2005

Maize Breeding

J. S. C. Smith
Pioneer Hi-Bred International, Inc.

O. S. Smith
Pioneer Hi-Bred International, Inc.

Kendall R. Lamkey
Iowa State University, krlamkey@iastate.edu

Maize Breeding

Abstract

Maize (Zea mays L.) is a remarkable plant. Human societies depend upon maize for food, health, scientific knowledge, economic growth, culture and spirituality. Maize breeders have improved productivity through selection on phenotype. Future improvements in maize productivity will require more effective utilization of genetic resources including direct selection upon genotype. Success will require a greater understanding of the complex biology of quantitative traits and a more thorough evaluation of the broader genetic base of maize. Maize breeders are fortunate and privileged to work with a species that encompasses a broad array of diversity and which provides a rich source of learning. In the future, technological developments must increasingly be considered and applied within a more holistic context including stewardship, sustainability, and equity.

MAIZE BREEDING

J.S.C. Smith[1], O.S. Smith[1], K.R. Lamkey[2]

[1] *Pioneer Hi-Bred International Inc., 7300 NW 62nd Ave., Johnston, Iowa 50131,USA*
[2] *Department of Agronomy, Iowa State University, Ames, Iowa 50011, USA*

ABSTRACT - Maize (*Zea mays* L.) is a remarkable plant. Human societies depend upon maize for food, health, scientific knowledge, economic growth, culture and spirituality. Maize breeders have improved productivity through selection on phenotype. Future improvements in maize productivity will require more effective utilization of genetic resources including direct selection upon genotype. Success will require a greater understanding of the complex biology of quantitative traits and a more thorough evaluation of the broader genetic base of maize. Maize breeders are fortunate and privileged to work with a species that encompasses a broad array of diversity and which provides a rich source of learning. In the future, technological developments must increasingly be considered and applied within a more holistic context including stewardship, sustainability, and equity.

KEY WORDS: Biotechnology; Corn; Genetic diversity; Genetic resources; Genomics; Genotype; Germplasm; Maize; Phenotype; Plant breeding; Transgenics.

INTRODUCTION

Maize is a most important and treasured resource providing food, fodder, and industrial raw materials. The species is extremely adaptable being grown from Northern Europe and Northern Asia to Southern parts of South America at all latitudes and at many altitudes. Maize is an important study resource providing for intellectual growth in science and the humanities. Maize culture binds together societies by providing food, knowledge, economic opportunities, intellectual growth, and spiritual nourishment. "Maize is, at once, a food staple, a so-cial safety net, a survival strategy and a cultural icon" (CARLSEN, 2004).

The conduct and impact of plant breeding and agriculture transcend national boundaries and generations. Maize exemplifies co-dependence between humans and cultivated plant species. Human civilization is dependent upon the quality of stewardship provided in agriculture, in crop improvement and in the conservation of genetic resources. Humans break these bonds of dependence at their peril. Thus, although our immediate focus is on US maize breeding we are confident that many, if not all readers will relate to common issues in their countries and regions.

The genetic potential of maize was originally carried in the genes of the wild grass, teosinte. The small female spikes of teosinte were transformed into the cobs of maize through selections made by seed gatherers and farmers some 8-10,000 years ago in the vicinity of Oaxaca, Mexico. Maize was then transported in trade and by human migration throughout much of the continent of South and North America; then from the early 16th century, throughout much of the rest of the world. Large phenotypic differences between maize and teosinte obscured the identity of the wild progenitor of maize for centuries. Recent genetic analyses coupled with precision phenotyping (DOEBLEY and STEC, 1991; MATSUOKA *et al.*, 2002a; DOEBLEY, 2004) confirmed earlier genetic studies (BEADLE, 1980) showing that the defining differences between maize and teosinte reside at relatively few loci. By attaining sufficient fluency in reading the genetic language of domestication scientists confirmed an ancient belief that teosinte is the ancestor of maize. An abiding common theme begins to emerge: The importance of attaining a more thorough understanding of the complex genetics that reside in the genus, *Zea*.

* For correspondence (fax: +1 515 334 7022; e.mail: stephen.smith@pioneer.com).

U.S. MAIZE PRODUCTION;
DEVELOPING THE GENETIC BASE

Most of the genetic base supporting US maize production traces to the Corn Belt race which originated through hybridization in the 19th century of two races, the Southern Dents and the Northern Flints (ANDERSON and BROWN, 1952). Southern dent corns were grown by indigenous inhabitants of the area which today is the southwestern U.S. as far back as 1100-1900 BC (HARD and RONEY, 1998). Northern Flint varieties had been cultivated in the area now known as New England since at least 1000 AD. By combining in its heritage two genetically different phylogenies (DOEBLEY et al., 1986), the Corn Belt Dent race encompasses a relatively broad array of genetic diversity. Nonetheless, additional, although usually challenging opportunities to further improve the germplasm base of US maize reside among the greater breadth of global maize diversity (HOLLEY and GOODMAN, 1988; POLLAK, 2003).

STRATEGIES TO INCREASE
U.S. MAIZE PRODUCTION

Decades before Gregor Mendel studied inheritance, farmer breeders in the U.S. appreciated the benefits of cross-breeding and by 1813 were developing new strains of corn through controlled pollinations (ANDERSON and BROWN, 1952). ANDERSON and BROWN (1952) concluded that…"For all the country…there is detailed evidence (in 1850) of the purposeful blending of diverse varieties… the controlled breeding of new varieties by farmers themselves was more frequent than anyone would believe… Some… had highly elaborate methods of selection… The open-pollinated varieties of maize that dominated the Corn Belt of the United States for over half a century were the creation of farmers and corn breeders." STURTEVANT (1899) documented the popular use of 69 open-pollinated varieties of flint corn and 323 varieties of dent corn.

However, USDA data (1866-2004) show US average maize yields flat at approximately 25 bu/a from 1866 to 1930. Low average US maize yields, relative to those attained in subsequent decades (approximately 130-140 bu/ac in the 2000s), were due to deficiencies in the genetic make-up of varieties and in crop husbandry practices. Prior to the 1930s a combination of poor agronomic practices, including soil erosion, poor soil fertility practices, and low plant populations, together with slow progress in genetic gain lead to low yields. Demands for increased amounts of maize were met by taking wetlands and prairie into cultivation, so there was little incentive to select for increased yield per unit area. Corn shows were still immensely popular, so selection focused on visual appearance of the ear, and selection for stand establishment, especially as the Corn Belt moved north. It was not until the end of the 1930s, by which time most of the acreage suitable for cultivation had come under the plough, and with increased demands for maize due to the coming of World War II that imperatives for increased productivity became pre-eminent.

IMPROVING PRODUCTIVITY
OF US MAIZE 1930-2000

There remained a dichotomy of thought on the direction for improving maize yields in the 1930s. "One school regarded the ear as a thing of beauty and more or less assumed that the characteristics associated with its beauty were of value from the standpoint of production… The other school placed first emphasis on productiveness and quality and stressed the necessity of field selection of seed ears from standing stalks, resistant to disease" (JENKINS, 1936). Henry Wallace exemplified the inquiring mind that placed emphasis on raising productivity and the application of scientific principles to achieve that goal. WALLACE (1923) demonstrated a correlation of only 0.2 between the judged score for ear appearance and yield noting that it was "the tendency of the judges to emphasise…length of ear, whereas Mother Nature,… lays her outstanding emphasis on weight of kernel". WALLACE (1923) concluded that "the corn judges did not know so very much about the factors which make for yield."

By the late 1930's a convergence of the need to improve productivity and evolving scientific knowledge began to result in varieties with improved productivity. Even before the re-discovery of Mendel's laws of genetics, W.J. Beal, had used detasseling crossing plots to make hybrids in 1881. However, it was pioneering studies on inbreeding that lead to the isolation of inbred lines and the discovery of the tremendous hybrid vigour in crosses between these lines that enabled improved productivity through hybrid selection. A Burr-Leaming double cross was subsequently developed by the Connecticut Experiment Station in 1917; 10 bushels of hybrid seed

were sold in 1922 (JENKINS, 1936). Then, following the re-discovery of Mendel's laws, and most especially from the 1930s, maize breeders developed a series of tools including inbreeding, hybridization, pedigree breeding, statistics, quantitative genetics, plot mechanization, cytoplasmic male sterility, mutation breeding, computer technology, off-season nurseries, molecular engineering, transgenic traits, di-haploid breeding, remote sensing, and a huge array of analytical technologies. These tools allowed breeders to more effectively change the genotype by selection on the phenotype as demonstrated by dramatic changes in grain yields per unit area accrued since the 1930's (DUVICK et al., 2004a,b).

IMPROVING FUTURE PRODUCTIVITY OF U.S. MAIZE

The current rate of genetic gain (approx. 1% per yr) must be maintained or preferably increased to meet demands for food, feed and industrial raw materials in a fashion that also helps protect the environment. To achieve these objectives will require improved efficiencies based upon capabilities to identify associations of alleles that will provide the genotypes with greater performance potentials in target agricultural environments. The task is extremely challenging, due to the inherent complexity of biological systems and the unpredictability of weather. One perception is that plant breeding today appears to be in a similar position occupied by medicine in the 1860s. Then, if the patient survived it was largely in spite of the best medical treatment that was available at the time. The challenge for continuing genetic gain will be to understand enough of the biological complexity so that selection upon genotype will have the desired phenotypic response in relation to agronomic performance.

GENETIC RESOURCES

Significant increases in the productivity of maize germplasm have been provided by a gene from *Bacillus thuringensis* (*Bt*). Transgenic approaches have provided levels of pest resistance not attained during several previous decades of breeding. However, this is an unfair evaluation of the potential of native genetic resources given the disparity of financial, technical and human resources that have been applied to transgenic approaches compared to those

applied to the evaluation and development of maize germplasm *per se*. Transgenic approaches to product development require significantly increased efforts in backcrossing, laboratory support, and data generation for regulatory approval and most require decades of research and development (GOODMAN, 2004). Studies of genetic gain (DUVICK et al., 2004a,b) demonstrate the contributions of native *Zea* germplasm to increasing productivity through enhancing biotic and abiotic stress resistances. In addition, exotic maize germplasm, although challenging to identify and adapt, can further increase US maize yields (HOLLEY and GOODMAN, 1988, 1995; HOLLAND et al., 1996; NASS and COORS, 2003; POLLAK, 2003). It is therefore crucially important to maintain significant effort on germplasm improvement because this is where the vast majority of alleles impacting traits of agronomic significance reside. If instead resources were focused on a narrow array of genetic diversity then there would be lost opportunities for further improvement of quantitative traits, lost opportunities for adaptation to changing climates, lost opportunities to optimally adapt varieties to new methods of crop husbandry, and a higher likelihood of loosing potentially useful germplasm through genetic erosion. Investments made into genomics and other tools to provide improved understanding of the genetics of agronomic traits and the opportunities so provided would be largely wasted if allelic diversity was lost through failures in stewardship of genetic resources. Maize improvement programs should take advantage of and apply the new tools being developed and utilize all the germplasm that is available.

INTEGRATING NEW KNOWLEDGE INTO MAIZE BREEDING

The degree of genetic complexity underlying quantitative traits has long perplexed researchers and breeders. The genetic control of quantitative traits was early a subject of keen interest (JOHANNSEN, 1903; EAST, 1915) following the re-discovery of Mendel's research in the early 1900s. The intractability of comprehending genetic control of complex traits was evidenced by DARLINGTON and MATHER (1949) who wrote: "It has been suggested that polygenes are essentially different from the major genes with discontinuous effect which typify Mendelian inheritances, in that they may be confined to genetically inert heterochromatic regions of the chromosomes". And, a more recent text for

plant breeders stated: "Quantitative genetic effects cannot generally be ascribed with certainty to particular loci and the number of loci controlling quantitative characters cannot be determined with any degree of precision" (WILLIAMS, 1964). Even now the genetic control of most quantitative traits still remains unknown more than half a century after the molecular structure of DNA was discovered (WATSON and CRICK, 1953). These fundamental gaps in our knowledge are largely due to the lack of tools available to quantify and track alleles with small genetic effects that interact with each other and with environmental factors.

A key learning from plant breeding is that irrespective of how complex the trait is, generally, if breeders develop methods to accurately measure the trait they can improve it by selection. Therefore, plant breeding conforms to a property of highly complex genetic systems, which is their ability to respond to directed selection. Nonetheless, new approaches may be required to keep pace with the food and environmental needs of today's rapidly expanding world population. Therefore plant breeding is undergoing a revolution where the goal is to develop tools that allow direct selection on the genotype to produce changes in the phenotype. How to produce favourable phenotypic changes by direct selection upon the genotype is one, if not the most important challenges of this decade and is being addressed in species from humans to bacteria and fungi. The process has already started in crop plants with the development of transgenics using genes from other species, and is moving to modifying the expression of native genes, as their function is being discovered. Consequently, it is the more complete understanding of the genetic control of quantitative traits which remains both the most challenging and the most ultimately rewarding goal in applying the science of genetics to plant breeding.

Most applications of trait mapping today involve the identification of a set of Quantitative Trait Loci (QTL) which then serve as a target genotype. Marker assisted selection is then applied to create the target genotype from the well-adapted genetic backgrounds that were individually missing all of the favourable allele combinations. This approach has been successful for simply inherited traits (FLINT-GARCIA et al., 2003). It is an approach that represents the current state of knowledge and capabilities which are relatively rudimentary and simplistic when the reality of complex biology and interactions with numerous unpredictable environmental factors, including weather, are considered. A greater appreciation and understanding of the biological complexities of how plants respond to stress including comprehending the genetic networks that underlie these responses will be required to allow breeders to select more effectively for combinations of alleles that will respond optimally in specific environments and management systems. Selection will depend on both genetic background and target environment (PECCOUD et al., 2004; PODLICH et al., 2004). Iterative mapping conducted over multiple cycles of breeding (PODLICH et al., 2004) will likely be required. Precision phenotyping is also an essential component to better comprehend genetic control and to successfully employ marker aided selection. SCHON et al., (2004) demonstrate that for polygenic traits such as grain yield no more than 60% of the genetic variation may be explainable by marker associations. Consequently, phenotypic selection will be an enduring component of successful plant breeding.

Developing more efficient breeding practices based upon a more complete comprehension of highly complex systems of biology and genetics will require that breeding programs become more effective vehicles of sustained research and learning (COOPER et al., 2004). Molecular characterisation will include data from the physical map, the genetic map, transcription profiling (GUO et al., 2004), proteome profiling, and metabolome profiling. Phenotypic data will be collected with greater precision and linked to genomic data. There will be a shift in focus from descriptions of individual genes to a more complete understanding of gene networks. Target environments will be better characterized and increased efforts will be made to integrate environmental effects with changes in gene expression. The breeding environment will become a richer learning environment; predictions and hypotheses will be tested during breeding and resultant knowledge will be shared through dynamic models. Information management systems will evolve to allow high volume exploratory research in genomics, gene discovery, gene-to-phenotype modeling of transgenic and natural variation, classification of target environments, experimental design and analysis. High performance computing will continue to evolve to enable modeling of breeding strategies and the rapid prototyping of new strategies. Significant investments will be required from both the public and the private sectors. Maize breeders are privileged and fortunate to work with a species that has been, and remains a deep well of learning.

EVOLVING ROLES OF THE PUBLIC AND PRIVATE SECTORS IN US MAIZE BREEDING; THE PUBLIC SECTOR

The record of genetic gain in US maize hybrids is dependent upon contributions from both the public and private sectors. The foundations of scientific knowledge have largely been laid by the public sector. And public sector breeders developed many inbred lines that were used directly as parents of US hybrids through to the 1980s. Today, U.S. maize breeding is dominated by the private sector. FREY (1996) in an inventory of human resources in plant breeding showed that there were 545 SYs devoted to maize breeding, which represents 25% of the SYs devoted to plant breeding of all crops in the U.S. Of these SYs, 510 (94%) were in the private sector, 27 (5%) were in the state agricultural experiment stations, and 8 (1%) were with the USDA-ARS. In contrast, 65% of soybean breeders and 41% of wheat breeders were in the private sector.

The intense concentration of maize breeders in the private sector raises several important questions regarding the interactions and roles of the private sector and public sector regarding research, education, and breeding goals. Those most frequently asked are:

1. Public breeders are redundant with private breeders taking their place, so why do we need public corn breeders?
2. What has been the impact of public corn breeders?
3. Why should public corn breeders be developing cultivars?
4. Where should research related to breeding be focused in the public corn breeding programs?

The traditional response to this set of questions has been that the public sector serves three basic roles - enhancement of germplasm and genetic diversity, education of the next generation of plant breeders, and basic research including education of graduate students. These roles are clearly important, but they have generally been met with a paucity of funding.

Genetic diversity is the raw material of selection and is critically important to maintaining long-term selection progress. Continuing development of an expanded germplasm base is a natural role for the public sector and one that the public sector has credentials in respect of the development of many historically inbred lines of key importance to US maize production and breeding (DARRAH and ZUBER, 1986)

and in the evaluation and introduction of new germplasm to the US (HOLLEY and GOODMAN, 1988, 1995; HOLLAND et al., 1996; NASS and COORS, 2003; POLLAK, 2003). As the US hybrid seed industry has evolved and matured, however, the role of public inbred lines has become increasingly unclear. This is mainly because heterotic groups in the public and private sectors have naturally evolved away from one another making it difficult to find niches for public germplasm in private breeding programs. With the exception of the Germplasm Enhancement of Maize (GEM) program (NASS and COORS, 2003; POLLAK, 2003), which has been but modestly funded, genetic diversity has been a difficult concept to relate to the public and thus to receive funding at the level that is needed for sustainable increases in productivity and stewardship of genetic resources.

Education of future plant breeders is the most frequently cited role of public maize breeding programs. The great majority of new plant breeders are hired by the private sector with only a small percentage going back into the public sector. Education of course is one of the missions of land grant universities, but it is not a mission of the USDA - Agricultural Research Service where the bulk of public funding of maize breeding resides. Again, with a few notable exceptions, graduate student education in plant breeding has become essentially an unfunded mandate of land grant universities.

Graduate student education is intimately tied to having strong research programs; without a strong research program there cannot be a strong education program. If the premise that plant breeding graduate student training needs to be based on research programs where the focus is on plant phenotypes plants is true, then the surest way to maintain strong graduate student education programs is to maintain core research funding in applied plant breeding. If this premise is not true, then future plant breeders can be hired from biochemistry, molecular biology, and other biological sciences that are not focused on plant phenotypes. We affirm that continued focus on phenotype and genotype is essential to a successful future for maize breeding.

HEISEY et al. (2001) indicated that private investment in plant breeding is related to the cost of research innovation, market structure and organization of the seed industry, ability to appropriate returns on research, and farmer profitability. The public sector shares the same costs of research innovation as the private sector, but can lack the private sectors ability to appropriate returns on research in-

novation. Research innovation in the public sector can simply be adopted by the private sector with little or no direct return to the public sector on the specific investment in research innovation or the research innovation may occur in crops where farmers traditionally save seed, which also results in no direct return on research innovation. The social return on public research innovation is however, large, but the knowledge generated is an impure public good that is often difficult to place value on.

The future of public sector maize breeding programs depends on returning to the core land grant missions of research, education, and outreach. The research and education components of the land grant missions have been largely fulfilled by public maize breeding programs. Critically important basic research is being conducted in the public sector including research in association genetics (THORNSBURRY *et al.*, 2001), evolution (MATSUOKA *et al.*, 2002b; VIGOUROUX *et al.*, 2002; DOEBLEY, 2004) and genetic diversity (MATSUOKA *et al.*, 2002a; LIU *et al.*, 2003), transposable elements (MCCLINTOCK, 1950), genetic structure (FU and DOONER, 2002), genome structure (GAUT and DOEBLEY, 1997), genetic mapping and sequencing (see Maize Genetics and Genomics Database at www.maizegdb.org) but often at institutions where linkages to maize breeding programs require formal collaborations with breeders in other universities. The outreach component however has gone unfulfilled or has been narrowly focused on industry and peer scientists. Refocusing outreach on farmers and consumers can lead to a social revitalization of public maize breeding. Public maize breeding should provide farmers with data that aids in decision making to achieve their goals. And educating consumers on the importance of providing stewardship of resources is an important component of persuading governments to make investments into genetic resource conservation and base-broadening that are essential for food, health and economic security.

PRIVATE SECTOR CORN BREEDING AND RESEARCH

The private commercial sector played an early role in developing both inbreds and hybrids because of the availability of reasonably well-adapted germplasm, the ability to utilise scientific knowledge, and perceived commercial opportunities including those supported by the elementary form of intellectual property protection (IPP) afforded by hybrids.

Development of germplasm is a critical component of successful and sustainable maize breeding. With regard to germplasm diversity developed and used by Pioneer in US corn production we can state that Raymond Baker, who was hired by Henry Wallace as the first corn breeder for the Pioneer Seed company in the 1920s, cast a very broad net in terms of evaluating adapted US maize landraces. Baker and colleagues evaluated virtually all US maize landraces for which they could obtain seed. BAKER (1984) noted that "Many open-pollinated plants were semi-barren and it seemed almost all lodged badly. It is hard to believe that corn hybrids as resistant to lodging could have come from the weak-rooted, stalk-rot susceptible, open-pollinated varieties we started with." A comparison of the pedigree backgrounds for Pioneer brand hybrids that have been widely used in the US central Corn Belt during the period 1930-1999 (SMITH *et al.*, 2004) indicates dependence upon direct use of public inbred lines as parents of hybrids during the 1930s and 1940s. From the 1950s onward an increasing number of the inbred parents of these Pioneer hybrids were proprietary. The proprietary germplasm developed by Pioneer differed from the widely used germplasm developed by the public sector although there was common dependence on Reid Yellow Dent germplasm through pedigrees tracing to the Iowa Stiff Stalk Synthetic population originally developed by G.F. Sprague at the USDA-ARS when he was at Iowa State University. And associations based upon molecular data of US hybrids that were widely used in the late 1980s demonstrated that most Pioneer brand hybrids differed genetically from most of the competitor hybrid germplasm (SMITH *et al.*, 1992). Given the importance of continuing to further develop the germplasm base it is therefore a matter of concern that incentives to encourage private investments into base-broadening are not more adequately provided for by currently available IP regimes (DONNENWIRTH *et al.*, 2004).

The private sector has increased investments in corn research and product development during the decades of the 1990s and 2000s in response to new commercial and scientific opportunities. Biotechnology requires significant investments but, in return, offers prospects of increasing the value of seed for the customer coupled with more effective intellectual property protection and thus provides opportunities for recouping research investments. Further investments are being made into research that will increase abilities to make practical use of new knowledge of the genetics of complex traits and of complex inter-

actions between target environments and plant genotypes. The complexities of interacting biological systems and unpredictable environmental conditions mandate that maize breeders will always be seeking to enhance existing strategies for sourcing, characterizing and combining useful allelic diversity to improve both the on-farm predictability and performance levels of new varieties. Abilities to obtain effective intellectual property protection on new inbreds and hybrids developed from these investments are prerequisites to allow funding into such intellectually challenging research by the private sector.

CONCLUSIONS

Successful maize breeding and production are dependent upon the development of adapted germplasm and a continual commitment to research. Maize has provided a source for critically important fundamental insights into basic aspects of genetics including initially startling and unexpected revelations such as the genetics of transposable elements (McCLINTOCK, 1950) and the lack of co-linearity among genes within species (FU and DOONER, 2002). Plant breeders have integrated information and technologies from research and so continued the evolution of breeding strategies, including, for example, the use of Mutator elements to identify and to clone genes. Breeders have been adept at developing practical strategies that have allowed increasingly effective phenotypically based selection.

DNA sequence, gene-expression and high-throughput marker technologies now make possible the routine availability of genotypic and phenotypic data in unprecedented amount and detail. Marker assisted enhancement of progress toward a target genotype that has already been identified is already routinely used in plant breeding. The challenge for the future is to develop both the germplasm base and the knowledge base to thereby predict, define and create new gene combinations that will contribute improved performance. Much more complete understanding of genetic resource diversity and of genotype, phenotype, the target environment and their interactions will be required. There is therefore no shortage of basic and applied research that will be necessary to further improve the effectiveness and efficiency of plant breeding, including abilities to more effectively source alleles from a broader base of genetic diversity. And secure long-term financial support for genetic resource conservation is fundamentally important. It would be a catastrophic error of monumental proportions if genetic resources that could be more effectively identified and accessible in the future as complex genetics are increasingly well understood have in the meanwhile been left to disappear or to die.

There are numerous important roles for publicly funded researchers, publicly funded plant breeders and commercially funded plant breeders to play in further progressing the sustainable productivity of global agriculture. For example, breeders, like physicists after World War II also need to consider the biological, social and ethical implications of their science. The record of human existence demonstrates a remarkable record of technological development. The development of agriculture and continued abilities to develop varieties that have improved performance due to their genetic content demonstrates ingenuity by individual farmers and researchers over centuries. The conduct of agriculture determines sustainability of food, health, livelihoods and the environment. Future demands to develop crops and agricultural systems will require continued demonstrations of human ingenuity in the development and application of technologies to support agriculture. Perhaps yet more challenging and of even greatest importance will be to increase the store of wisdom and so harness human technological ingenuity and to develop productive and sustainable agriculture founded on biological principles providing equitable benefits.

REFERENCES

ANDERSON E., W.L. BROWN, 1952 Origin of corn belt maize and its genetic significance. pp 124-148. *In*: J.W. Gowen (Ed.), Heterosis. Iowa State University Press, Ames, IA.

BAKER R., 1984 Some of the open-pollinated varieties that contributed the most to modern hybrid corn. pp. 1-19. *In*: Proc. 20th Ann. Illinois Corn Breeders School. Univ. Illinois, Urbana-Champaign, IL.

BEADLE G.W., 1980 The Ancestry of Corn. Scientific American **242:** 112-119.

CARLSEN L., 2004 The movement to defend traditional maize. Americas Program (Silver City, NM: Interhemispheric Resource Center, June 24, 2004).

COOPER M., O.S. SMITH, G. GRAHAM, L. ARTHUR, L. FENG, D.W. PODLICH, 2004 Genomics, genetics and plant breeding: A private sector perspective. Crop Sci. **44:** 1907-1913.

DARLINGTON C.D., K. MATHER, 1949 The elements of genetics. Allen & Unwin, London.

DARRAH L.L, M.S. ZUBER, 1986 United States farm maize germplasm base and commercial breeding strategies. Crop Sci. **26:** 1109-1113.

DOEBLEY J.F., 2004 The genetics of maize evolution. Ann. Rev. Genet. **38:** 37-59.

DOEBLEY J.F., A. STEC, 1991   Genetic analysis of the morphological differences between maize and teosinte. Genetics **129**: 285-295.

DOEBLEY J., L. LUKENS, 1998   Transcriptional regulators and the evolution of plant form. Plant Cell **10**: 1075-1082.

DOEBLEY J.F., M.M. GOODMAN, C.W. STUBER, 1986   Exceptional genetic divergence of Northern Flint Corn. Amer. J. Bot. **73**: 64-69.

DONNENWIRTH J., J. GRACE, S. SMITH, 2004   Intellectual Property Rights, Patents, Plant Variety Protection and Contracts: A perspective from the Private Sector. I.P. Strategy Today **9**: 19-34.

DUVICK D.N., J.S.C. SMITH, M. COOPER, 2004a   Changes in performance, parentage and genetic diversity of successful corn hybrids, 1930-2000. pp. 65-97. *In:* C.W. Smith, J. Betran, E.C.A. Runge (Eds.), Corn: Origin, History, Technology, and Production, John Wiley & Sons Inc., N.J.

DUVICK D.N., J.S.C. SMITH, M. COOPER, 2004b   Long-term selection in a commercial hybrid maize breeding program. Plant Breed. Rev. **24**: 109-151.

EAST E.M., 1915   Studies on size inheritance in *Nicotiana*. Genetics **1**: 164-176.

FLINT-GARCIA S.A., L.L. DARRAH, M.D. MCMULLEN, B.E. HIBBARD, 2003   Phenotypic versus marker-assisted selection for stalk strength and second-generation European corn borer resistance in maize. Theor. Appl. Genet. **107**: 1331-1336.

FREY K.J., 1996   National Plant Breeding Study I. Spec. Rep. 98. Iowa Agric. and Home Econ. Station, Ames, IA.

FU H., H.K. DOONER, 2002   Intraspecific violation of genetic colinearity and its implications in maize. Proc. Natl. Acad. Sci. USA **99**: 9573-9578.

GAUT B., J. DOEBLEY, 1997   DNA sequence evidence for the segmental allotetraploid origin of maize. Proc. Natl. Acad. Sci. USA **94**: 6809-6814.

GOODMAN M.M., 2004   Plant breeding requirements for applied molecular biology. Crop Sci. **44**: 1913-1914.

GUO M., M.A. RUPE, C. ZINSELMEIER, J. HABBEN, B.A. BOWEN, O.S. SMITH, 2004   Allelic variation of gene expression in maize hybrids. Plant Cell **16**: 1707-1716.

HARD R.J., J.R. RONEY, 1998   A massive terraced villa complex in Chihuahua, Mexico, 3,000 years before present. Science **279**: 1661-1664.

HEISEY P.W., C.S. SRINIVASAN, C. THIRTLE, 2001   Public sector plant breeding in a privatizing world. Economic Research Service, U.S. Department of Agriculture, Agriculture Information Bull. No. 772, Washington D.C.

HOLLAND J.B., M.M. GOODMAN, 1995   Combining ability of tropical maize accessions with US germplasm. Crop Sci. **35**: 767-773.

HOLLAND J.B., M.M. GOODMAN, F. CASTILLO-GONZALEZ, 1996   Identification of agronomically superior Latin American maize accessions via multi-stage evaluations. Crop Sci. **36**: 778-784.

HOLLEY R.N., M.M. GOODMAN, 1988   Yield potential of tropical hybrid maize derivatives. Crop Sci. **28**: 213-218.

JENKINS M.T., 1936   Corn Improvement. USDA Yearbook of Agriculture. US Government Printing Office, Washington, DC.

JOHANNSEN W., 1903   Uber Erblichkeit in populationen und in reined Linien. Gustav Fischer, Jena.

LIU K., M.M. GOODMAN, S. MUSE, J.S.C. SMITH, E.S. BUCKLER, J. DOEBLEY, 2003   Genetic structure and diversity among maize inbred lines as inferred from DNA microsatellites. Genetics **165**: 2117-2128.

MATSUOKA Y., Y. VIGOUROUX, M.M. GOODMAN, J. SANCHEZ G., E. BUCKLER, J. DOEBLEY, 2002a   A single domestication for maize shown by multilocus microsatellite genotyping. Proc. Natl. Acad. Sci. USA **99**: 6080-6084.

MATSUOKA Y., S.E. MITCHELL, S. KRESOVICH, M. GOODMAN, J. DOEBLEY, 2002b   Microsatellites in Zea - variability, patterns of mutations, and use for evolutionary studies. Theor. Appl. Genet. **104**: 436-450.

MCCLINTOCK B., 1950   The origin and behaviour of mutable loci in maize. Proc. Nat. Acad. Sci. USA **36**: 344-355.

NASS L.L., J.G. COORS, 2003   Potential of exotic x adapted maize germplasm for silage. Maydica **48**: 197-206.

PECCOUD J., K. VANDER VELDEN, D.W. PODLICH, C.R. WINKLER, W.L. ARTHUR, M. COOPER, 2004   The selective values of alleles in a molecular network model are context dependent. Genetics **166**: 1715-1725.

PODLICH D.W., C.R. WINKLER, M. COOPER, 2004   Mapping as you go: An effective approach for marker-assisted selection of complex traits. Crop Sci. **44**: 1560-1571.

POLLAK L.M., 2003   The History and Success of the Public-Private Project on Germplasm Enhancement of Maize (GEM). Adv. Agronomy **78**: 45-87.

SCHON C.C., H.F. UTZ, S. GROH, B. TRUBERG, S. OPENSHAE, A.E. MELCHINGER, 2004   Quantitative trait locus mapping based on resampling in a vast maize testcross experiment and its relevance to Quantitative Genetics for complex traits. Genetics **167**: 485-498.

SMITH J.S.C., O.S. SMITH, S. WRIGHT, S.J. WALL, M. WALTON, 1992   Diversity of U.S. hybrid maize germplasm as revealed by Restriction Fragment Length Polymorphisms. Crop Sci. **32**: 598-604.

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 1999. Crop Sci. **44**: 1935-1946.

STURTEVANT E.L., 1899   Varieties of Corn. Bulletin No. 57, USDA, Washington, DC.

THORNSBURRY J.M., M.M. GOODMAN, J. DOEBLEY, S. KRESOVICH, D. NIELSEN, E.S. BUCKLER IV., 2001   *Dwarf8* polymorphisms associated with variation in flowering time. Nature Genetics **28**: 286-289.

VIGOUROUX Y., C.T. HITTINGER, K. HOUCHINS, L. SCHULZ, M. MCMULLEN, S. KRESOVICH, Y. MATSUOKA, J. DOEBLEY, 2002   Identifying genes of agronomic importance in maize by screening microsatellites for evidence of selection during domestication. Proc. Natl. Acad. Sci. USA **99**: 9650-9655.

WALLACE H.A., 1923   What is in the corn judge's mind? Jour. Amer. Soc. Agron. pp. 300-304.

WATSON J.D., F.H.C. CRICK, 1953   Molecular structure of nucleic acids; A structure for Deoxyribose Nucleic Acid. Nature **171**: 737-738.

WILLIAMS W., 1964   Genetical Principles and Plant Breeding. Blackwell Scientific Publications, Oxford, UK.