Chapter 1
Wild Relatives of Maize

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Abstract Crop domestication changed the course of human evolution, and domestication of maize (*Zea mays* L. subspecies *mays*), today the world's most important crop, enabled civilizations to flourish and has played a major role in shaping the world we know today. Archaeological and ethnobotanical research help us understand the development of the cultures and the movements of the peoples who carried maize to new areas where it continued to adapt. Ancient remains of maize cobs and kernels have been found in the place of domestication, the Balsas River Valley (~9,000 years before present era), and the cultivation center, the Tehuacan Valley (~5,000 years before present era), and have been used to study the process of domestication. Paleogenomic data showed that some of the genes controlling the stem and inflorescence architecture were comparable to modern maize, while other genes controlling ear shattering and starch biosynthesis retain high levels of variability, similar to those found in the wild relative teosinte. These results indicate that the domestication process was both gradual and complex, where different genetic loci were selected at different points in time, and that the transformation of teosinte to maize was completed in the last 5,000 years. Mesoamerican native cultures

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domesticated teosinte and developed maize from a 6 cm long, popping-kernel ear to what we now recognize as modern maize with its wide variety in ear size, kernel texture, color, size, and adequacy for diverse uses and also invented nixtamalization, a process key to maximizing its nutrition.

Used directly for human and animal consumption, processed food products, bioenergy, and many cultural applications, it is now grown on six of the world's seven continents. The study of its evolution and domestication from the wild grass teosinte helps us understand the nature of genetic diversity of maize and its wild relatives and gene expression. Genetic barriers to direct use of teosinte or *Tripsacum* in maize breeding have challenged our ability to identify valuable genes and traits, let alone incorporate them into elite, modern varieties. Genomic information and newer genetic technologies will facilitate the use of wild relatives in crop improvement; hence it is more important than ever to ensure their conservation and availability, fundamental to future food security. In situ conservation efforts dedicated to preserving remnant populations of wild relatives in Mexico are key to safeguarding the genetic diversity of maize and its genepool, as well as enabling these species to continue to adapt to dynamic climate and environmental changes. Genebank ex situ efforts are crucial to securely maintain collected wild relative resources and to provide them for gene discovery and other research efforts.

Keywords Maize wild relatives · Crop domestication · Teosinte · *Tripsacum* · In situ conservation · Ex situ conservation · Plant genetic resources

1.1 Introduction

All the rain gods participated in the project –the blue, the white, the yellow, and the red gods- and in a final effort, Nanáhuatl struck the mountain and made it release its treasure. The mountains spilled out white corn, black corn, yellow corn, and red corn (The legend of the Suns, Aztec mythology).

1.1.1 Origin of the Crop and Brief History of Use Worldwide

Domestication of maize (*Zea mays* L. ssp. *mays*) happened during the last ~9000 years before present (BP) from its wild relative grass teosinte (*Z. mays* ssp. *parviglumis* H. H. Iltis and Doebley). This process took place in the Balsas River Valley of southern Mexico (Matsuoka et al. 2002; Piperno et al. 2009), with subsequent introgression from *Z. mays* ssp. *mexicana* (Schrad.) H. H. Iltis and Doebley into highland Mexican maize (van Heerwaarden et al. 2011).

Archaeological remains of maize cobs, pollen, starch grains, kernels, phytoliths, and ceramics indicate early use of maize by at least 8700 years BP (Piperno et al. 2009; Ranere et al. 2009) and a widespread dispersal through the Americas, reaching

Ecuador (6400–5000 BP), Peru (4800–4600 BP), Colombia (4745–4380 BP), the Caribbean (1140–1350 B. P.), and Puerto Rico (3295–2890 BP) (Bonzani and Oyuela-Caycedo 2006).

Following diversification in the Mexican highlands, maize was introduced to the southwestern USA by 4000 BP, according to archaeological evidence from the temperate highlands of the Colorado Plateau and the lowlands deserts of southern Arizona (Vierra 2005; Huckell 2006), via the inland Mexican route (da Fonseca et al. 2015). Soon after introduction in the southwestern USA, maize agriculture was adopted by locals, whereas in the highlands, maize agriculture was initiated between 2400 and 1800 BP, despite evidence of earlier presence of maize (Wills 1988; Huckell 2006; Cordell and McBrinn 2012). One theory attributes the difference in time of adoption for cultivation to insufficient adaptation of the early introduced materials to the highland environmental conditions (Matson 1991).

The earliest evidence for the introduction of maize into the temperate northeast of the continent is 275 AD (Ohio) and 460 AD (southern Ontario) (Hart and Means 2002). Using tree ring calibrated radiocarbon dating; Little (2002) found that maize was introduced into the lower Hudson River valley around 1000 AD. Maize cultivation thus spread from west to east, evidenced by archaeological samples recovered more frequently from New England that date to the period of 900 to 1500 AD (Hart and Means 2002; Little 2002).

During the late 1500s AD, maize spread by various routes into Europe, Africa, and Asia (Dubreuil et al. 2006; Rebourg et al. 2003) and during the 1600s AD into Africa (McCann 2005). The spread of maize along a north-south axis, as opposed to a west-east direction post domestication, was relatively slow due to the need to adapt to local day length to initiate flowering (Hung et al. 2012).

Mir et al. (2013) proposed a preliminary overview of the global movement of maize germplasm by analyzing 784 different landrace populations with 17 unlinked SSR molecular markers. Their results classified the maize germplasm of the Americas based on their geographic origins into seven different groups (US Northern Flints, Mexican highland, tropical lowlands, Andes, middle North American, South American, and middle South American). By associating the levels of similarity with other landraces from other continents, Mir et al. (2013) revealed a migration route (Fig. 1.1). Previously documented diffusion of US Northern Flints through Europe, from northern France eastwards, starting in the sixteen century was confirmed, as well as their contribution to the Pyrenean-Galician landraces. A predominance of US Northern Flints in the admixed ancestry of Portuguese landraces suggested a hybrid origin, and perhaps a second independent introduction of US Northern Flint into Portugal, possibly via Portuguese expeditions in North America in the early sixteen century. Middle Eastern and Eastern African maize introductions traced back to the middle North American maize germplasm, contradicting previous reports of early diffusion of Caribbean maize through Southern Europe into Egypt (ca. 1517) and onward throughout Eastern Africa (Portères 1955). The same source of maize was introduced to into northern China (Mir et al. 2013).

Traces of ancestry from the Mexican highlands cluster were found throughout eastern Asia, along the coasts, suggesting maritime introduction(s), initiating in

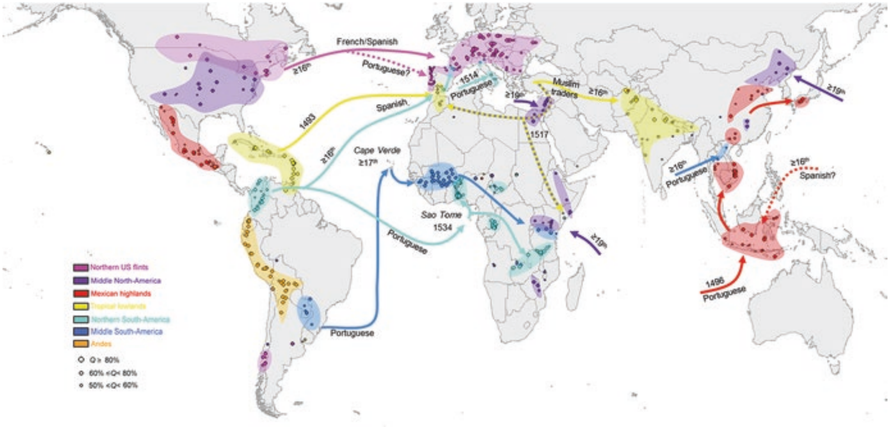

Fig. 1.1 Map of hypothetical major routes of global maize diffusion out of the Americas (Mir et al. 2013)

Indonesia and diffusing northwards and toward Japan. The tropical lowland cluster contributed to southern Spanish maize, in agreement with reports that Columbus traveled back to Spain with maize from the Caribbean. The same ancestry was found in Moroccan landraces, and in those of western Asia, from Nepal to Afghanistan. However, tropical lowland ancestry decreases southeastwards through Asia, where Mexican ancestry becomes predominant, suggesting that Asia was the contact zone between these two diffusion routes (Mir et al. 2013).

The northern South American cluster was present as a second contributor to southern European landraces, even exceeding the Tropical lowland ancestry in some Pyrenean, Italian, southern Spanish, and Galician landraces. Some northern South American and middle South American contributions to western sub-Saharan African landraces were also identified (Mir et al. 2013). Finally, the Andean ancestral cluster did not show clear evidence of direct diffusion out of the Americas. This may be due to its relative geographical isolation from main trading routes and adaptation to extreme high altitude conditions, as reported by Gouesnard et al. (2002).

1.1.2 *Modern Day Use*

Maize has emerged as a crop of global importance due to its multiple uses as a human food, as a feedstock for livestock and bioenergy, and for important components for industrial products, made possible by the unparalleled crop genetic diversity that has supported adaptation to a tremendous range of agroecological conditions and production challenges. The world's most multipurpose crop, maize, serves as a food staple for hundreds of millions of people in the developing world, feed for billions of livestock, and raw material for an increasing number of industrial and biofuel uses. Cultivated on 222 million hectares (Mha) globally (FAOSTAT 2014), maize is fundamental to global food and economic security, and of immense historical and current cultural value, providing 20% of the total calories in human diets in 21 low-income countries, and over 30% in the 12 countries that are home to a total of more than 310 million people (Anon Maize Phase II, CGIAR-Research Program on Maize Anon 2016).

Globally, about 1016.73 million metric tons of maize are produced every year – the highest among major staple cereals (FAOSTAT 2014). It is cultivated in 160 countries on all continents except Antarctica (Fowler 2006; Ben-Ari and Makowski 2014), and from 58 N latitude to 40 S, in tropical, subtropical, and temperate environments, and from sea level to 3,800 m (Paliwal 2000; Farnham et al. 2003). The leading countries for world production (percent) are the USA (35), China (25), Brazil (7.7), Argentina (3.2), Ukraine (2.7), Mexico (2.5), India (2.2), and Indonesia (1.8) (FAOSTAT 2014). Maize hybrids with increased production per unit area are required to feed the world's ever-growing population. The introduction of new improved maize varieties into west and central Africa has moved more than one million people per year out of poverty since the mid-1990s (Alene et al. 2009). Each decade since the 1970s, global maize yield has increased, but yield gains have not occurred in all areas and have actually decreased in some (Hengsdijk and Langeveld 2009). Globally, maize yields are increasing in 70% of the planted area (103 Mha), stagnating in 26%, and decreasing in 3% (Ray et al. 2012, 2013). Some of these increases reflect step changes as countries modernize production methods and technologies and do not necessarily indicate a permanent trend.

A recent study of genetic gain for US maize (Smith et al. 2014) showed the rate of genetic gain increased compared to results from a previous survey conducted a decade earlier. Duvick and Cassman (1999) show the proportion of yield gain due to improved genetics increased from approximately 50% to 75%. If yield gains due to improved farm management cannot keep pace with those of the past decades, increasing the rate genetic gain to increase yield becomes more imperative (Cassman et al. 2003; Lobell et al. 2009). Coupled with the need to improve sustainability of global production, the demand for genetic contributions continues to accelerate.

A rich body of literature testifies not only to the importance and success of efforts to increase maize productivity in the temperate USA over time but also to understanding the basis for these improvements. Duvick (1977) tested production of popular hybrids grown over a period of 40 years at a range of plant densities, demonstrating that hybrids were selected over time for increased yield and positive agronomic trait performance under increased plant density, while individual plant yield did not increase. There has been no published evidence that contradicts the statement that yield on a single hybrid plant basis has not changed. Over the 40-year period that spanned the transition from production of open pollinated varieties to double-cross hybrids and then to single-cross hybrids, yield increases averaged 115 kg/ha/yr. (United States Department of Agriculture National Agricultural Statistics Service (USDA-NASS) 2004). Duvick (2005) provides an excellent review of the research conducted to examine the factors contributing to this progress, via improved agronomics, new breeding methods, and the interaction of the two. Changing management practices, earlier planting dates made possible by increased abiotic stress tolerance and use of seed treatments, use of mechanized harvest equipment, increased application of nitrogen fertilization, and an average increase in plant density of 1000 plants/ha/yr. contributed to major technological achievement. Major plant traits underwent modification in this period. Improved root and stalk health and strength resulted in erect plants at harvest and reduced lodging, which enabled mechanized harvesting. More upright leaf angles reduced shading of lower leaves in the canopy, increasing photosynthetic capacity. Reduced tassel size allowed more photosynthate to be partitioned to the ear. Improving stay-green (delayed senescence) extended the grain fill period relative to the plant's life cycle. Improved biotic stress tolerance and selection for resistance to disease and insect pests contributed to plant health and grain yield. The delay between time of pollen shed and silk emergence, known as the anthesis-silking interval, decreased as abiotic stress tolerance improved. Stronger silking under high density or drought stress reduced grain loss due to poor grain fill. Selection against barrenness (failure to produce an ear) under high plant density was important. These traits and more, coupled with longer grain fill period and rapid dry-down at harvest, supported increased production, movement of production areas to higher latitude environments, and increased global grain trade.

During the 1970s to the 1990s, research expenditures for maize increased, devoted to integration and application of new biotechnology tools in plant breeding and also to increased expenditures for more maize breeders, testing locations, and numbers of yield test plots (Duvick and Cassman 1999). The trend in increased research costs per unit of genetic gain for maize continued into the second decade of the twenty-first century (Smith et al. 2014). This implies that "the marginal yield increase per unit of research investment has decreased substantially over time" (Grassini et al. 2013).

Over the past 20 years, the maize seed industry has become increasingly international, with vast resources consolidated in and deployed by a few major international companies in North and South American and in Europe. The public sector breeding effort has simultaneously been reduced in scope. This is cause for concern, as the status of genetic diversity deployed commercially vs. genetic vulnerability is unknown.

Society depends upon agriculture being successful over centuries and beyond, and access to diverse genetic resources is key. The Rockefeller Foundation provided support from 1945–1960 to collect races of maize representing the diversity of maize grown across the Americas, which provide the main basis for characterization and classification, including understanding comparative germplasm constitution and phylogenies (Brown and Goodman 1977). The few racial complexes that have attained global importance include the Mexican Dents, Corn Belt Dents, Tusóns, Caribbean Flints, Northern Flints and Flouries, and the Catetos or Argentine Flints, although additional races contribute regional importance (Goodman 1978).

Maize serves as a model organism for biological research worldwide. The genetic discoveries of Barbara McClintock (1956, 1984) led to insights into the diversity of the maize genome, the discovery of transposable elements, and the revolutionary understanding that the genome is dynamic and subject to rearrangement essentially continually generating new diversity. More than 50 years passed before the role of these elements in regulating genes was understood (Biemont and Vierira 2006). Today's technologies enable innovative research to understand gene function and to capture traits from the wild relatives, which previously has not been possible. The sequencing of the maize genome and publication of B73 ReGen_v1 (Schnable et al. 2009) marked a paradigm shift as genomic information became readily available for researchers to use in both basic and applied endeavors to understand maize genetic diversity and capture useful diversity for crop improvement and food security. Today, we are well-equipped to conduct research to better utilize not only maize landraces but also the wild relatives.

1.1.3 Challenges in Cultivation

1.1.3.1 Pests, Diseases, and Edaphic and Climatic Limitations

Mesoamerica and the northern part of South America are the regions where the greatest maize diversity originated. The diversity of environmental conditions supported development of maize varieties well adapted to specific soil and climatic conditions as well as to biotic and abiotic stresses. Cultural practices in the communities where landraces are grown, which affect the production systems used and the patterns of dietary consumption and ritual uses of maize, have been found to be also closely correlated with patterns of maize diversification and variation (Louette and Smale 1998).

Over its vast geographical distribution, maize encounters a large number of diverse pests and pathogens during its life-span. Leaf blights and foliar diseases, stalk rots, and ear molds that may or may not produce toxins, and an array of insects that either directly cause economic damage or vector diseases, all challenge maize production. Tropical landraces and inbreds from Africa and Asia typically offer some level of resistance to diseases and insect pests endemic to those production areas. Disease-causing organisms include viruses, bacteria, fungi, spiroplasma, and mycoplasma, and other pathogens, all of which are under constant selection pressure to evolve virulence alleles to overcome host resistance alleles. More than 50 viruses have been identified as infecting maize (Lapierre and Signoret 2004). At least a dozen viruses from eight families cause significant agronomic problems in maize worldwide (Louie 1999; Redinbaugh and Pratt 2008).

Worthy of considerable note among emerging diseases is maize lethal necrosis (MLN) in sub-Saharan Africa, which can result in total yield loss. Estimated losses of 126,000 metric tons occurred in 2012 in Kenya alone. First reported in September 2011 (Wangai et al. 2012a, b), MLN results from a coinfection of maize chlorotic mottle virus (MCMV) and sugarcane mosaic virus (SCMV) (Goldberg and Brakke 1987; Niblett and Claflin 1978; Uyemoto et al. 1980). It can be mechanically transmitted by a number of insects, including maize thrips (*Frankliniella williamsi*, Cabanas et al. 2013) and casual introduction into plant tissue via abrasion and seed transmission (Jensen et al. 1991; Mahuku et al. 2015). Massive efforts have been undertaken to identify MLN-tolerant germplasm, and the genetics and inheritance of MLN resistance is complex. Gowda et al. (2015) used genome-wide association study (GWAS) and genome selection (GS) tools to examine a wide variety of maize breeding program resources, including ones from African countries and from the Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), and identified a series of single nucleotide polymorphisms (SNPs) localized to eight of the ten chromosomes and six detected quantitative trait loci (QTLs). CIMMYT's information portal reports progress in development and release of MLN-tolerant germplasm (http://mln.cimmyt.org/mln-resistanttolerant-germplasm/).

Late wilt of maize, caused by the fungus *Harpophora maydis*, is a soilborne and seedborne fungus (Pésci and Németh 1998) considered to be an invasive species. Important and known to occur in Egypt since 1963 (Samra et al. 1962, 1963) and India (Payak et al. 1970), it has also been reported in Hungary (Pésci and Németh 1998) and in Portugal and Spain (Molinero-Ruiz et al. 2010). This disease presents serious threats to global maize production, given the risks of pathogen movement through contaminated soil and/or infested seed.

Finally, tar spot of maize appears to be increasing in impact in Mexico and Central America and can cause estimated yield loss up to 30% or more (Hock et al. 1995). Tar spot predisposes the plant to subsequent infestation by other pathogens and also reduces grain quality and the quality of fodder (Bajet et al. 1994). It is caused by the interaction of two fungi, *Phyllachora maydis* and *Monographella maydis*, and has been found historically at high elevations in cool, humid areas of Latin America but has proliferated and spread to South American tropics and parts of North America.

Other diseases such as common and southern rust have serious impacts as well. Continual breeding effort is needed to overcome development of more virulent strains and races of pathogens. There are landraces like Tuxpeño Crema, a subpopulation of landrace Tuxpeño, from Mexico that is well known for its resistance to tropical foliar diseases (Rodriguez et al. 1998). A popcorn landrace, Palomero Toluqueño, was found to have resistance to the maize weevil, *Sitophilus zeamais* (Arnason et al. 1994); this resistance may be due to biochemical composition, pericarp hardness, or both, which are genetically controlled. A few Caribbean landraces were found to be tolerant to larger grain borer (*Prostephanus truncatus*) (Kumar 2002). There are Mexican maize landraces that offer various types of abiotic stress tolerance; sources include Conico, Conico Norteño, Bolita, Breve de Padilla, Nal Tel, Tuxpeño (drought tolerant), Oloton (acid soil tolerant), and Chalqueño × Ancho de Tehuacan cross (alkalinity tolerant) (Prasanna 2012). Some of the derived lines from La Posta Sequia, an open pollinated variety developed by CIMMYT, are tolerant to both drought and heat stresses (Cairns et al. 2013).

1.1.3.2 Nutritional, Functional Use

The nutritional safety and health of people are vital requisites for the progress of societies. Maize is a widely consumed and multipurpose crop that provides many constituents required for human nutrition, including carbohydrates, fiber, protein, vitamins, and some micronutrients. It provides over 20% of the total calories consumed in 21 countries and over 30% in 12 countries that are home to a total of more than 310 million people (Shiferaw et al. 2011).

Maize landraces exhibit diverse grain colors, including white, light and dark yellow, orange, red, blue, and purple. Typical yellow maize contains many important vitamins with the notable exception of vitamin B-12. Vitamin A, as provitamin A carotenoids, and vitamin E, as tocopherols, are the predominant fat-soluble vitamins found in maize. Both carotenoids and tocopherols play important roles as antioxidants among other functions (Kurilich and Juvik 1999). In humans, these carotenoids have been implicated in preventing various eye and cardiovascular diseases, as well as several types of age-related diseases, most likely via their role as antioxidants and/or as regulators of the immune system. Even though carotenoids are yellow-orange phytopigments, orange or yellow grain color is not necessarily correlated with provitamin A concentrations due to variable accumulations in seed coat, endosperm, and germ (Harjes et al. 2008). Consumption of orange maize has been demonstrated to improve total body vitamin A stores as effectively as supplementation (Gannon et al. 2014) and significantly improve visual function in marginally vitamin A-deficient children (Palmer et al. 2016).

Other pigment molecules found in maize are anthocyanins. These flavonoid compounds (cyanidin, pelargonidin, and peonidin) range from red to blue in color, giving some maize varieties an almost black or red pigmentation (Boyer and Shannon 1987). Flavonoids are not considered essential nutrients, but are strongly recommended for optimal health due to their potent antioxidant behaviors (Gropper et al. 2005).

Vitamin E constituents are found in significant amounts in maize seed (Grams et al. 1970; Reiners and Gooding 1970). Water-soluble vitamins are found principally in the endosperm, although the highest concentrations are in the aleurone layer. The process of nixtamalization (cooking maize with lime, heat, and/or pressure) can change the composition of nutritional state and sometimes release compounds with high nutritional value.

Significant advances have been made in genetic enhancement of maize for nutritional value. Biofortified provitamin A maize is an example for an efficacious source of vitamin A when consumed as a staple crop (Welch and Graham 2004). Exogenous and endogenous fortification efforts to improve the levels of limiting amino acids, provitamin A carotenoids, B vitamins, and trace minerals are gaining emphasis in the battle against malnutrition problems in high-risk populations who rely on maize as a staple food (*Giuliano* 2017; Muzhingi et al. 2017).

1.1.3.3 Anticipating Climate Change

As the planet warms, we are already seeing the impact of inconsistent weather patterns and extreme weather events on global maize production. Ray et al. (2014) noted that across the nine major grain belts of the globe, 41% of inter-year yield variation was due to climate variability, and the percentage effect of climate variability on yield variability increased to 60–75% for the USA and China. The global movement of seeds, soil, and pests plays a significant role in the pace of development of new production threats across global production areas. Modern genetic and breeding technologies, coupled with big data analytics, will be necessary to assist in identification of germplasm that may offer useful alleles from non-elite sources such as the landraces and wild relatives. Important to enabling these processes are systematic genotyping and phenotyping activities to document genetic resource performance under a variety of edaphic and biologically challenging conditions. Maize and maize wild relative germplasm must be available for these efforts, critical for food security.

1.2 Maize Wild Relatives

Archaeological and Molecular Evidence Links Modern Maize to Its Wild Relatives

The genus *Tripsacum* is the closest wild relative of *Zea*, and the genera have been estimated to have diverged between 4.5 and 5.2 million years ago, based on comparative DNA sequence data and mutation rates per nucleotide under neutral selection (Hilton and Gaut 1998; Buckler and Stevens 2005). *Tripsacum* comprises 15–16 perennial species. Members of the genus are widely distributed in the Americas, from northeastern and north central USA to Mexico and Central America, the West Indies, and South America to Bolivia and Paraguay (Doebley 1983; Blakey et al. 2007).

Hilton and Gaut (1998) estimated that the time of divergence between *Z. luxurians* (Durieu and Asch.) R. M. Bird and *Z. mays* ssp. *parviglumis* occurred at least 100,000 years ago. However, White and Doebley (1999) stated that estimates may be inaccurate and depend upon improved knowledge of mutation rates for specific genes; thus estimates must be validated by fossil records. They also provided a summary of divergence times as follows:

- The genera *Zea* and *Tripsacum* diverged between 2.3–2.6 m yr. and 4.5–4.8 m yr.
- The age of the *Zea* genepool is between 0.7 m yr. and 4.7 m yr., possibly between 1.2 and 1.4 m yr.
- *Z. mays* and *Z. luxurians* represent potentially the first phylogenetic divergence within *Zea* and occurred approximately 700,000 yr. ago.

Considering the short span of time between divergence and domestication of the genus *Zea*, it is not surprising that considerable diversity resides in the wild relatives of maize, including both sister genera, *Zea* and *Tripsacum* (Smith et al. 2017).

Based on biochemical and molecular data, it has been shown that the domestication of maize took place in the Balsas River Basin in southwestern Mexico about 9000 years B.P. and that *Z. mays* spp. *parviglumis* is the closest extant wild relative of maize (Doebley et al. 1987; Doebley 1990a, b; Matsuoka et al. 2002). However, in the case of landraces, which by origin are more similar to *Z. mays* ssp. *parviglumis*, their predominant distribution was in the Mexican highlands, the natural habitat for *Z. mays* ssp. *mexicana*. Using single nucleotide polymorphisms (SNPs), van Heerwaarden et al. (2011) genotyped the *Zea* subspecies *parviglumis* and *mexicana* and landraces from across the Americas demonstrating that the two subspecies were less differentiated from each other than from the landraces, identifying much more admixture between the landraces and *Z. mays* ssp. *mexicana* than between the landraces and *Z. mays* ssp. *parviglumis*. These results suggested that *Z. mays* ssp. *mexicana* had an important role in the adaptation of maize to the highlands.

Further studies analyzed the morphological differences between maize and teosinte. An example of this is the degree of apical dominance; *Z. mays* ssp. *parviglumis* shows numerous lateral branches and tillers in contrast to maize, where the plant is usually an unbranched single stalk. Doebley et al. (1997) identified the gene responsible for the differences in plant architecture, *teosinte branched1* (*tb1*), which encodes a transcription factor that represses the growth of axillary organs. Studer et al. (2011) demonstrated that a transposable element insertion in the upstream regulatory region of *tb1* locus acts as an enhancer of the expression of the gene. Using a diverse array of teosinte populations, teosinte inbreds, maize landraces, and maize inbreds in this study, the authors also found that the allele that confers the maize phenotype was segregating in some teosinte populations, suggesting that the process of domestication acted on standing variation present in teosinte. The distal and proximal components in the complex control region were found to contribute independently to phenotypic traits such as tillering and also to internode length and cupules per rank.

Another example of contrasting phenotypes between maize, *Z. mays* ssp. *parviglumis* and other teosintes, is the structure of the female infructescence. Teosinte presents numerous spikelets of disarticulating seeds covered by a hard protective casing (glumes), whereas maize produces only a small number of infructescences with naked grains attached to the cob. This variation is explained by a single locus, *teosinte glume architecture* (*tga1*) (Wang et al. 2005). Several other domestication loci have been identified through different genetic approaches (Ross-Ibarra et al. 2007).

With the development of new genomic technologies, the understanding of the domestication process in maize is improving. In two independent studies, Ramos-Madrigal et al. (2016) and Vallebueno-Estrada et al. (2016) sequenced the genomes of ancient cobs from the San Marcos caves in the Tehuacan Valley of Puebla state in Mexico. Vallebueno-Estrada et al., returned to the original cave sites and discovered additional specimens, dated about 5000 years old, and sequenced the genomes. Their results identified modern maize variants of the loci *tb1* and *bt2* (*brittle2*, glycogen biosynthesis, increasing the starch content and sweetness of the kernels), but the locus *tga1* was a teosinte (*Zea mays* ssp. *parviglumis)* variant. Ramos-Madrigal et al. (2016) sequenced the genome of the original cob discovered by the archaeologist Richard MacNeish in the mid-1960s and stored in a museum in Andover, Massachusetts (Janzen and Hufford 2016). The sequencing results showed modern variants of the loci *td1* (related to inflorescence architecture), *zmgl* (circadian clock and flowering time), *ba1* (lateral meristem development), *bt2*, and *tga1*. They also found the *Zea mays* ssp. *parviglumis* variants for the loci *zagl1* (related to ear shattering), *su1*, and *wx1* (starch biosynthesis).

In both cases, the genome of the ancient cob was more closely related to modern maize than to teosinte; however, genes related to the domestication syndrome were different between modern landraces and improved maize lines (Allaby 2014; Ramos-Madrigal et al. 2016). The results showed that the ancient genome had multiple loci selected at different points in time and that the domestication process of maize was still on going.

Archaeological, botanical, and genetic evidence indicate that *Z. mays* spp. *mays* was domesticated in the Balsas River Valley of southern Mexico from its wild relative, one of the teosintes (*Z. mays* spp. *parviglumis*). Extensive molecular analysis indicated that maize arose through a single domestication event about 9000 years BP (Matsuoka et al. 2002; Piperno et al. 2009). These same studies located the populations of Balsas teosinte, considered to be the most closely related to extant maize, at the intersection of the states of Michoacán, Guerrero, and Estado de México, suggesting that maize diverged from an ancestral teosinte population in the Balsas River Valley (Fig. 1.2; Matsuoka et al. 2002; Doebley 2004; Piperno et al. 2009). Phytolith and starch grain evidence indicate that maize was present in the Balsas River Valley by 8700 years BP (Piperno et al. 2009); however, the most ancient Mexican maize specimens are two inflorescence fragments found in the Guilá Naquitz cave from the highlands of Oaxaca, averaging 6,235 years BP (Piperno and Flannery 2001; Benz 2001).

Unlike the specimens found in the Guilá Naquitz cave, the materials found in the San Marcos cave in the Tehuacan Valley of Puebla state are remarkably uniform and present polystichous cobs, dating to between 5300 and 5000 years BP (Benz and Long 2000). Morphometric examination of these specimens suggested that these materials were fully domesticated since they showed morphological traits indistinguishable from those found in some extant landraces (Benz and Iltis 1990). The changes in the cob architecture were considered the result of early efforts to gain access to the grains (improved seed retention and harvestability) and increase productivity. Recent paleogenomic studies on ancient cobs from the Tehuacan Valley have shown that even some of the genes controlling the stem and inflorescence architecture were comparable to modern maize, while other genes controlling ear shattering and starch biosynthesis still retained high levels of variability, similar to those found in the wild relative teosinte. As more paleogenomic information is generated, using samples from different time periods, the shifting forces behind the transformation of teosinte into maize will be elucidated.

1.2.1 Maize Crop Wild Relatives (CWR) and Their Genepool Classifications

> … no more useless grasses from the standpoint of human consumption could be devised than the American relatives of maize. (J.H. Kempton 1937)

No one would disagree that the hard-coated, seemingly inedible, seeds of the teosintes, at that time classified in the genus *Euchlaena*, and those of *Tripsacum*,

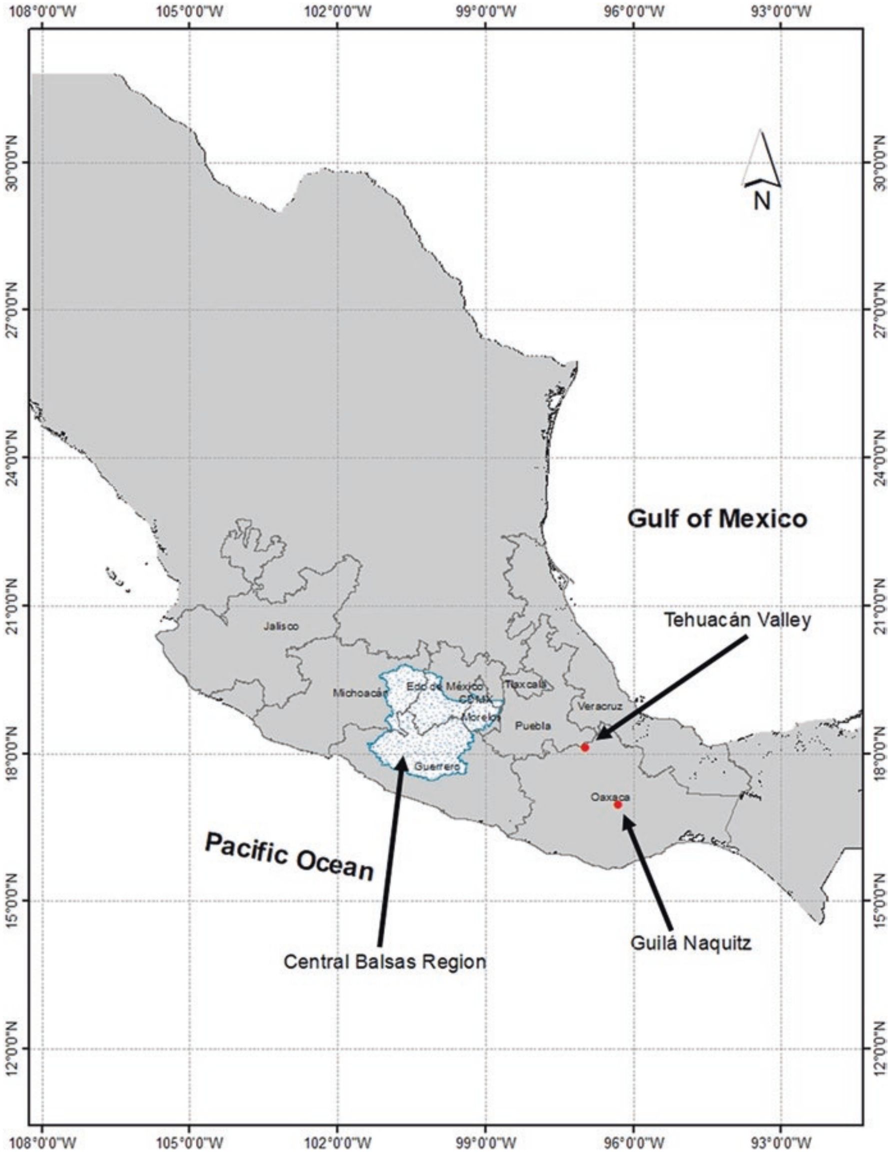

Fig. 1.2 Map of the locations of the Guilá Naquitz cave and the Tehuacan valley archaeological sites (red circles) and with the modern distribution of the populations of *Zea mays* ssp. *parviglumis* H. H. Iltis and Doebley from the Central Balsas River Valley (area outlined in blue)

bear little resemblance to the highly edible kernels of maize. This incongruity alone generated decades of research and, at times, heated debates, about the origin of maize and the identification of its extant wild relatives. As early as 1939, George Beadle published a short review of the evidence – cytology and hybridization data –

that supported the hypotheses of a very close relationship between maize and teosinte and a more distant relationship between these taxa and the genus *Tripsacum*. However, many were not convinced, and it was only when Beadle returned to maize research in the 1970s (as a retired Nobel Prize winner) that he was able to carry out the key experiments, based on simple Mendelian genetics, that, along with the advent of molecular biology, started the paradigm shift in our understanding of the genetic processes that led to the origin of maize as a domesticated crop plant (Beadle 1972, 1980; Doebley 2001, 2004; Berg and Singer 2003). This continues to be a very active area of research, both biological and archaeological, as described in the previous section. Here we describe the relationships among maize and its closest wild relatives, using the currently accepted taxonomy [See recent reviews of *Zea* (Hufford et al. 2012) and *Tripsacum* (Blakey et al. 2007)].

The two genera that form the genepool of maize, *Zea* and *Tripsacum*, comprise subtribe Tripsacinae, tribe Andropogoneae, and subfamily Panicoideae of family Poaceae (Grass Phylogeny Working Group 2001). They represent the genetic diversity that is potentially available to the target crop species, either through direct hybridization or artificial means, such as embryo rescue. All taxa are classified based on the ease of genetic exchange with the crop (Harlan and de Wet 1971). In Fig. 1.3, we present the genepools in a pyramid format, with maize (*Z. mays* ssp. *mays*) at the apex, representing the primary genepool, all other taxa in the genus *Zea* (the "teosintes") as the secondary genepool, and all of the species in the genus *Tripsacum* at the base of the pyramid, as the tertiary genepool.

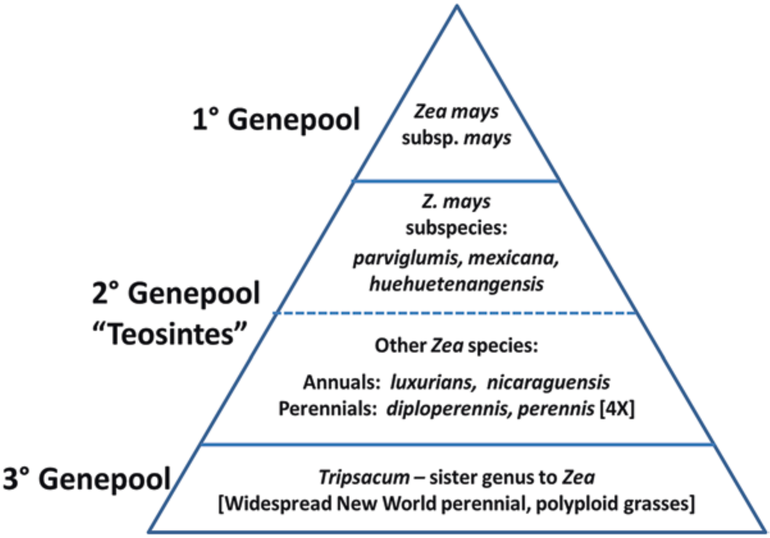

Fig. 1.3 Genepool classifications of maize and its wild relatives

Within the teosintes, we have split the three subspecies of *Z. mays*, all of which are annuals and can readily cross with maize, from the other three *Zea* species, one of which (Z. *luxurians*) is an annual and two of which, Z. *diploperennis* Iltis, Doebley and Guzman and *Zea perennis* (Hitchc.) Reeves & Manglesdorf, are perennials, and diploid or tetraploid, respectively. These three *Zea* species show increasing incompatibilities with maize, but all share the same base chromosome number, n = 10.

At the outer edge of the maize genepool, the tertiary level, the base chromosome number shifts to n = 18 in *Tripsacum* spp., all of which are perennials. This difference in chromosome numbers provides an effective barrier to genetic exchange between *Zea* and *Tripsacum*. However, a recent comparison of the maize and diploid *Tripsacum dactyloides* L. genomes indicates that they contain very similar gene contents, in contrast to major differences between the two in the composition and abundance of the transposable element families (Chia et al. 2012). These results confirm that *Tripsacum* is indeed part of the maize genepool but that access to the abundant, potentially useful, diversity in *Tripsacum* for maize improvement may only be attainable directly in the future via gene editing technologies (Smith et al. 2017).

Tripsacum species display considerable variation in ploidy level: a few are strictly diploid, others show a range from diploid to tetraploid and, in some cases, pentaploid and hexaploid, while still others are strictly tetraploid. The complexity of this ploidy variation has still not been fully explored: in a survey of ploidy levels (2x, 3x, 4x, 5–6x) in 174 Mexican populations, 15 out of 37 ploidy level-taxon combinations (41%) had never been reported before, and in more than half of the cases, the "new" ploidy was triploid (Berthaud et al. 1997). There has been no subsequent investigation of this phenomenon in the 20 years since these results were published.

Ploidy level is intimately associated with the reproductive system of species in the maize genepools. In *Tripsacum* species, all of the diploids are sexual, while the polyploids exhibit facultative diplosporic, pseudogamous apomixis. This signifies a complete breakdown of meiosis in the embryo sac and the development of embryos that are genetically identical to the maternal plant. Endosperm development does require fertilization by a reduced or unreduced sperm cell. Male meiosis is also disrupted, resulting in 25% of the pollen grains with variable ploidy (Farquharson 1955; Burson et al. 1990; Leblanc et al. 1995). Despite this dysfunction, sexual offspring are produced on rare occasions by the apomictic polyploids (Grimanelli et al. 2003). This low level of sexual reproduction allows for gene flow among diploid and polyploid species in areas of sympatry. This could account for the complex pattern of overlapping and highly variable morphology seen in the centers of species diversity in Mexico and Guatemala (Randolph 1970; Li et al. 1999; Springer and Dewald 2004).

An interesting case that illustrates the commonality of the *Zea* and *Tripsacum* genomes, as well as the complexities and consequences of the reproductive biology in the group, is the species *T. andersonii* J.R. Gray, a natural *Tripsacum* x *Zea* hybrid (Talbert et al. 1990; Larson and Doebley 1994; Berthaud et al. 1997). Diploid *Zea luxurians* was identified as the *Zea* parent, while triploid *T. latifolium* (2n = 3x = 54), the result of a hybridization between *T. latifolium* Hitchc. (2x) and

T. maizar Hern.-Xol. and Randolph (2x), is proposed to be the *Tripsacum* parent (Berthaud et al. 1997). *T. andersonii*, commonly known as Guatemala grass, with its abundant vegetative growth, has become a global forage success story (see Sect. 1.3).

1.2.2 Distribution/Habitat/Abundance

The center of diversity for both *Zea* and *Tripsacum* is Mexico and Guatemala. Excluding the global distribution of maize, the main difference between the ranges of the two genera is that *Tripsacum* is much more widespread than *Zea* (teosintes) (see maps Figs. 1.4 and 1.5). *Tripsacum* species are distributed from the central and eastern USA to Paraguay, growing from sea level to nearly 2,700 m in tropical and subtropical forests, savannas, grasslands, dry scrubland, and temperate forests. The only cold-tolerant taxon in the maize genepool is *Tripsacum dactyloides*, which allowed it to expand its range to most of the central and eastern parts of the continental USA, as the glaciers receded. The distribution of the teosintes is restricted to central Mexico, with scattered sites in Central America and a few sites in northern Mexico (Fig. 1.5). In Mexico, the distribution of the teosintes has been described in detail (Wellhausen et al. 1952; Sánchez-González and Ordaz 1987; Wilkes 1967; Taba 1995; Sánchez-González and Ruiz-Corral 1996), and most of

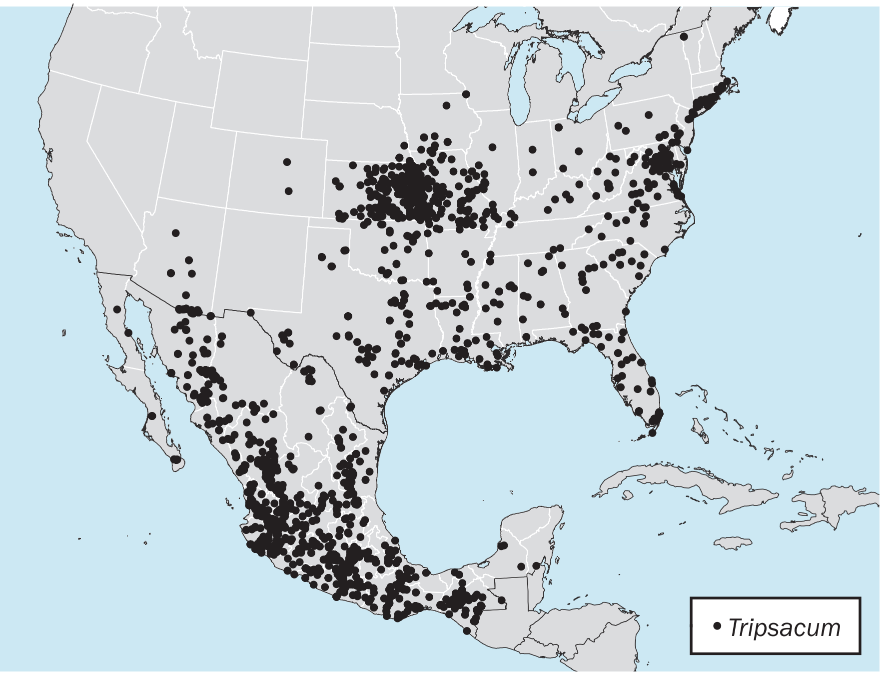

Fig. 1.4 Map of center of diversity and widespread distribution for *Tripsacum* L. in North America

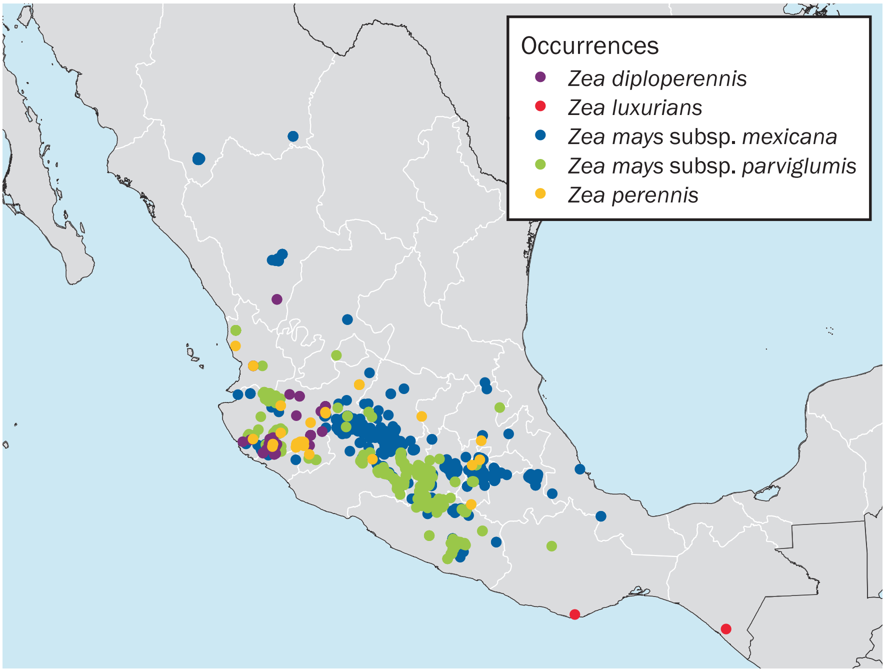

Fig. 1.5 *Zea* L. center of diversity and widespread distribution map in North America

the information regarding several species of teosinte has been updated by Sánchez-González et al. (1998). It was estimated that about 20% of teosinte populations remain uncollected in their potential areas of distribution. Despite this lack of information, teosinte has been monitored more or less regularly, and the reported distribution is considered to be accurate (Sánchez-González and Ordaz 1987; Sánchez-González et al. 1998).

The genus *Zea* includes cultivated maize (*Z. mays* spp. *mays*) and its closest wild relatives, the teosintes (spp. *parviglumis* and spp. *mexicana*, both present in Mexico in the mesic low and middle altitude of southwestern Mexico and across the cooler high elevations of the Mexican Central Plateau, respectively (Fig. 1.5), and spp. *huehuetenangensis*, found only in western Guatemala). Additionally, the genus also includes the species *Z. diploperennis* (diploid) and *Z. perennis* (tetraploid) both perennial and narrowly distributed along the mountain slopes of western Mexico. Finally, *Z. luxurians* and *Z. nicaraguensis* Iltis & Benz, annual, flood-tolerant species, are present in southeastern Guatemala and the Pacific Coast of Nicaragua (Iltis and Doebley 1980; Doebley and Iltis 1980).

The genus *Tripsacum* (L.) has its center of diversity in Mexico and Guatemala and is widely distributed in Mexico and the USA; however, the species-level classification is not always reliable due to weaknesses in the current taxonomy, based entirely on morphology. For this reason individual species are not indicated in the *Tripsacum* distribution map (Fig. 1.4). A fairly recent survey (1989–1992) described three groups of *Tripsacum* species in Mexico, organized by geography (Berthaud et al. 1995, 1997). A more recent review of the genus (Blakey et al. 2007) summarizes the current state of the taxonomy. A modern monographic treatment of the genus is critically needed.

1.2.3 Utilization

1.2.3.1 Breeding and the Relative Importance of CWR (Use to Date, Valuation)

The use of CWR for plant improvement has a variable record of success, depending on the species and biological barriers. This notably includes maize, and the high levels of genetic diversity known to exist in the wild relatives have been essentially untapped for the improvement of elite maize germplasm. While studies indicate that useful genetic variation in wild species can be introgressed and expressed in a maize background, we are unaware of any commercial temperate maize production with wild relative introgressions. Biological challenges in the form of abiotic or biotic stress tolerance or novel applications may increase the need for access to expanded genetic variation, and newer genetic technologies may ease the process of tapping CWR variation for the development of high-performing varieties.

Hybrids between tetraploid perennial teosintes and maize have low fertility and produce few viable kernels. Incompatibility factors can disrupt hybridizations attempted using weedy types of teosinte as female. Three genetic systems conferring cross incompatibility have been described in *Zea*: teosinte crossing barrier1-strong (*Tcb1-s*) found in teosinte and gametophyte factor1-strong (*Ga1-s*) and *Ga2-s* found in maize and teosinte (Evans and Kermicle 2001; Kermicle and Evans 2010).

Teosinte may be a source of alleles for useful agronomic traits; it is often found sympatric with maize and is thus subjected to the same biotic and abiotic stresses. In fact, teosinte may also provide useful alleles for insect resistance, as reviewed by de Lange et al. (2014). A gray leaf spot (GLS) study utilizing a population of more than 900 near-isogenic lines (NILs) derived from multiple teosinte accessions introgressed into a B73 background demonstrated that teosinte is a source of novel disease resistance alleles (Lennon et al. 2016).

Comparative genetic mapping in maize and *Tripsacum* has demonstrated significant conservation of synteny between the two species (Blakey 1993) which is also supported by studies of a translocation of *Tripsacum* sequence onto maize chromosome 2 (Maguire 1962). Studies of *Tripsacum* addition lines of maize (Galinat 1973) demonstrated that *Tripsacum* carried genomic blocks with dominant loci able to complement multiple genetically linked recessive maize mutants. The whole genome duplication (WGD) present in maize (Schnable et al. 2009; Swigonová et al. 2004) occurred before the split of the *Zea* and *Tripsacum* lineages (Bomblies and Doebley 2005; Chia et al. 2012). Fractionation of duplicate genes from the *Zea*-*Tripsacum* WGD has been shown to be ongoing in the maize lineage, with some retained gene copies present in some maize haplotypes but missing from others (Hirsch et al. 2016; Schnable et al. 2016). Therefore, it is likely that homeologous regions in the *Tripsacum* genome may have some degree of reciprocal gene loss events relative to gene loss events in maize and thus contain ancestral maize genes lost from the maize lineage.

Existing genetic and genomic resources for *Tripsacum* have largely been generated as outgroups for molecular evolution studies in maize (as reviewed by Blakey et al. 2007)). As part of Hapmap2, 8x short-read shotgun data was generated from *Tripsacum* (Chia et al. 2012), and additional lower pass genomic data generated for several other *Tripsacum* species (Zhu et al. 2016). Pacific Biosciences (PacBio) long-read sequencing was used to generate a set of full-length transcript sequences from *Tripsacum dactyloides*. Data were generated using RNA isolated from three vegetative tissues to increase the overall fraction of expressed transcripts sampled. The same technology has been employed to generate full-length transcript sequences in maize (Wang et al. 2016), enabling comparisons of transcript isoforms based on full-length reads.

Previous analyses based on short-read data found that syntenic genes are more than twice as likely to exhibit conserved alternative splicing patterns as nonsyntenic genes (Mei et al. 2017a) but that in some cases alternative splicing had diverged between maize homeologs with one copy retaining an ancestral splicing pattern shared with sorghum (Mei et al. 2017b). Using data from orthologous genes in maize, *Tripsacum*, sorghum, setaria, and *Oropetium* genus, a set of genes with uniquely high rates of nonsynonymous substitution in *Tripsacum* was identified. These genes are enriched among other genes which were also targets of selection during the adaption of domesticated maize to temperate climates through artificial selection. A metabolic pathway identified through this method, phospholipid metabolism, has plausible links to cold and freezing tolerance and shows functional divergence between maize and *Tripsacum*.

Resistance to biotic stresses in teosinte has been well documented. De la Paz-Gutiérrez et al. (2010) found teosinte to be more resistant than maize to 66 genera of insects. Nault and Gordon (1982) found *Z. perennis* and *Z. diploperennis* teosintes to be resistant to several important viruses to which all other *Zea* tested were susceptible. In addition, abiotic stress resistance is also easy to find in teosinte. *Z. luxurians*, *Z. nicaraguensis*, and *Z. mays* ssp. *huehuetenangensis* (Iltis and Doebley) Doebley all grow in areas that receive frequent rainfall and have been found to possess unique flooding and waterlogging resistance (Mano et al. 2005; Mano and Omori 2007, 2013, 2015). Examples of successful introgression of maize crop wild relatives were summarized in Smith et al. (2017) and include: (1) resistance to gray leaf spot from *Z. mays* ssp. *mexicana* (Lennon et al. 2016), (2) resistance to a range of pests and diseases (de Lange et al. 2014), (3) resistance to the parasitic weed *Striga* from *Z. diploperennis* (Rich and Ejeta 2008), (4) flooding tolerance potential from *Z. diploperennis* (Mano et al. 2013) and the mapping of a mechanism of protection from waterlogging from chromosome 3 of *Z. nicaraguensis* (Watanabe et al. 2017), and (5) a report from Wang et al. (2008a) that germplasm contributed by teosinte (*Z. mays* ssp. *parviglumis*) was associated with higher yields in maize when evaluated at Jinan and Weifang, China. Reported uses of *Tripsacum* include: (1) resistance to *Striga* (Gurney et al. 2003), to western corn rootworm (Prischmann et al. 2009), and to common rust from *T. dactyloides* (Bergquist 1981) and (2) resistance to northern corn leaf blight from *T. floridanum* Porter ex Vasey (Hooker 1981).

The potential of the genetic diversity stored in wild species banks for use in crop improvement appears to be much greater than previously imagined. Recent increase in the use of wild resources has occurred because of the recognition of the potential utility of CWR for food security and the development of advanced biotechnologies (Honsdorf et al. 2014; Langridge and Fleury 2011). The examples reviewed here and in other studies (Brozynska et al. 2016; Ford-Lloyd et al. 2011; Hajjar and Hodgkin 2007; Maxted and Kell 2009; Zamir 2001) demonstrate that there is a wealth of genetic diversity retained in wild relatives of various crops, much of which remains to be explored. The rapid improvement of biotechnological tools such as diverse omics approaches has resulted in promising advances and no doubt will become routine in plant breeding programs. Advanced biotechnologies, such as genome editing and cisgenesis/intragenesis, are continuously being refined and will accelerate the demand for and use of genetic diversity retained in CWR, contributing to agriculture sustainability.

1.2.3.2 Desirable Characters: From the Perspective of Use

Rapid progress of advanced biotechnologies that can aid in bridging genotype-phenotype associations will facilitate the use of CWR for crop improvement. Thus far, a number of QTL and SNPs associated with agronomically and ecologically important traits have been identified in wild species using linkage analyses, GWAS, and combined analyses of “omics” approaches and linkage mapping.

Teosinte should offer useful functional variation to improve maize traits that are not immediately apparent nor easily measured in a teosinte background, including improved nutritional quality (Melhus 1948; Swarup et al. 1995; Wang et al. 2008b; Flint-Garcia et al. 2009), productivity (Cohen and Galinat 1984; Magoja and Pischedda 1994; Casas Salas et al. 2001; Wang et al. 2008b), and cross-incompatibility factors, some of which are very strong and apparently unique to teosinte (Kermicle 2006; Kermicle and Evans 2010). Useful variation has been identified in teosinte and incorporated into the domesticated gene pool via hybridization and backcrossing and/or selection in a few cases. Research to date supports the further use of teosinte to provide useful phenotypic variation for maize improvement. Despite arguments to the contrary, it is also known that introgression occurs in maize via gene flow from teosinte and is an ongoing process in the center of origin (Warburton et al. 2011; Hufford et al. 2013). In addition, various desirable characteristics have been transferred into maize by substituting three of the maize chromosomes with three chromosomes from *Z. perennis*, which was achieved by creating a BC1F3 generation of maize perennial teosinte BC1F3 (Tang et al. 2005). Important agronomic traits, such as male flowering, kernel number, and kernel weight, analyzed in teosinte NILs resulted in the identification of extreme days to anthesis teosinte alleles and a QTL for kernel number that does not segregate in maize x maize populations (Liu et al.

2016a). It has been repeatedly cautioned that teosinte has been vastly underused for the improvement of maize because the time and uninterrupted effort needed is very high; however, the possibility of eventual discovery of unique and useful alleles is great (Goodman 1998; Goodman et al. 2014).

The use of both wild *Zea* species and exotic maize landraces, the majority of which are adapted to tropical and subtropical growing environments, is rare in breeding programs despite their richer sequence diversity compared to elite temperate maize germplasm. The Germplasm Enhancement of Maize (GEM) project is one systematic and collaborative effort to move useful sequence diversity from exotic germplasm (landraces) to elite temperate maize breeding populations (Salhuana and Pollak 2006). The project has released >300 lines for public use since its inception (http://www.public.iastate.edu/~usda-gem/). Many other projects have also used exotic sources to create populations and incorporate important traits, including drought stress resistance (Meseka et al. 2013), nutritional characteristics (Menkir et al. 2015), cell wall digestibility (Brenner et al. 2012), and aflatoxin accumulation resistance (Warburton et al. 2013). Increased sequence variation in tropical maize may be higher because a second bottleneck occurred when maize moved from Mexico into more northern climates in the USA and also because gene flow between tropical maize and sympatric teosinte continues to bring in new variation from maize CWR (Warburton et al. 2011; Hufford et al. 2013). Appropriate tropical maize germplasm could be used as a bridge between temperate breeding pools and maize CWR.

Researchers have suggested methods to introgress useful traits from teosinte into maize breeding pools, including sequential backcrossing (Casas Salas et al. 2001), joint multiple population analysis, GWAS, and GS via high throughput sequencing and genotyping technologies (Sood et al. 2014; Baute et al. 2015). Generating large-scale genomic information from cereal CWR is now much more economical than ever, and much progress has already been made in sequencing and resequencing CWR to date, including studies published by Brozynska et al. (2016). Using sequence information to guide introgression for genomic regions known to be associated with useful traits will improve the efficiency of this process, while minimizing linkage drag from outside of genomic regions of interest. This process must minimize perturbing favorable linkage blocks in established heterotic patterns and the yield potential of the resulting backcrossed progeny.

Maize wild relatives can be used less directly to tap the allelic diversity necessary to incorporate new traits. If a beneficial allele can be found in an exotic source such as landraces or wild species, the sequence information itself may be sufficient to seek and identify the same allele in a more elite maize line and introgress it into the elite breeding pool via marker-assisted backcrossing, thus reducing potential genetic drag from wide crosses of unadapted germplasm or those with poor agronomics. Alternatively, if this sequence diversity does not exist in elite maize breeding pools, it may be possible to use the information from exotic sources to guide improvement in the elite temperate genome. Once a precise genomic region is identified via genetic mapping or other "omic" studies of landraces or wild species, the causal mutation defining the beneficial allele from the exotic source can be characterized. If the sequence change is small, this information can be used to improve elite breeding lines via genome editing. The resulting improved line may be more acceptable to large private companies who must control the intellectual property rights associated with the line.

Combining phenotyping of a large maize-teosinte introgression population and high-density SNP genotyping could enhance our ability to understand the genetic basis underlying morphological changes during maize domestication. Results from different studies show that the maize-teosinte NIL population is very useful for mapping genes and subsequent fine-mapping, as well as for introducing unique alleles into the maize gene pool. Elucidating the genetic architecture of various agronomic and domestication traits is essential to the positional cloning of important genes and to providing resources for improving the yield potential of maize.

1.2.3.3 Challenges to Increased Use

Notwithstanding new techniques to edit and engineer genes and genomes, one economical and efficient solution for the need for new sequence variation to continue to improve crop species is to tap existing sequence variation that often already exists in expanded gene pools represented in the CWR collections (Michael and Van Buren 2015; Brozynska et al. 2016) and allow new diversity to evolve under natural settings (Meilleur and Hodgkin 2004).

Several biological challenges impede more frequent use of wild *Zea* species or *Z. mays* landraces in elite temperate maize breeding. These include photoperiod sensitivity; division of tropical and temperate maize in their adaptation, and the fact that most landraces and all CRW are tropical; carefully balanced heterotic patterns into which most elite maize is assigned, and which introgression of exotic germplasm would disturb; and the very high yield demanded by growers, which is generally suppressed for a necessary number of generations by genetic drag during introgression. Introgression of a few genes, with a quick return to the background of the recurrent parent, avoids the problems associated with a complete mixing. However, since most agronomically important traits are under the control of many genes, this may not be a viable breeding option unless a few QTLs or genes have a large effect on the phenotype.

Maize breeders and plant breeders in general are often reluctant to introduce sources of exotic germplasm into their programs since many deleterious alleles may be introduced as well as a few valuable alleles. Initial screening of the aforementioned NIL population, in which exotic alleles are introgressed into an adapted background (Liu et al. 2016b), can identify useful exotic alleles in a genetic background that can be more easily incorporated into breeding programs. For many, if not most traits, the use of alleles from teosinte may not ultimately be necessary since sufficient allelic resources exist within cultivated maize, a famously diverse crop (Buckler et al. 2006).

The creation of genetic resources, and efforts to characterize and move traits from maize CRW to elite breeding lines, such as the teosinte NILs created by Liu et al. (2016a), ongoing work by the CIMMYT Seeds of Discovery program, the teosinte GWAS studies being run by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), and efforts to conserve the CWR and other valuable maize germplasm should be well supported as a public good in order to contribute to mainstream breeding and sustainable production.

Domestication greatly reduced genetic diversity in modern maize compared with teosinte, a reduction that may ultimately limit maize productivity. It is nearly impossible to directly identify traits in teosinte that may be used for maize improvement because of extreme maladaptiveness of teosinte in temperate trials. The identification of useful variation from teosinte can also be slowed by a lack of genetic resources available to support the study of variation, particularly for quantitative traits that cannot be estimated for breeding purposes in a teosinte background (including most yield, ear, kernel, and plant morphology traits). However, the recent release of 928 near-isogenic introgression lines (NILs) from 10 *Z. mays* ssp. *parviglumis* accessions in a B73 background provides an opportunity to measure the phenotypic effect of teosinte sequence variation on cultivated maize (Liu et al. 2016a) and complements older teosinte-maize introgression resources (Briggs et al. 2007). Linkage analysis of the newest NILs have already identified positive alleles from teosinte on traits including male flowering time, number of kernel rows, and 50-kernel weight in maize (Liu et al. 2016b). With the NILs, the gap between teosinte and maize is narrowed, and it becomes feasible for modern corn breeders to identify and use alleles that were lost during domestication.

Particularly for traits where sufficient sequence variation does not exist in the domesticated gene pool, investment in the identification and transfer of new sequence variation from CWR is long overdue. The consequence of a narrow genetic base in maize has been tragically demonstrated in the past. The genetic base of commercial maize is believed to have become much narrower as heterotic patterns have been refined over the past 45 years, which may increase vulnerability to new epidemics and yield loss. Use of genome selection and focused haplotype identification is driving further loss of genetic diversity. Combined with changing weather patterns and less predictable maize growing environments, the potential cost of loss due to increased genetic vulnerability is much larger than the cost of investment in reducing genetic vulnerability.

1.3 Wild Utilized Species (Uses Other than for Maize Improvement: Forage)

1.3.1 What Are They and Where and How Are They Used

T. dactyloides, or eastern gamagrass, has been used for forage and fodder in the USA, where it has earned several endearing nicknames, such as, “queen of forages,” “Cadillac of forages,” and “ice cream grass,” due to its high palatability and digestibility (Blakey et al. 2007). Throughout the tropics, a type of *Tripsacum*, often called “Guatemala grass,” has been used to feed livestock in various forms – pasture, hay, silage, and green “cut and carry” fodder – often in former British colonies. There is considerable confusion about the species name(s) for this germplasm. Even on the Food and Agriculture Organization (FAO) website (http://www.fao.org), the information for *T. andersonii* and *T. laxum* Nash is identical, “…since both names are used.”

Both *T. floridanum* and *T. dactyloides* are used in xeriscaping in South Florida, where both taxa are still found in natural populations. In its center of origin and diversity in Mexico and Guatemala, 12 out of the 15–16 taxa in the genus *Tripsacum* are found, but as of yet, there has been no significant development of the forage potential of these grasses in the region.

1.3.2 Distribution and Habitat

In the USA, *T. dactyloides* can be found growing in small colonies covering a region from Connecticut west to Nebraska and across the south from Texas to Florida (see Fig. 1.4). Moist areas, such as streambanks and floodplains, are common habitats where *T. dactyloides* occurs in multiple ploidy levels within the same area, although the diploid form is found primarily in prairie habitats west of the Mississippi River, due to its greater drought tolerance (de Wet et al. 1982, 1985).

1.3.3 Potential for Expanded Use

Tripsacum species, primarily *dactyloides* and *andersonii/laxum*, are cited as having many strengths, such as high forage quality and yield potential and tolerance to both poor drainage and drought, but also some key limitations, including difficulties in establishment, susceptibility to continuous grazing, and low seed production. Good management practices, such as frequent cuttings, are strongly recommended [see Fact Sheets at http://www.tropicalforages.info; Heuzé et al. 2015]. As the agronomic potential of *Tripsacum* is starting to be realized through its increasing use for pasture, forage, and soil erosion control throughout the world (Springer and Dewald 2004), continued improvement and development of the genus is predicated upon a strong commitment to the preservation of natural populations and the development of germplasm resources.

1.4 Conservation Status of CWR and WUS

1.4.1 In Situ

Currently, there is no a national strategy for in situ conservation of wild relatives of maize in either Mexico or Guatemala. Most of the efforts have been concentrated on ex situ conservation and primarily for teosinte. The lack of in situ conservation poses a risk to the wild genetic resources of maize and limits their potential utilization in breeding programs. Occasionally, teosinte will be enclosed in a natural protected area; however it is not for a specific protection goal as these areas are targeting other species. Figure 1.6 indicates *Zea* populations located within protected areas (Fig. 1.7).

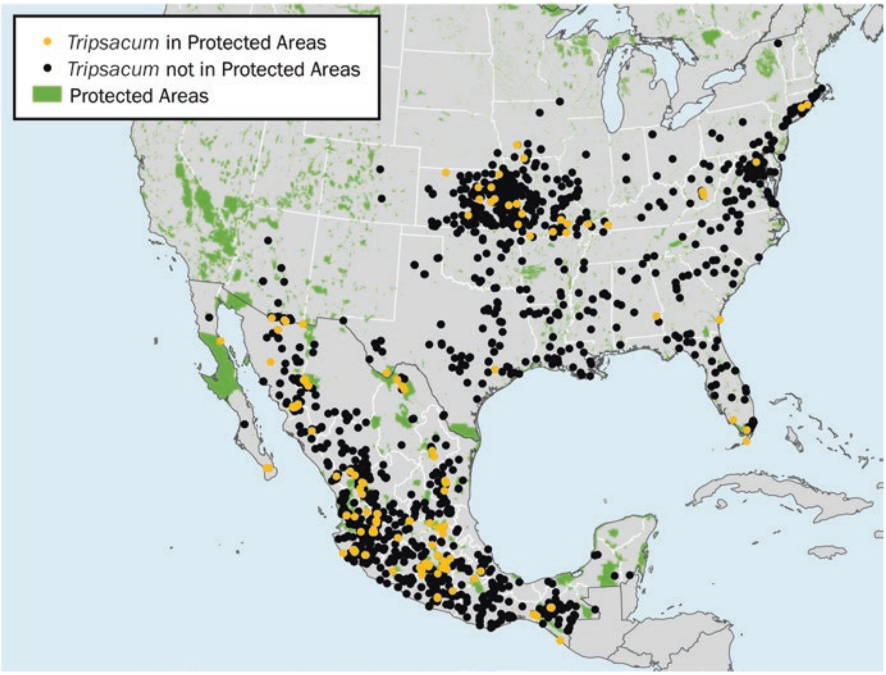

Fig. 1.6 *Tripsacum* L. distribution map for in situ conservation status in North America. All *Tripsacum* individuals located inside and outside protected natural areas are shown

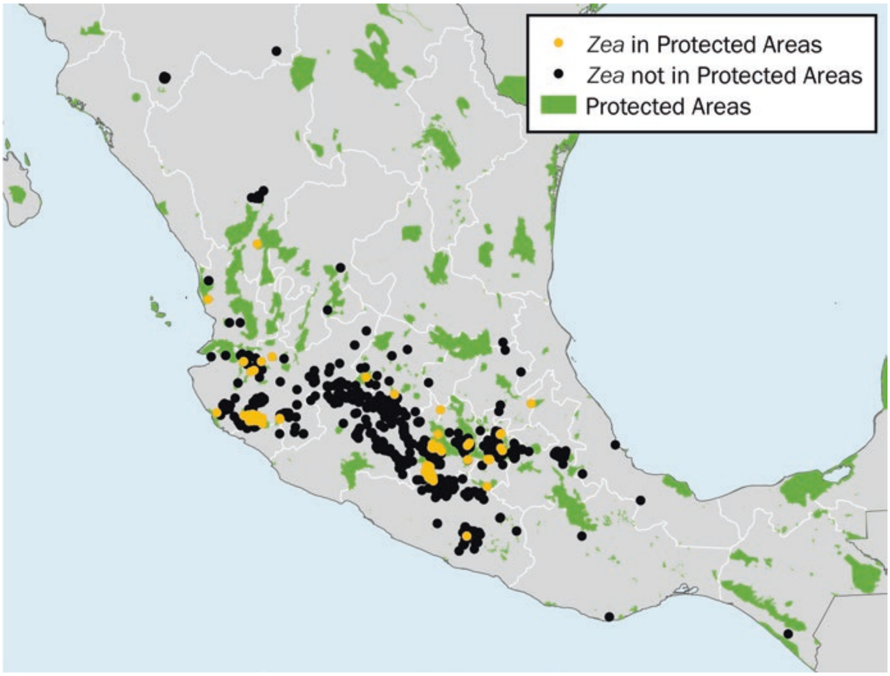

Fig. 1.7 *Zea* L. distribution map for in situ conservation status in North America. All *Zea* individuals located inside and outside protected natural areas are shown

Table 1.1 Teosinte germplasm collections in North America. Numbers of accessions reported in GRIN-Global for USDA and CIMMYT collections (November 2017). Data for the University of Guadalajara collection provided by D. J.J. Sanchez (November 2017); data for INIFAP provided by Dr. G. Esquivel-Esquivel (November 2017)

Species/subspecies	University of Guadalajara	INIFAP	CIMMYT	USDA	All
Zea mays ssp. *mexicana* (Schrad.) H. H. Iltis and Doebley	291	283	111	253	938
Z. mays ssp. *huehuetenangenis* (Iltis and Doebley) Doebley	197	198	84	130	609
Z. mays ssp. *huehuetenangensis* (Iltis and Doebley) Doebley			1	7	8
Z. diploperennis Iltis, Doebley and Guzman	14	7	3	13	37
Z. perennis (Hitchc.) Reeves and Manglesdorf	7	4	2	10	23
Z. luxurians (Durieu and Asch.) R. M. Bird	2		1	20	23
Z. nicaraguensis Iltis and Benz			12	1	13
Unknown		5	58		63
Total accessions	511	497	272	434	1714

1.4.2 Ex Situ

1.4.2.1 Status (Genebank Coverage and Gaps)

Only four genebanks in the world hold significant germplasm collections of the teosintes (*Z.* spp. other than maize), and three of them are located in Mexico (Table 1.1). The total number of reported accessions is 1349, but there is much redundancy across these collections. Other than the two Mexican subspecies of *Z. mays*, most taxa number very few collections, partly because their natural distributions are restricted. Only the collections held at CIMMYT and USDA are freely accessible to the public. Tripsacum germplasm is generally maintained as field-grown live plants. Only four collections are known: CIMMYT, USDA (Woodward, OK, and Miami, FL), and Instituto Nacional de Investigaciones Forestales y AgroPecuarias (INIFAP [Verdineño Station, Nayarit, Mexico]). The USDA genebank maintains a small number of *Tripsacum* accessions as seeds.

1.4.2.2 Current Activities (Exploration, Regeneration, Others)

CIMMYT is due to begin construction of a screen house dedicated to teosinte seed regeneration in winter 2018. This facility will be built in the same experimental station where the *Tripsacum* live collection is maintained. It is hoped that consolidation of these CWR conservation activities in one site will bring about increased efficiencies and effectiveness and attract other institutions interested in regeneration of their collections, in a site where controlled pollinations are assured. The USDA regenerates a limited number of accessions each year in greenhouse conditions, due to plant photoperiod and adaptation needs.

1.4.3 Suggestions on Ways to Improve Conservation

There is a need to identify those geographies where native populations are at greatest risk. Collection for ex situ conservation and in situ conservation of prioritized CWR could be intensively focused in the geographic regions harboring the greatest richness of taxa (Castañeda-Álvarez et al. 2016). Instead of focusing on a single beneficial trait, the overall genetic provenance and adaptive value in each CWR species should also be taken into account to prioritize CWR and guide efficient and effective conservation strategies. Knowledge of the conservation status (in situ and ex situ) of CWR and use of geographic and ecological variation metrics as a proxy for gap analysis modeling can maximize the efficiency of conservation actions. Global initiatives (Dempewolf et al. 2014; Vincent et al. 2013) have increased CWR conservation efforts and should be complemented by regional and national actions (Meilleur and Hodgkin 2004). Collaborations between local institutions or organizations can help to build agreements for effective in situ or ex situ conservation and foster sharing of wild resources. International CWR exchanges and/or introductions could also greatly benefit the extensive conservation and utilization of CWR.

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References

Alene AD, Menkir A, Ajala SO, Badu-Apraku B, Olanrewaju AS, Manyong VM, Ndiaye A (2009) The economic and poverty impacts of maize research in West and Central Africa. Ag Econ 40:535–550

Allaby RG (2014) Domestication syndrome in plants. In: Smith C (ed) Encyclopedia of global archeology. Springer, New York, pp 2182–2184

Anon (2016) Maize Phase II, CGIAR-Research Program on Maize. Maize Agri-Food systems Proposal 2017–2022. CGIAR, Montpellier. https://library.cgiar.org/bitstream/handle/10947/4403/2.%20MAIZE%20AFS-CRP%20and%20FP%20Narratives%20Proposal%202017-2022%20(July%2030,%202016).pdf?sequence=1

Arnason JT, Baum B, Gale J, Lambert JDH, Bergvinson D, Philogene BJR, Serratos JA, Mihm J, Jewell DC (1994) Variation in resistance of Mexican landraces of maize to maize weevil Sitophilus zeamais, in relation to taxonomic and biochemical parameters. Euphytica 74:227–236

Bajet NB, Renfro BL, Valdez Carrasco JM (1994) Control of tar spot of maize and its effect on yield. Int J Pest Manag 40:121–125

Baute GJ, Dempewolf H, Rieseberg LH (2015) Using genomic approaches to unlock the potential of CWR for crop adaptation to climate change. In: Redden R, Yadav SS, Maxted N, Dulloo ME, Guarino L, Smith P (eds) Crop wild relatives and climate change. Wiley, Hoboken, pp 268–280. https://doi.org/10.1002/9781118854396.ch15

Beadle GW (1972) The mystery of maize. Field Mus Nat Hist Bull 43:2–11

Beadle GW (1980) The ancestry of corn. Sci Am 242:112–119

Ben-Ari T, Makowski D (2014) Decomposing global crop yield variability. Environ Res Lett 9(2014):114011 (10pp). https://doi.org/10.1088/1748-9326/9/11/114011

Benz BF (2001) Archeological evidence of teosinte domestication from Guilá Naquitz, Oaxaca. Proc Natl Acad Sci U S A 98:2101–2103

Benz BF, Iltis H (1990) Studies in archeological maize I: the “wild” maize from San Marcos cave reexamined. Am Antiq 55(3):500–511

Benz BF, Long A (2000) Prehistoric maize evolution in the Tehuacan valley. Curr Antropol 41:459–465

Berg P, Singer M (2003) George beadle: an uncommon farmer. The emergence of genetics in the 20th century. Cold Springs Harbor Laboratory Press, Cold Spring Harbor

Bergquist RR (1981) Transfer from *Tripsacum dactyloides* to corn of a major gene locus conditioning resistance to Puccinia sorghi. Phytopathology 71:518–520

Berthaud J, Savidan Y, Barre M, Leblanc O (1995) *Tripsacum*: its diversity and conservation. In: Taba S (ed) Maize genetic resources. Maize Program special report. CIMMYT, Mexico, D.F., pp 74–85

Berthaud J, Savidan Y, Barre M, Leblanc O (1997) Tripsacum. In: Fucillo D, Sears L, Stapleton P (eds) Biodiversity in trust. Cambridge University Press, Cambridge, UK

Biemont C, Vierira C (2006) Junk DNA as an evolutionary force. Nature 443:521–524

Blakey CA (1993) A molecular map in *Tripsacum dactyloides*, Eastern Gamagrass. University of Missouri, Missouri, Columbia

Blakey C, Costich D, Sokolov V, Islam-Faridi M (2007) *Tripsacum* genetics: from observations along a river to molecular genomics. Maydica 52:81–99

Bomblies K, Doebley JF (2005) Molecular evolution of floricaula/leafy orthologs in the andropogoneae (poaceae). Mol Biol Evol 22:1082–1094

Bonzani RM, Oyuela-Caycedo A (2006) The gift of the variation and dispersion of maize: social and technological context in Amerindian societies. In: Staller JE, Tykot RH, Benz BF (eds) Histories of maize. Academic, Burlington, pp 344–356

Boyer CD, Shannon JC (1987) Carbohydrates of the kernel. In: Watson SA, Ramstad PE (eds) Corn: chemistry and technology. American Association of Cereal Chemists, St. Paul, pp 253–272

Brenner EA, Blanco M, Gardner C, Lübberstedt T (2012) Genotypic and phenotypic characterization of isogenic doubled haploid exotic introgression lines in maize. Mol Breed 30:1001–1016. https://doi.org/10.1007/s11032-011-9684-5

Briggs WH, McMullen MD, Gaut BS, Doebley J (2007) Linkage mapping of domestication loci in a large maize teosinte backcross resource. Genetics 177:1915–1928. https://doi.org/10.1534/genetics.107.076497

Brown WL, Goodman MM (1977) Races of corn. In: Sprague GF (ed) Corn and corn improvement, Chapter 2. American Society of Agronomy, Madison, pp 49–88

Brozynska M, Furtado A, Henry RJ (2016) Genomics of crop wild relatives: expanding the gene pool for crop improvement. Plant Biotechnol J 14:1070–1085. https://doi.org/10.1111/pbi.12454

Buckler ES, Stevens NM (2005) Maize origins, domestication and selection. In: Motley TJ, Zerega N, Cross HB (eds) Darwin’s Harvest. New approaches to the origins, evolution, and conservation of crops. Columbia University Press, New York, pp 67–90

Buckler ES, Gaut BS, McMullen MD (2006) Molecular and functional diversity of maize. Curr Opin Plant Biol 9:172–176. https://doi.org/10.1016/j.pbi.2006.01.013

Burson BL, Voigt PW, Sherman RA, Dewald CL (1990) Apomixis and sexuality in Eastern Gamagrass. Crop Sci 30:86–89

Cabanas D, Watanabe S, Higashi CHV, Bressan A (2013) Dissecting the mode of Maize chlorotic virus (*Tombusviridae*: *Machlomovirus*) transmission by *Frankliniella williamsi* (*Thysanoptera*: *Thripidae*). J Econ Entomol 106:16–24. https://doi.org/10.1603/EC12056

Cairns J, Crossa J, Zaidi PH, Grudloyma P, Sanchez C, Araus JJ, Thaitad S, Makumbi D, Magorokosho C, Banziger M, Menkir A, Hearne S, Atlin GN (2013) Identification of drought, heat, and combined drought and heat tolerant donors in maize. Crop Sci 53:1335–1346

Casas Salas JF, Sánchez Gonzalez JJ, Ramírez Díaz JLD, Ron Parra J, Montes Hernandez S (2001) Rendimiento y sus componentes en retrocruzas maíz-teocintle. Rev Fitotec Mex 24(1):17–26

Cassman KG, Dobermann A, Walters DT, Yang HS (2003) Meeting cereal demand while protecting natural resources and improving environmental quality. Annu Rev Environ Resour 28:315–358. https://doi.org/10.1146/annurev.energy.28.040202.122858

Castañeda-Álvarez NP, Khoury CK, Achicanoy HA, Bernau V, Dempewolf H, Eastwood RJ, Guarino L, Harker RH, Jarvis A, Maxted N, Müller JV, Ramirez-Villegas J, Sosa CS, Struik PC, Vincent H, Toll J (2016) Global conservation priorities for crop wild relatives. Nat Plants 2:16022

Chia JM, Song C, Bradbury PJ, Costich D, de Leon N, Doebley J, Elshire RJ, Gaut B, Geller L, Glaubitz JC et al (2012) Maize hapmap2 identifies extant variation from a genome in flux. Nat Genet 44:803–807

Cohen JI, Galinat WC (1984) Potential use of alien germplasm for maize improvement. Crop Sci 24:1011–1015

Cordell LS, McBrinn ME (2012) Archeology of the southwest. Academic, San Diego

da Fonseca RR, Smith BD, Wales N, Cappellini E, Skoglund P, Fumagalli M, Samaniego JA, Carøe C, Ávila-Arcos MC, Hufnagel DE, Korneliussen TS, Vieira FG, Jakobsson M, Arriaza B, Willerslev E, Nielsen R, Hufford MB, Albrechtsen A, Ross-Ibarra J, Gilbert MTP (2015) The origin and evolution of maize in the southwestern United States. Nat Plants. https://doi.org/10.1038/NPLANTS2014.3

De la Paz-Gutiérrez S, Sánchez-González JJ, Ruíz-Corral JA (2010) Diversidad de especies insectiles en maíz y teocintle en México. Folia Entomol Mex 48:103–118

De Lange E, Balmer D, Mauch-Mani B, Turlings TCJ (2014) Insect and pathogen attack and resistance in maize and its wild ancestors, the teosintes. New Phytol 204:329–341

De Wet JMJ, Harlan JR, Brink D (1982) Systematics of *Tripsacum dactyloides* (Gramineae). Am J Bot 69:1251–1257

De Wet JMJ, Cohen CE, Brink D (1985) Seed proteins and systematics of *Tripsacum*. Biochem Syst Ecol 13:231–237

Dempewolf H, Eastwood RJ, Guarino L, Khoury CK, Müller JV, Toll J (2014) Adapting agriculture to climate change: a global initiative to collect, conserve, and use crop wild relatives. Agroecol Sustain Food Syst 38:369–377

Doebley JF (1983) The taxonomy and evolution of Tripsacum and teosinte, the closest relatives of maize. In: Gordon DT, Knoke JK, Naul LR (eds), Proc Intl Maize Virus Disease Colloquium and Workshop, the Ohio State University, Ohio Agricultural Research and Development Center, Wooster, Ohio. August 1982. Ohio State University, p. 15–28

Doebley J (1990a) Molecular systematics of *Zea* (Gramineae). Maydica 35:143–150

Doebley J (1990b) Molecular evidence for gene flow among *Zea* species. Bioscience 40(6):443–448

Doebley J (2001) George Beadle's other hypothesis: one-gene, one-trait. Genetics 158:487–493

Doebley J (2004) The genetics of maize evolution. Ann Rev Genet 38:37–59

Doebley J, Iltis HH (1980) Taxonomy of *Zea* (Gramineae). I. A subgeneric classification with key to taxa. Am J Bot 67:982–993

Doebley J, Goodman M, Stuber CW (1987) Patterns of isozyme variation between maize and Mexican annual teosinte. Econ Bot 41(2):234–246

Doebley J, Stec A, Hubbard L (1997) The evolution of apical dominance in maize. Nature 386:4856–4488

Dubreuil P, Warburton ML, Chastanet M, Hoisington D, Charcosset A (2006) More on the introduction of temperate maize into Europe: large-scale bulk SSR genotyping and new historical elements. Maydica 51:281–291

Duvick DN (1977) Genetic rates of gain in hybrid maize yields during the past 40 years. Maydica 22:187–196

Duvick DN (2005) Genetic progress in yield of United States maize (*Zea mays* L.). Maydica 50:193–202

Duvick DN, Cassman KG (1999) Post–Green revolution trends in yield potential of temperate maize in the North-Central United States (1999). Agronomy & Horticulture – Faculty Publications. Paper 96. http://digitalcommons.unl.edu/agronomyfacpub/96

Evans MMS, Kermicle JL (2001) *Teosinte crossing barrier1*, a locus governing hybridization of teosinte with maize. Theor Appl Genet 103:259–265. https://doi.org/10.1007/s001220100549

FAOSTAT (2014) Statistics database. Food and agriculture Organization of the United. Nations, Rome. http://faostat.fao.org

Farnham DE, Benson GO, Pearce RB (2003) Corn perspective and culture. In: White P, Johnson LA (eds) Corn: chemistry and technology, 2nd edn. American Association of Cereal Chemists International, St. Paul, pp 1–33

Farquharson LI (1955) Apomixis and polyembryony in *Tripsacum dactyloides*. Am J Bot 42:737–743

Flint-Garcia SA, Bodnar AL, Scott MP (2009) Wide variability in kernel composition, seed characteristics, and zein profiles among diverse maize inbreds, landraces, and teosinte. Theor Appl Genet 119:1129–1142. https://doi.org/10.1007/s00122-009-1115-1

Ford-Lloyd BV, Schmidt M, Armstrong SJ, Barazani O, Engels J, Hadas R, Maxted N (2011) Crop wild relatives-undervalued, underutilized and under threat? Bioscience 61:559–565

Fowler C (2006) The New York Times Upfront

Galinat WC (1973) Intergenomic mapping of maize, teosinte and tripsacum. Evolution 27:644–655

Gannon B, Kaliwile C, Arscott SA, Schmaelzle S, Chileshe J, Kalungwana N, Mosonda M, Pixley K, Masi C, Tanumihardjo SA (2014) Biofortified orange maize is as efficacious as a vitamin A supplement in Zambian children even in the presence of high liver reserves of vitamin A: a community-based, randomized placebo-controlled trial. Am J Clin Nutr 100(6):1541–1550

Giuliano G (2017) Provitamin A biofortification of crop plants: a gold rush with many miners. Curr Opin Biotechnol 44:169–180. https://doi.org/10.1016/j.copbio.2017.02.00

Goldberg KB, Brakke MK (1987) Concentration of maize chlorotic mottle virus increased in mixed infections with maize dwarf mosaic virus, strain-B. Phytopathology 77:162–167. https://doi.org/10.1094/Phyto-77-162

Goodman MM (1978) A brief survey of the races of maize and current attempts to infer their racial relationships, Chapter 10. In: Walden DB (ed) Maize breeding and genetics. Wiley, New York, pp 143–158

Goodman MM (1998) Research policies thwart potential payoff of exotic germplasm. Diversity (Basel) 14:30–35

Goodman MM, Holland JB, Sanchez Gonzalez JJ (2014) Breeding and diversity. In: Wusirika RM, Lai BJ, Kole C (eds) Genetics, genomics and breeding of maize. CRC Press, New York, pp 14–50

Gouesnard B, Rebourg C, Welcker C, Charcosset A (2002) Analysis of photoperiod sensitivity within a collection of tropical maize populations. Genet Resour Crop Evol 49:471–481

Gowda M, Das B, Makumbi D, Babu R, Semagn K, Mahuku G, Olsen MS, Bright JM, Beyene Y, Prasanna BM (2015) Genome-wide association and genomic prediction of resistance to maize lethal necrosis disease in tropical maize germplasm. Theor Appl Genet 128:1957–1968

GPWG [Grass Phylogeny Working Group] (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). Ann Mo Bot Garden 88:373–457

Grams GW, Blessin CW, Inglett GE (1970) Distribution of tocopherols within the corn kernel. J Am Oil Chem Soc 47:337–339

Grassini P, Eskridge KM, Cassman KG (2013) Distinguishing between yield advances and yield plateaus in historical crop production trends. Nat Commun. https://doi.org/10.1038/ncomms3918

Grimanelli D, Garcia M, Kaszas E, Perotti E, Leblanc O (2003) Heterochronic expression of sexual reproductive programs during apomictic development in Tripsacum. Genetics 165:1521–1531

Gropper SS, Smith JL, Groff JL (2005) Perspective: phytochemicals and herbal supplements in health and disease. In: Howe E, Feldman E, Harkrader S, Roybal M (eds) Advanced nutrition and human metabolism, 4th edn. Thomson Wadsworth, Belmont, pp 123–127

Gurney AL, Grimanelli D, Kanampiu F, Hoisington D, Scholes JD, Press MC (2003) Novel sources of resistance to Striga hermonthica in *Tripsacum dactyloides*, a wild relative of maize. New Phytol 160:557–568

Hajjar R, Hodgkin T (2007) The use of wild relatives in crop improvement: a survey of developments over the last 20 years. Euphytica 156:1–13

Harjes CE, Rocheford TR, Bai L, Brutnell TP, Kandianis CB, Sowinski SG, Stapleton AE, Vallabhaneni R, Williams M, Wurtzel ET, Yan J, Buckler ES (2008) Natural genetic variation in lycopene epsilon cyclase tapped for maize biofortification. Science 319:330–333

Harlan JR, de Wet J (1971) Toward a rational classification of cultivated plants. Taxon 20(4):509–517

Hart JP, Means BK (2002) Maize and Villages: a summary and critical assessment of current northeast early late prehistoric evidence, Chapter18. In: Hart JP, Reith CB (eds) Northeast subsistence-settlement change: AD 700–1300. University of the State of New York, The State Education Department, Albany, pp 345–358

Hengsdijk H, Langeveld JWA (2009) Yield trends and yield gap analysis of major crops in the world. Werkdocument 170. Statutory Research Tasks Unit for Nature and the Environment, Wageningen, 170pp

Heuzé V, Tran G, Nozière P, Salgado P, Lebas F (2015) Guatemala grass (*Tripsacum andersonii*). Feedipedia, a programme by INRA, CIRAD, AFZ and FAO. https://feedipedia.org/node/365. Last updated on 11 May 2015, 14:30

Hilton H, Gaut BS (1998) Speciation and domestication in maize and its wild relatives: evidence from the Globulin-1 gene. Genetics 150:863–872

Hirsch C, Hirsch CD, Brohammer AB, Bowman MJ, Soifer I, Barad O, Shem-Tov D, Baruch K, Lu F, Hernandez AG, Fields CJ, Wright CL, Koehler K, Springer NM, Buckler E, Buell CR, de Leon N, Kaeppler SM, Childs KL, Mikel M (2016) Draft assembly of elite inbred line ph207 provides insights into genomic and transcriptome diversity in maize. Plant Cell 28:2700

Hock J, Kranz J, Renfro BL (1995) Studies on the epidemiology of the tar spot disease complex of maize in Mexico. Plant Pathol 44:490–502

Honsdorf N, March TJ, Berger B, Tester M, Pillen K (2014) High-throughput phenotyping to detect drought tolerance QTL in wild barley introgression lines. PLoS One 9:e97047

Hooker AL (1981) Resistance to *Helminthosporium turcicum* from *Tripsacum floridanum* incorporated into corn. Maize Genet Coop Newsl 55:87–88

Huckell LW (2006) In: Staller JE, Tykot RH, Benz BF (eds) Histories of maize: multidisciplinary approaches to the prehistory, linguistics, biogeography, domestication, and evolution of maize. Elsevier Academic, Amsterdam, pp 97–107

Hufford M, Bilinski P, Pyhajarvi T, Ross-Ibarra J (2012) Teosinte as a model system for population and ecological genomics. Trends Genet 28(12):606–615

Hufford MB, Lubinksy P, Pyhajarvi T, Devengenzo MT, Ellstrand NC, Ross-Ibarra J (2013) The genomic signature of crop-wild introgression in maize. PLoS Genet 9:e1003477. https://doi.org/10.1371/journal.pgen.1003477. [erratum: 9:10.1371/annotation/2eef7b5b-29b2-412f-8472-8fd7f9bd65ab]

Hung HY, Shannon LM, Tian F, Bradbury PJ, Chen C, Flint-Garcia SA, McMullen MD, Ware D, Buckler ES, Doebley JF, Holland JB (2012) *ZmCCT* and the genetic basis of day-length adaptation underlying the post-domestication spread of maize. Proc Natl Acad Sci U S A. https://doi.org/10.1073/onas.1203189109

Iltis HH, Doebley JF (1980) Taxonomy of *Zea* (Gramineae). II. Subspecific categories in the Zea mays complex and a generic synopsis. Am J Bot 67:994–1004

Janzen GM, Hufford MB (2016) Crop domestication: a sneak-peek into the midpoint of maize evolution. Curr Biol 23:1240–1242. https://doi.org/10.1016/j.cub.2016.10.045

Jensen SG, Wysong DS, Ball EM, Higley PM (1991) Seed transmission of maize chlorotic mottle virus. Plant Dis 75:497–498

Kempton JH (1937) Maize – our heritage from the Indian. (1937) Annual report of the Board of Regents of the Smithsonian Institution, pp 385–408

Kermicle JL (2006) A selfish gene governing pollen-pistil compatibility confers reproductive isolation between maize relatives. Genetics 172:499–506. https://doi.org/10.1534/genetics.105.048645

Kermicle JL, Evans MMS (2010) The *Zea mays* sexual compatibility gene ga2: naturally occurring alleles, their distribution, and role in reproductive isolation. J Hered 101:737–749. https://doi.org/10.1093/jhered/esq090

Kumar H (2002) Resistance in maize to the larger grain borer*, Prostephanus truncates* (Horn) (Coleoptera: Bostrichidae). J Stored Prod Res 38:267–280

Kurilich AC, Juvik JA (1999) Quantification of carotenoid and tocopherol antioxidants in Zea mays. J Agric Food Chem 47:1948–1955

Langridge P, Fleury D (2011) Making the most of ‘omics’ for crop breeding. Trends Biotechnol 29:33–40

Lapierre H, Signoret P-A (eds) (2004) Virus and virus diseases of Poaceae (Gramineae). Technology and engineering, Institut National de la Recherche Agronomique. France, Paris

Larson SR, Doebley J (1994) Restriction site variation in the chloroplast genome of Tripsacum (Poaceae): phylogeny and rates of sequence evolution. Syst Bot 19:21–34

Leblanc O, Peel MD, Carman JG, Savidan Y (1995) Megasporogenesis and megagametogenesis in several Tripsacum species (Poaceae). Am J Bot 82:57–63

Lennon JR, Krakowsky M, Goodman M, Flint-Garcia S, Balint-Kurti PJ (2016) Identification of alleles conferring resistance to gray leaf spot in maize derived from its wild progenitor species teosinte. Crop Sci 56:209–218

Li YG, Dewald CL, Sims PL (1999) Genetic relationships within *Tripsacum* as detected by RAPD variation. Ann Bot 84:695–702

Little EA (2002) Kautantouwit’s legacy: calibrated dates on prehistoric maize in New England. Am Antiq 67:109–118

Liu Z, Cook J, Melia-Hancock S, Guill K, Bottoms C, Garcia A, Ott O, Nelson R, Recker J, Balint-Kurti P, Larsson S, Lepak N, Buckler E, Trimble L, Tracy W, McMullen MD, Flint-Garcia SA (2016a) Expanding maize genetic resources with pre-domestication alleles: maize-teosinte introgression populations. Plant Genome 9. https://doi.org/10.3835/plantgenome2015.07.0053

Liu Z, Garcia A, McMullen MD, Flint-Garcia SA (2016b) Genetic analysis of kernel traits in maize-teosinte introgression populations. G3 (Bethesda) 6:2523–2530. https://doi.org/10.1534/g3.116.030155

Lobell DB, Cassman KG, Field CB (2009) Crop yield gaps: their importance, magnitude and causes. Annu Rev Environ Resour 34:179–204. https://doi.org/10.1146/annurev.environ.041008.093740

Louette D, Smale M (1998) Farmers’ seed selection practices and maize variety characteristics in a traditionally-based Mexican community. CIMMYT Economics working paper no. 98-04. CIMMYT, Mexico, D. F.

Louie R (1999) Diseases caused by viruses. In: White DG (ed) Compendium of corn diseases. APS Press, St. Paul, pp 49–55

Magoja JL, Pischedda G (1994) Maize x teosinte hybridization. In: Bajaj YPS (ed) Biotechnology in agriculture and forestry, vol 25. Springer, Berlin, pp 84–101

Maguire MP (1962) Common loci in corn and tripsacum. J Hered 53:87–88

Mahuku G, Lockhart BE, Wanjala B, Jones MW, Kumunye JN, Stewart LR, Cassone BJ, Sevgan S, Nyasani JO, Kusia E, Kumar PL, Niblett CL, Kiggundu GA, Pappu HR, Wangai A, Prasanna BM, Redinbaugh MG (2015) Maize lethal necrosis (MLN), and emerging threat to maize-based food security in Sub-Saharan Africa. Phytopathology 105(7):956–965. https://doi.org/10.1094/PHYTO-12-14-0367-FI

Mano Y, Omori F (2007) Breeding for flooding tolerant maize using “teosinte” as a germplasm resource. Plant Root 1:17–21. https://doi.org/10.3117/plantroot.1.17

Mano Y, Omori F (2013) Relationship between constitutive root aerenchyma formation and flooding tolerance in *Zea nicaraguensis*. Plant Soil 370:447. https://doi.org/10.1007/s11104-013-1641-0

Mano YY, Omori F (2015) Flooding tolerance in maize (*Zea mays* subsp. *mays*) F1 hybrids containing a QTL introgressed from teosinte (*Zea nicaraguensis*). Euphytica 205:255–267. https://doi.org/10.1007/s10681-015-1449-5

Mano YY, Muraki M, Fujimori M, Takamizo T, Kindiger B (2005) Identification of QTL controlling adventitious root formation during flooding conditions in teosinte (*Zea mays* ssp. *huehuetenangensis*) seedlings. Euphytica 142:33–42. https://doi.org/10.1007/s10681-005-0449-2

Matson RG (1991) The origins of southwestern agriculture. University of Arizona Press, Tucson

Matsuoka Y, Vigouroux Y, Goodman MM, Sanchez GJ, Buckler E, Doebley J (2002) A single domestication for maize shown by multilocus microsatellite genotyping. Proc Natl Acad Sci U S A 99:6080–6084

Maxted N, Kell SP (2009) Establishment of a global network for the in situ conservation of crop wild relatives: status and needs. Food and Agriculture Organization of the United Nations Commission on Genetic Resources for Food and Agriculture, Rome

McCann J (2005) Maize and grace. Harvard University Press, Massachusetts

McClintock B (1956) Controlling elements and the gene. Cold Spring Harb Symp Quant Biol 21:197–216

McClintock B (1984) The significance of responses of the genome to challenge. Science 226:792–801

Mei W, Boatwright JL, Feng G, Schnable JC, Barbazuk WB (2017a) Evolutionarily conserved alternative splicing across monocots. Genetics. https://doi.org/10.1534/genetics.117.300189

Mei W, Liu S, Schnable JC, Yeh CT, Springer NM, Schnable PS, Barbazuk WB (2017b) A comprehensive analysis of alternative splicing in paleopolyploid maize. Front Plant Sci 8:694

Meilleur BA, Hodgkin T (2004) In situ conservation of crop wild relatives: status and trends. Biodivers Conserv 13:663–684

Melhus LE (1948) Exploring the maize germplasm of the tropics. In: Proceedings of the 3rd annual hybrid corn industry research conference, Chicago. 1–2 Dec 1948. American Seed Trade Association, Washington, DC, pp 7–19

Menkir A, Rocheford T, Maziya-Dixon B, Tanumihardjo S (2015) Exploiting natural variation in exotic germplasm for increasing provitamin: a carotenoids in tropical maize. Euphytica 205:203–217. https://doi.org/10.1007/s10681-015-1426-z

Meseka S, Fakorede M, Ajala S, Badu-Apraku B, Menkir A (2013) Introgression of alleles from maize landraces to improve drought tolerance in an adapted germplasm. J Crop Improv 27:96–112. https://doi.org/10.1080/15427528.2012.729259

Michael TP, Van Buren R (2015) Progress, challenges and the future of crop genomes. Curr Opin Plant Biol 24:71–81. https://doi.org/10.1016/j.pbi.2015.02.002

Mir C, Zerjal T, Combes V, Dumas F, Madur D, Bedoya C, Dreisigacker S, Franco J, Grudloyma P, Hao PX, Hearne S, Jampatong S, Laloë D, Muthamia Z, Nguyen T, Prasanna BM, Taba S, Xie CX, Yunus M, Zhang S, Warburton ML, Charcosset A (2013) Out of America: tracing the genetic footprints of the genetic diffusion of maize. Theor Appl Genet 126:2671–2682. https://doi.org/10.1007/s00122-013-2164-z

Molinero-Ruiz ML, Melero-Vara JM, Mateos A (2010) *Cephalosporium maydis*, the cause of late wilt in maize, a pathogen new to Portugal and Spain. Plant Dis 94(3):379

Muzhingi T, Palacios-Rojas N, Miranda A, Cabrera ML, Yeum KJ, Tang G (2017) Genetic variation of carotenoids, vitamin E and phenolic compounds in Provitamin A biofortified maize. J Sci Food Agric 97:793–801. https://doi.org/10.1002/jsfa.7798

Nault LR, Gordon DT (1982) Response of annual and perennial teosintes (*Zea*) to six maize viruses. Plant Dis 66:61–62. https://doi.org/10.1094/PD-66-61

Niblett CL, Claflin LE (1978) Corn lethal necrosis a new virus disease of corn in Kansas. Plant Dis Rep 62:15–19

Paliwal RL (2000) Origin, evolution, and spread of maize. In: Paliwal RL, Granados G, Lafitte HR, Vlollc AD (eds) Tropical maize: production and improvement. FAO, Rome, pp 5–11

Palmer AC, Healy K, Barffour MA, Siamusantu W, Chileshe J, Schulze KJ, West KP, Labrique AB (2016) Provitamin A carotenoid-biofortified maize consumption increases pupillary responsiveness among Zambian children in a randomized controlled trial. J Nutr. https://doi.org/10.3945/jn.116.239202

Payak MM, Lal S, Lilaramani M, Renfro BL (1970) *Cephalosporium maydis* – a new threat to maize in India. Indian Phytopathol 23(3):562–569

Pésci S, Németh L (1998) Appearance of *Cephalosporium maydis* Samra, Sabet, and Hingorani in Hungary. Facul Lanbouw En Toegep Biolog Wetenschappen 63:873–877

Piperno DR, Flannery KV (2001) The earliest archeological maize (*Zea mays* L.) from highland Mexico: new accelerator mass spectrometry dates and their implications. Proc Natl Acad Sci U S A 98:2101–2103

Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium B.P. Maize from the central Balsas river valley, Mexico. Proc Natl Acad Sci U S A 106:5019–5024

Portères R (1955) L'introduction du maïs en Afrique. J Agric Trop Bot Appl 2:221–231

Prasanna BM (2012) Diversity in global maize germplasm: characterization and utilization. J Biosci 37:843–855

Prischmann DA, Dashiell KE, Schneider DJ, Eubanks MW (2009) Evaluating *Tripsacum*-introgressed maize germplasm after infestation with western corn rootworms (Coleoptera: Chrysomelidae). J Appl Entomol 133:10–20. https://doi.org/10.1111/j.1439-0418.2008.01311.x

Ramos-Madrigal J, Smith BD, Moreno-Mayar JV, Gopalakrishnan S, Ross-Ibarra J, Gilbert MTP, Wales N (2016) Genome sequence of a 5,310-year-old maize cob provides insights into the early stages of maize domestication. Curr Biol 26:3195–3201

Randolph LF (1970) Variation among *Tripsacum* populations of Mexico and Guatemala. Brittonia 22:305–337

Ranere AJ, Piperno DR, Holst I, Dickau R, Iriarte J (2009) The cultural and chronological context of early Holocene maize and squash domestication in the central Balsas river valley, Mexico. Proc Natl Acad Sci U S A 106:5014–5018

Ray DK, Ramankutty N, Mueller ND, West PC, Foley JA (2012) Recent patterns of crop yield growth and stagnation. Nat Commun 3:1293. https://doi.org/10.1038/ncomms2296

Ray DK, Mueller ND, West PC, Foley JA (2013) Yield trends are insufficient to double crop production by 2050. PLoS One 8:1–8, e66428

Ray DK, Gerber JS, MacDonald GK, West PC (2014) Climate variation explains a third of global crop yield variability. Nat Commun. https://doi.org/10.1038/ncomms6989

Rebourg C, Chastanet M, Gousenard B, Welcker C, Dubreuil P, Charcosset A (2003) Maize introduction into Europe: the history reviewed in the light of molecular data. Theor Appl Genet 106:895–903

Redinbaugh MG, Pratt RC (2008) Virus resistance. In: Hake S, Bennetzen JL (eds) Handbook of maize: its biology. Springer, New York, pp 255–270

Reiners RA, Gooding CM (1970) Corn oil. In: Inglett GE (ed) Corn: culture, processing, products. Avi Publishing, Westport, pp 241–261

Rich PJ, Ejeta G (2008) Towards effective resistance to Striga in African maize. Plant Signal Behav 3:618–621

Rodriguez MG, Miguel-Chavez RS, Larque-Saavedra A (1998) Physiological aspects in Tuxpeno maize with improved drought tolerance. Maydica 43:137–141

Ross-Ibarra J, Monrell PL, Gaut S (2007) Plant domestication, a unique opportunity to identify the genetic basis of adaptation. Proc Natl Acad Sci U S A 104:8641–8648

Salhuana W, Pollak L (2006) Latin American maize project (LAMP) and germplasm enhancement of maize (GEM) project: generating useful breeding germplasm. Maydica 51:339

Samra AS, Sabet KA, Hingorani MK (1962) A new wilt of maize in Egypt. Plant Dis Rptr 46:481–483

Samra AS, Sabet KA, Hingorani MK (1963) Late wilt disease of maize caused by *Cephalosporium maydis*. Phytopathology 53(4):402–406

Sánchez-González JJ, Ordaz L (1987) Systematic and ecogeographic studies on crop gene pools: 2. El teocintle en México: distribución y situación actual de las poblaciones. IBPGR, Rome

Sánchez-González JJ, Ruiz-Corral JA (1996) Distribución del teocintle en México. In: Serratos JA, Willcox MC, Castillo F (eds) Memoria del Foro: Flujo genético entre maíz criollo, maíz mejorado y teocintle: implicaciones para el maíz transgénico. INIFAP, CIMMYT, CNBA, El Batán, pp 20–38

Sánchez-González JJ, Kato-Yamamake TA, Aguilar-Sanmiguel M, Hernández Casillas JM, López-Rodriguez A, Ruiz-Corral JA (1998) Distribución y caracterización del teocintle. Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias. Centro de Investigación Regional del Pacífico Centro. Libro técnico No. 2. CIPAC-INIFAP-SAGAR, Guadalajara

Schnable PS, Ware D, Fulton RS, Stein JC, Wei F, Pasternak S, Liang C, Zhang J, Fulton L, Graves TA, Minx P, Reily AD, Courtney L, Kruchowski SS, Tomlinson C, Strong C, Delehaunty K, Fronick C, Courtney B, Rock SM, Belter E, Du F, Kim K, Abbott RM, Cotton M, Levy A, Marchetto P, Ochoa K, Jackson SM, Gillam B, Chen W, Yan L, Higginbotham J, Cardenas M, Waligorski J, Applebaum E, Phelps L, Falcone J, Kanchi K, Thane T, Scimone A, Thane N, Henke J, Wang T, Ruppert J, Shah N, Rotter K, Hodges J, Ingenthron E, Cordes M, Kohlberg S, Sgro J, Delgado B, Mead K, Chinwalla A, Leonard S, Crouse K, Collura K, Kudrna D, Currie J, He R, Angelova A, Rajasekar S, Mueller T, Lomeli R, Scara G, Ko A, Delaney K, Wissotski M, Lopez G, Campos D, Braidotti M, Ashley E, Golser W, Kim H, Lee S, Lin J, Dujmic Z, Kim W, Talag J, Zuccolo A, Fan C, Sebastian A, Kramer M, Spiegel L, Nascimento L, Zutavern T, Miller B, Ambroise C, Muller S, Spooner W, Narechania A, Ren L, Wei S, Kumari S, Faga B, Levy MJ, McMahan L, Van Buren P, Vaughn MW, Ying K, Yeh CT, Emrich SJ, Jia Y, Kalyanaraman A, Hsia AP, Barbazuk WB, Baucom RS, Brutnell TP, Carpita NC, Chaparro C, Chia JM, Deragon JM, Estill JC, Fu Y, Jeddeloh JA, Han Y, Lee H, Li P, Lisch DR, Liu S, Liu Z, Nagel DH, McCann MC, SanMiguel P, Myers AM, Nettleton D, Nguyen J, Penning BW, Ponnala L, Schneider KL, Schwartz DC, Sharma A, Soderlund C, Springer NM, Sun Q, Wang H, Waterman M, Westerman R, Wolfgruber TK, Yang L, Yu Y, Zhang L, Zhou S, Zhu Q, Bennetzen JL, Dawe RK, Jiang J, Jiang N, Presting GG, Wessler SR, Aluru S, Martienssen RA, Clifton SW, McCombie WR, Wing RA, Wilson RK (2009) The B73 maize genome: complexity, diversity, and dynamics. Science 326(5956):1112–1115. https://doi.org/10.1126/science.1178534

Schnable J, Zang Y, Ngu DWC (2016) Pan-grass syntenic gene set (sorghum referenced). Figshare. https://doi.org/10.6084/m9.figshare.3113488.v1

Shiferaw B, Prasanna BM, Hellin J, Banziger M (2011) Crops that feed the world. 6. Past successes and future challenges to the role played by maize in global food security. Food Sec 3:307–327

Smith JSC, Cooper M, Gogerty J, Loeffler C, Borcherding D, Wright K (2014) Yield gains contributed by plant breeding in US maize 1930–2011. In: Smith JSC, Specht J, Diers B, Carver B (eds) Yield gains in major US field crops. Crop Science Society of America, Madison, pp 125–171

Smith JS, Gardner CAC, Costich DE (2017) Ensuring the genetic diversity of maize and its wild relatives. In: Watson D (ed) Achieving sustainable cultivation of Maize, Volume 1: from improved varieties to local applications. Burleigh Dodds Science Publishing Ltd, Sawston, pp 3–50. https://doi.org/10.19103/AS.2016.0001.02

Sood S, Flint-Garcia S, Willcox MC, Holland JB (2014) Mining natural variation for maize improvement: selection on phenotypes and genes. In: Tuberosa R, Graner A, Frison E (eds) Genomics of plant genetic resources. Springer, Dordrecht, pp 615–649. https://doi.org/10.1007/978-94-007-7572-5_25

Springer TL, Dewald CL (2004) Eastern gamagrass and other Tripsacum species. In: Moser LE, Burson BL, Sollenberger LE (eds) Warm-season (C4) grasses agronomy monograph 45. American Society of Agronomy, Madison, pp 955–973

Studer A, Zhao Q, Ross-Ibarra J, Doebley J (2011) Identification of a functional transposon insertion in the maize domestication gene *tb1*. Nat Genet 43:1160–1163

Swarup S, Timmermans MC, Chaudhuri S, Messing J (1995) Determinants of the high-methionine trait in wild and exotic germplasm may have escaped selection during early cultivation of maize. Plant J 8:359–368. https://doi.org/10.1046/j.1365-313X.1995.08030359.x

Swigonová Z, Lai J, Ma J, Ramakrishna W, Llaca V, Bennetzen JL, Messing J (2004) Close split of sorghum and maize genome progenitors. Genome Res 14:1916–1923

Taba S (1995) Teosinte: geographic variations and conservation. In: Taba S (ed) Maize genetic resources. Maize program special report. CIMMYT, Mexico, D.F.

Talbert LE, Doebley JF, Larson S, Chandler VL (1990) *Tripsacum andersonii* is a natural hybrid involving *Zea* and *Tripsacum*: molecular evidence. Am J Bot 77(6):722–726

Tang Q, Rong T, Song Y, Yang J, Pan G, Li W, Huang Y, Cao M (2005) Introgression of perennial teosinte genome into maize and identification of genomic in situ hybridization and microsatellite markers. Crop Sci 45:717–721. https://doi.org/10.2135/cropsci2005.0717

USDA-NASS (2004) State level data for field crops. Grains. Corn area, yield, production, price per unit, and value of production [Online]. Available by NASS. https://www.nass.usda.gov/Statistics_by_Subject/

Uyemoto JK, Bockelman DL, Claflin LE (1980) Severe outbreak of corn lethal necrosis disease in Kansas. Plant Dis 64:99–100. https://doi.org/10.1094/PD-64-99

Vallebueno-Estrada M, Rodríguez-Arévalo I, Rougon-Cardoso A, Martínez-González J, García Cook A, Montiel R, Vielle-Calzada JP (2016) The earliest maize from San Marcos Tehuacán is a partial domesticate with genomic evidence of inbreeding. Proc Natl Acad Sci U S A 113:14151–14156

van Heerwaarden JV, Doebley J, Briggs WH, Glaubitz JC, Goodman MM, Sanchez Gonzalez JJ, Ross-Ibarra J (2011) Genetic signals of origin, spread and introgression in a large sample of maize landraces. Proc Natl Acad Sci U S A 108:1088–1092

Vierra BJ (2005) The late archaic across the borderlands: from foraging to farming. University of Texas Press, Austin

Vincent H, Wiersema J, Kell S, Fielder H, Dobbie S, Castañeda-Álvarez NP, Maxted N (2013) A prioritized crop wild relative inventory to help underpin global food security. Biol Conserv 167:265–275

Wang H, Nussbaum-Wagle T, Li B, Zhao Q, Vigoroux Y, Faller M, Bomblies K, Lukens L, Doebley JF (2005) The origin of the naked grains of maize. Nature 436:714–719

Wang L, Xu C, Qu M, Zhang J (2008a) Kernel amino acid composition and protein content of introgression lines from Zea mays ssp. Mexicana into cultivated maize. J Cereal Sci 48:387–393. https://doi.org/10.1016/j.jcs.2007.09.014

Wang LZ, Yang AF, He CM, Qu ML, Zhang JR (2008b) Creation of new maize germplasm using alien introgression from *Zea mays* ssp. *mexicana*. Euphytica 164:789–801. https://doi.org/10.1007/s10681-008-9730-5

Wang B, Tseng E, Regulski M, Clark TA, Hon T, Jiao Y, Lu Z, Olson A, Stein JC, Ware D (2016) Unveiling the complexity of the maize transcriptome by single-molecule long-read sequencing. Nat Commun 7:11708

Wangai A, Sikinyi E, Ochieng J, Miyogo S, Karanja T, Odour H, Kimani E, Irungu J, Kinyua Z, Ngaruiya P, Ligeyo D, Kipkemboi S (2012a) Joint assessment report: report on status of maize lethal necrosis disease and general maize performance. Ministry of Agriculture, Kenya. Online publication. http://www.fao.org/fileadmin/user_upload/drought/docs/Maize%20Lethal%20Necrotic%20Disease%20in%20Kenya_Joint%20Assessment%20Report%20(July%202012).pdf

Wangai AW, Redinbaugh MG, Kinyua ZM, Mahuku G, Sheets K, Jeffers D (2012b) First report of Maize chlorotic mottle virus and maize lethal necrosis in Kenya. Plant Dis 96:1582. https://doi.org/10.1094/PDIS-06-12-0576-PDN. [Abstract] [ISI]

Warburton ML, Wilkes G, Taba S, Charcosset A, Mir C, Madur D, Dreisigacker S, Bedoya C, Prasanna B, Xie C, Hearne S, Franco J (2011) Gene flow between different teosinte species and into the domesticated maize gene pool. Genet Resour Crop Evol 58:1243–1261

Warburton ML, Williams WP, Windham G, Murray S, Xu W, Hawkins L, Franco J (2013) Phenotypic and genetic characterization of a maize association mapping panel developed for the identification of new sources of resistance to *Aspergillus flavus* and aflatoxin accumulation. Crop Sci 53:2374–2383. https://doi.org/10.2135/cropsci2012.10.0616

Watanabe K, Takahashi H, Sato S, Nishiuchi S, Omori F, Malik AI, Colmer TD, Mano Y, Nakazono M (2017) A major locus involved in the formation of the radial oxygen loss barrier in adventitious roots of teosinte *Zea nicaraguensis* is located on the short-arm of chromosome 3. Plant, Cell Environ 40(2):304–316

Welch RM, Graham RD (2004) Breeding for micronutrients in staple food crops from a human nutrition perspective. J Exp Bot 55(396):353–364

Wellhausen EJ, Roberts LM, Hernandez XE (1952) Races of maize in Mexico. Bussey Institution of Harvard University, Cambridge

White SE, Doebley JF (1999) The molecular evolution of terminal *ear1*, a regulatory gene in the genus *Zea*. Genetics 153(3):1455–1462

Wilkes HG (1967) Teosinte: the closest relative of maize. Bussey Institution of Harvard University, Cambridge

Wills WH (1988) Early prehistoric agriculture in the American Southwest. School of American Research Press, Santa Fe

Zamir D (2001) Improving plant breeding with exotic genetic libraries. Nat Rev Genet 2:983–989

Zhu Q, Cai Z, Tang Q, Jin W (2016) Repetitive sequence analysis and karyotyping reveal different genome evolution and speciation of diploid and tetraploid *Tripsacum dactyloides*. Crop J 4:247–255