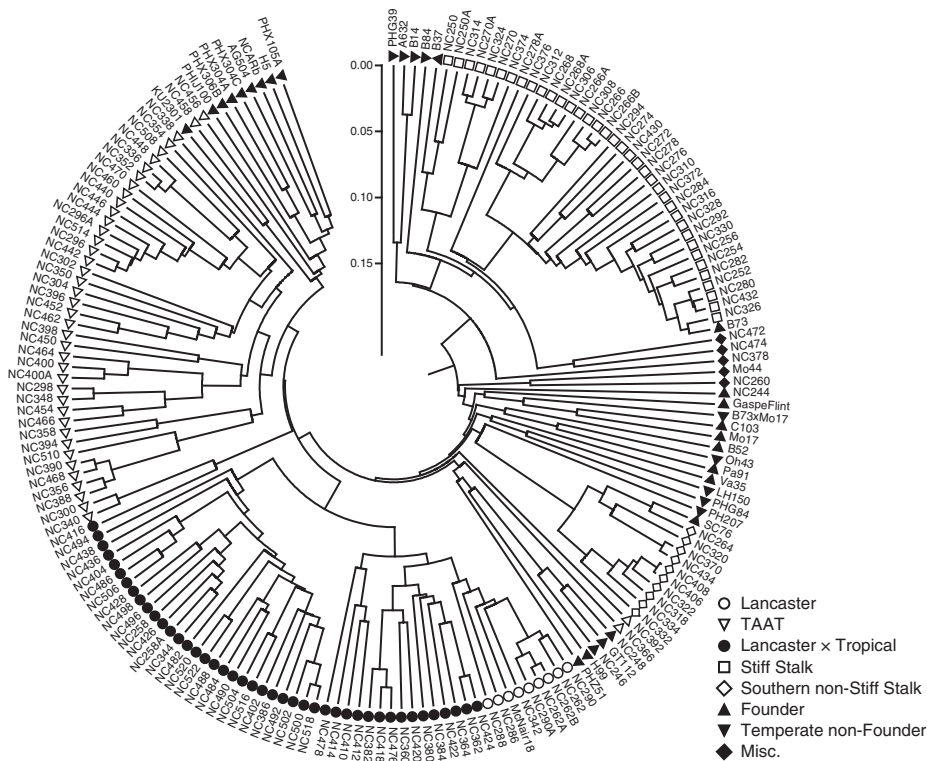


Fig. 1.1. Unbranched phylogeny of 146 NC inbred lines, 23 founders to the NC lines, and 11 common temperate lines (as points of reference) based on the shared allele distance among 632 single nucleotide polymorphisms and clustered with a UPGMA algorithm (Nelson 2009). Germplasm groups to which lines are assigned are given unique shapes.

maize-growing conditions. Uhr and Goodman (1995) reported the development of second-cycle inbreds (derived from intermating selected lines from the original set of matings) from this program. These TAAT lines represent a major breakthrough for a public maize breeding program: the creation of a unique heterotic group with high yield potential for use in combination with traditional U.S. Corn Belt Dent germplasm (Tallury and Goodman, 1999; Goodman 2004). The TROPHY (Tropical Hybrid) synthetics were formed by intermating descendants of intercrosses among the seven double-cross tropical hybrids. The TROPHY Elite and TROPHY

Composite populations are currently in their 6th and 10th cycles of selection, respectively, for yield and other traits of agronomic importance (Jines 2007). The TROPHY Low Moisture Composite was subjected to eight cycles of selection for low harvest grain moisture from 1984 to 1989 (Hawbaker and Goodman 1997); nine NC lines have been derived from this population. Lines from the tropical germplasm pool combine well with either Lancaster or Stiff Stalk lines.

The Lancaster \times Tropical germplasm pool (Fig. 1.1) was formed through intermating lines from the tropical and Lancaster germplasm pools, and encompasses 45 NC lines. The most common pedigrees in this pool are NC258 \times NC296 (the latter, a first-cycle TAAT line) and NC262 \times (Agroceres 155 \times Pioneer X105A). Many of the NC262 \times tropical lines are described in Lewis and Goodman (2003). The NC258 \times NC296 lines were described in the Ph.D. thesis of Molnár (2002). Lines from this germplasm pool combine well with Stiff Stalk lines.

The Stiff Stalk pool (Fig. 1.1) was initiated by Dr. D.H. Thompson, but most of the line releases were made after his retirement. Two Iowa Stiff Stalk Synthetic-derived lines, B37 and B73, are the key founders of this pool. B37 is a parent of NC250 [Nigerian Composite ARb \times B37²]. NC250 and B73 were used as parents in the development of 24 NC lines, many of which were derived through multiple backcrosses to B73. NC250 confers resistance to southern leaf blight (*Bipolaris maydis*) and gray leaf spot (*Cercospora zea-maydis*) while B73 provides superior yield and lodging resistance. B73 was also used as a backcross recurrent parent with donor line Pa91 in the development of eight NC lines that exhibit the superior agronomic characteristics of B73 and good seed quality and general plant health from Pa91.

The Southern Non-Stiff Stalk germplasm pool (Fig. 1.1) is composed primarily of 10 NC lines that were derived from SC76 in combination with B52 (a source of virus resistance) and Gaspé Flint (a source of earliness). The B52 \times SC76⁴ lines were all derived from a common BC2 parent from populations formed by Dr. Al Manweller at the University of South Carolina. Lines from the Southern Non-Stiff Stalk germplasm pool combine well with either Stiff Stalk or Lancaster lines.

Together, the NC inbred lines released by Dr. Goodman represent a unique combination of diverse, exotic germplasm, good disease resistance, and good yield potential in combination with U.S. germplasm. Furthermore, the development and release of the tropical-derived inbred lines is a practical demonstration of the utility of exotic maize germplasm for U.S. maize improvement. Dr. Goodman has guided this program for over 40 years from its inception as a problem in botanical taxonomy to its ultimate goal of improving U.S. maize while

simultaneously diversifying its genetic base to provide the raw material for continued gains from selection and to safeguard against vulnerabilities caused by a narrow germplasm base.

III. SERVICE TO HUMANKIND

During his research on the Latin American races of maize in the 1960s and 1970s, Dr. Goodman came to realize, perhaps better than anyone, the problems and limitations of the public maize germplasm collections. He made a systematic study of the availability of the collections originally made by the Rockefeller Foundation Program in the 1940s and 1950s in Latin America (the basis for the *Races of Maize* monographs) and found that many of the collections had been lost (Goodman 1984). Two of the Latin American gene banks that had housed most of the Latin American collections had been closed down, backup collections sent to the USDA had been discarded, and maintenance at the remaining Latin American facility in Mexico was poor (Timothy and Goodman 1979; Goodman 1984). As a result, many collections were lost.

Dr. Goodman's pointed critiques of the national and global germplasm collections demonstrated clearly a problem that had previously not been brought to the attention of the larger maize breeding and genetics community. He went beyond identifying the problem, however, and spearheaded a USDA-sponsored "major effort to regenerate, preserve, and evaluate the 25,000 or so, collections of maize stored in seed banks in several Latin American countries," according to Charlie Stuber (1986). Stuber continued:

This may sound like a simple project. However, the problems associated with political situations in Latin American countries, the logistics of transporting research supplies from the U.S. to Latin America, and transporting seed from Latin America have frequently been nearly insurmountable. Because of Dr. Goodman's commitment to the maintenance and preservation of these valuable genetic resources, his efforts have required numerous trips to Latin America and many ingenious methods to accomplish the job. I know of no other person in the U.S. who would be willing to devote the time and effort to this project as Dr. Goodman has done and continues to do.

Largely on the basis of his efforts to rescue the many endangered Latin American maize collections, in 1987 Dr. Goodman was awarded the O. Max Gardner Award, which recognizes faculty among all University of North Carolina system campuses who have "made the greatest contributions to the welfare of the human race."

The germplasm rescue project was a major success and has led to a substantially improved maize germplasm collection maintained by the USDA as well as improvements in other international and national collections. Further, this project led to the Latin American Maize Project (LAMP), which was guided substantially by Dr. Goodman, and involved the evaluation of Latin American racial accessions in the nations in which they were collected and exchange of collections for evaluation across countries (Salhuana et al. 1998). Beginning in 1994, after the Latin American Maize Project was completed, a unique cooperative project involving private industry, USDA, and state university researchers was initiated to incorporate germplasm from the superior Latin American accessions into elite, commercial Corn Belt Dent genetic backgrounds. This project, named the Germplasm Enhancement of Maize (GEM) project, continues today and has a primary objective of enhancing the genetic base of U.S. maize by developing maize lines that possess unique alleles from exotic germplasm sources in well-adapted genetic backgrounds to make them immediately useful to commercial breeding programs in the United States (Pollak and Salhuana 2001). In addition to the maize inbred line development program already described, Dr. Goodman directed the GEM project at NCSU, resulting in the release of numerous superior inbred lines containing significant amounts of exotic germplasm (Balint-Kurti et al. 2006; Carson et al. 2006). In our opinion, it is hard to imagine that programs remotely resembling the LAMP and GEM projects would have been initiated without the leadership provided by Dr. Goodman. More recently, Major Goodman was a co-organizer of the first meeting of the Maize Germplasm Network, a network of maize gene banks, sponsored by the Global Crop Diversity Trust, the World Bank, and CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo), with the goal of ensuring the maintenance and availability of precious maize germplasm resources by long-term financial commitments from donor agencies.

IV. MENTOR AND COLLEAGUE

In addition to his groundbreaking work to rescue, study, and make a valuable genetic resource of tropical maize germplasm, Dr. Goodman will leave an important legacy as a mentor of graduate students and postdoctoral researchers as well as an unusually helpful colleague to many maize researchers. As students of Major, we personally have witnessed his incredible dedication to maize research, the care he takes to ensure data are of the highest possible quality, his rigorous criticism of his own research, and his tremendous generosity of time and attention

paid to other researchers who seek his advice. It is not unusual even today for a steady stream of visitors to come to his lab to talk to him about statistical analyses, plant breeding, maize germplasm, and maize evolution. Although this usually prevents him from having uninterrupted time to pursue his own research, he never fails to go out of his way to provide assistance.

Major had only one experience as a formal course instructor, for multivariate statistics in the 1970s. Nevertheless, he spent a large amount of time teaching graduate students, usually in a very practical setting, such as the corn breeding nursery or while shelling selected ears. His method of teaching involves assigning each graduate student responsibility for some portion of the breeding nursery and giving each creative freedom to evaluate and select materials. He has an ability to guide a graduate student's career while allowing for maximum freedom in discovery and pursuing individual interests. Working by Major's side in the field and discussing breeding philosophy, objectives, and methods was often our most rewarding educational experience in graduate school. Another lesson learned early on from Major was a healthy dose of skepticism for one's own breeding materials. Although Major was convinced early in his career of the value of exotic maize germplasm, he has always cast a cold eye on his own inbred lines. For example, he taught us never to put too much trust in yield trial data from only one year or in the visual appearance of an inbred line. He is honest and sincere in his assessment of performance and potential, and hidden within his outwardly pessimistic sarcasm is a deep sense of optimism. Major's comments on his own germplasm have provided some classic examples of his darkly ironic sense of humor. We have all heard him call breeding material "good stuff," but only in reference to those ears that were being discarded or plants being eliminated from the breeding nursery. In contrast, he refers to most of his released inbred lines as "trash"!

The value of Major's training of students and postdoctoral researchers can be judged from the results. Numerous former students have gone to work in private seed industry, where they hold critical positions for breeding research and germplasm work. In fact, much of today's private sector effort to diversify the germplasm base of commercial hybrids is led by former students of Dr. Goodman. Others hold public sector positions in plant breeding and plant genetics, including one member of the National Academy of Sciences (John Doebley), three faculty members at NCSU, and the USDA-ARS National Program Leader for crop genetic resources. Finally, several students hold positions at universities, national programs, and breeding companies in other countries, including Mexico, France, and Colombia.

Major is well known for his penetrating insight into scientific questions, and he applies a similarly critical approach to his own work as well as that from other laboratories. Mangelsdorf (1983) wrote, "To me one of Dr. Goodman's most admirable qualities is his scrupulous intellectual honesty which compels him to be as critical of his own work as that of others." Similarly, Bruce Weir (1986) wrote: "I have found Major to be a stimulating and cooperative colleague over the past ten years. He has always been willing to share his statistical expertise, and has often given valuable criticism of my own work. I greatly respect his judgment." What we and many other of his students and colleagues have been lucky to observe is the incredibly kind and generous man behind the well-known skeptical scientist, who has gone beyond providing scientific training and advice and supported us in many ways beyond the professional.

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