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North American Crop Wild Relatives, Volume 2

Important Species

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This book is dedicated to the custodians of the diversity of wild plants in North America – past, present, and future

Foreword

Reinvesting in Crop Wild Relatives in North America

Nearly any place you hike a canyon, canoe a river, climb a mountain, wade a wet meadow, or weed a field in North America, you will come upon native plants that are close relatives of food, fiber, animal forage and feed, industrial oil, ornamental, and medicinal crops. On the fringes of muskegs from Hartley Bay in British Columbia to sites in northern California, you might come upon the Pacific crab apple (*Malus fusca* [Raf.] C. K. Schneid) around ancient fishing and gathering camps (Routson et al. 2012). In the watersheds of the St. Johns and Kissimmee Rivers in Florida, the vines of the rare Okeechobee gourd (*Cucurbita okeechobeensis* [Small] L. H. Bailey subsp. *okeechobeensis*) trail up into the branches of wild custard apples (*Annona glabra* L.) (Andres and Nabhan 1988; Nabhan 1989). Where I live and farm in Southern Arizona just north of the Mexican border, wild chiles (*Capsicum annuum* var. *glabriusculum* [Dunal] Heiser & Pickersgill) grow in desert canyons not far from wild grapes (*Vitis* L.), walnuts (*Juglans* L.), passion fruits (*Passiflora* L.), cassava (*Manihot* Mill), tomatillos (*Physalis* L.), and tepary beans (*Phaseolus acutifolius* A. Gray var. *acutifolius*) (Nabhan 1990; Nabhan 1991).

To many naturalists, these plants are but botanical curiosities, worthy of conservation without regard to historic or current human uses. But for crop geneticists and plant breeders, and a growing number of biodiversity conservationists, these species are especially worthy of protection, conservation, and evaluation because they may hold something of lasting value for the future of the way we live and eat on this planet.

These scientific and cultural values are exactly the reason why agricultural research and conservation management insights are not only so important but so timely. The chapters of this book represent the first comprehensive effort to assess wild crop genetic resources on our continent. Remarkably, this book arrives in our hands at just the moment in North American history when many of these plants are threatened by climate change yet also when these resources are most needed if future generations are to adapt.

The wildness in these plants confers distinct advantages not found in their domesticated cousins: tolerance to extremes of temperature and precipitation and resistance to the pests that lay waste to agricultural fields. This is why we are increasingly looking to the wild to strengthen our agriculture, particularly during this period of accelerated climate change. Farmers, orchardists, ranchers, and horticulturalists are already suffering from shifting and often heightened frequencies of drought, heat waves, catastrophic freezes, hurricanes, floods, and fires. And with the changes in these abiotic stressors come other biotic impacts to our farming systems and food security: previously unforeseen weeds, insect pests, and crop diseases that take a long-term toll on agricultural productivity and food safety.

During eras of political, economic, and environmental stress, humanity turns to consider a broader range of options than typically employed during "business as usual." This is one of those times – when agriculture is looking to draw upon a broader and deeper gene pool of crop genetic resources as a means to re-diversify and add resilience to the food plants that we depend on for survival. After decades of focusing on a relatively small genetic base of cultivated varieties for crop improvement, geneticists are now casting a much wider net, fortunately enabled by a broader portfolio of diagnostic techniques, micro-propagation practices, and biotechnologies used to select and transfer genes from wild relatives into food crops.

This is why the fact that forty-some crop wild relative species are included in the U.S. Fish and Wildlife Service's Endangered and Threatened Plant list is of great concern. To make matters worse, this list is likely to grow much larger (Rogers 2015). Analyses of North American seed plants facing extinction risks exacerbated by climate change and land use intensification (Zhang et al. 2016) would indicate that roughly 27% of the 4600 crop wild relatives documented to occur in the U.S. (Khoury et al. 2013) are likely to lose more than 80% of their habitat by the 2080s and will suffer a 50% retraction of their ranges.

As I read through the names on the current U.S. list of threatened and endangered crop wild relatives, I am struck by both their beauty and by the fragility of the plant species they represent:

- Texas wildrice (*Zizania texana* Hitchc.), an aquatic perennial with high allelic richness surviving along just a few stretches of the San Marcos River drainage of the Edwards Plateau in Texas
- The scrub plum (*Prunus geniculata* R. M. Harper) of Lake Wales Ridge in Florida, a small shrub with perfumed flowers valued by horticulturists as a showy and fragrant ornamental, closely related to the Chickasaw plum, with a fruit of probable hybrid origin that has been both culturally dispersed and cultivated for well over 150 years
- The Bakersfield prickly pear cactus [*Opuntia basilaris* Engelm. & J. M. Bigelow var. *treleasei* (J. M. Coult.) J. M. Coult. ex Toumey], with genes for drought resistance and production of compounds which protect against adult-onset diabetes, both of which desperately needed by farmers and consumers on our continent

- The puzzle sunflower (*Helianthus paradoxus* Heiser), a halophyte of the Pecos River in New Mexico and West Texas, which emerged from a chance hybrid of the common sunflower (*Helianthus annuus* L.) and the prairie sunflower (*Helianthus petiolaris* Nutt.) over 75,000 years ago, but is now far more salt tolerant than either of its parents, and most cultivated sunflower hybrids as well
- The Okeechobee gourd, a squash relative first described by John and William Bartram along the St. Johns River in Florida around the time of the Revolutionary War, which has barely survived the agricultural revolution that drained the Everglades for sugarcane production and diverted most rivers in Florida into croplands (Nabhan 1989)
- The Oahu cowpea (*Vigna o-wahuensis* Vogel), a rare perennial legume that has gone extinct on the very island in Hawaii where my daughter and grandson now live but which tenaciously hangs on for dear life in just seven small populations spread across four of the other Hawaiian Islands

I offer you these brief "personality profiles" to remind you that each of these valuable and endangered crop relatives has a distinctive character. The tasks of identifying, counting, tallying, mapping, monitoring, and managing the remaining populations of rare plant species on the verge of extinction are ever increasing. It is worth a moment of our time now and then to remember the complex ecological and human relationships surrounding each of these unique but declining plants.

It is important to remember that the contribution of wild relatives to crops is not a new phenomenon. In fact, these plants have naturally exchanged genes in traditional agricultural settings for millennia. We are all beneficiaries of such serendipitous crop diversification every time we sit down to eat a meal or drink a glass of wine or cider. They have been – and continue to be – our most useful "living library," a set of manuals to help us maintain our food security (Gruber 2017, Khoury 2015, and in this volume).

Several of the chapters in this book point out the importance of recognizing that many crop relatives remain economic crops and cultural resources in their own right. Plant breeders do not necessarily need to "improve" some of these plants to make them acceptable to the public. For example, the fresh and dried fruits of wild chiltepín peppers (*Capsicum annuum* var. *glabriusculum*) sell for more than USD $80 per pound in much of the U.S. Southwest and northwestern Mexico. One pound of American wildrice from Minnesota streams and lakes that is hand-harvested and wood-parched by Native American foragers garners prices of up to USD $17 on Amazon. On the southern edges of the Chihuahuan Desert, consumers are willing to pay five to ten times more for a delicious semi-cultivated potato called papita güera (*Solanum cardiophyllum* Lindl) than for domesticated potatoes of exotic origin. Yet the anciently cultivated genotypes of this species are hardly if at all represented in most potato gene banks, including those in Mexico and the USA.

Wild apples (*Malus* Mill.) prized for their tartness and flavor are now included in hard ciders in the USA and Canada. Legally collected or propagated rare food crops like Price's potato bean (*Apios priceana* B. L. Rob.), agaves (*Agave* L.), and cacti command high prices in horticultural trade. Wild prickly pears (*Opuntia* Mill.), pinyon nuts (*Pinus* L.), and ramps (*Allium tricoccum* Aiton) continue to attract almost as much attention from chefs and nutritional scientists as their cultivated counterparts do. Nevertheless, habitat fragmentation and other threats are diminishing foragers' access to these North American plants.

Beyond these direct uses, promising new applications of these plants are emerging from recent innovations in applied research. In Kansas, the Land Institute is newly domesticating perennial wild relatives of food crops, using intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D. R. Dewey) and rosinweed (*Silphium integrifolium* Michx.), a distant relative of sunflower, in their prairie-adapted polycultures (Dehaan et al. 2016; Van Tassel et al. 2017). In Missouri, botanists associated with the Missouri Botanical Garden and St. Louis University are evaluating wild relatives of commercially important fruit tree crops for development in their own right both as sources of food and as rootstocks, due to their hardiness and resistance to emerging insect pests and plagues (Allison Miller, pers. com).

In Illinois, integrated pest management teams have experimented with the native buffalo gourd (*Cucurbita foetidissima* Kunth) as a trap crop grown on the edges of squash and pumpkin fields to reduce larval damage to these crops and increase pollination efficiencies (Metcalf et al. 1980; Metcalf et al. 1982). In Arizona, our ecological research in the first in situ reserve for crop wild relatives in the USA [in Coronado National Forest] allowed us to determine how capsaicinoids and other secondary metabolites serve as "directed" chemical defenses against *Fusarium* fungi, insect pests, and seed-predating rodents in wild chiltepín peppers (Tewksbury and Nabhan 2001; Eich 2008). It may now be possible to differentially select and use the various capsaicinoids in the wild chile pepper arsenal for the discouragement of grain storage pests, prevention of fungal contamination of seeds, treatment of shingles, reduction of blood serum cholesterol and glucose, and management of attention-deficit disorders (Eich 2008; Barchenger and Bosland, this volume).

Thus, crop wild relatives are extremely valuable genetic resources, yet they also offer us their colorful and meaningful natural histories – stories of survival, if you will, of a more diverse portfolio of plants still available to humanity.

Thankfully, as many of the chapters in this book document, the conservation and use of wild relatives is getting more serious traction, with national and international initiatives looking to make a significant impact in the coming years. But these efforts are the tip of the iceberg of what is needed. As several contributions in this volume affirm, we must continue to invest in sufficiently supporting every link in the wild relative-food crop supply chain – from in situ conservation of natural habitats in national parks and biosphere reserves to ex situ seed banks, botanical gardens, and plant restoration efforts – if the entire supply and delivery system is to function for the future. It is not enough for land grant universities to invest millions in molecular biology laboratories if they end up closing down herbaria and cutting budgets of campus arboreta and experimental farms in the process. As Harvard conservation biologist E.O. Wilson once quipped, it is the "non-sexy" and more descriptive sciences of systematics, ethnobotany, biogeography, and seed storage physiology that have gotten us to where we are today.

These recently emerged opportunities will not bear fruit if our funding sources for habitat conservation and landscape management, for basic biology and seed banking, and for horticultural innovation and biomedical research focus only on the last few links of the wild relative-crop commodity supply chain. We not only need to diversify the genetic base of our food supply, we also need to diversify and sustain the many forms of conservation, restoration, and scholarly inquiry which together ensure access to these crop genetic resources.

Collectively, the chapters in this remarkable book provide a valuable overview of the best information and practices needed to safeguard and wisely use North America's crop wild relatives. Detailing the species native and naturalized in the continent and related to important food, fiber, animal forage and feed, industrial oil, ornamental, and medicinal crops, the authors outline their potential for use and highlight the conservation needs for the species. In bringing together for the first time this information from across the broad North American region, including Canada, Mexico, and the USA, the book provides access to critical conservation information for well over 600 promising plants. As this landmark volume attests, these plants are essential elements of North America's natural and cultural heritage. This book becomes the model for advancing the efforts needed to better care for this heritage for present and future generations. It provides us with operating instructions for wisely managing "our living library."

Tucson, AZ, USA Gary Paul Nabhan

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Preface

Wild plants useful to food and agriculture occupy a niche frequently outside the realm of both agricultural and natural resource professionals. The agricultural community tends to focus its attention on a handful of domesticated species, and the natural resource community tends to focus on legislatively regulated wild species (e.g., species that are rare, endangered, or indicators of ecosystems such as wetlands). The increasing challenges to agricultural production brought about in the coming decades by climate change, added to the biotic and abiotic stresses already present, will necessitate the use of novel genes from wild plant genetic resources to find solutions. The combined efforts of both the agricultural and the natural resource communities are critical to locate, conserve, manage, and make available these invaluable species for food and agricultural security of future generations.

The purpose of this two-volume book is to highlight the most important wild plant genetic resources that grow in North America. We define wild plant genetic resources as wild species with relevance for agriculture; these include the wild plant populations from which domesticated varieties evolved, crop wild relatives that can be used to improve contemporary crops, wild species that have a record of use by people, and any other wild species with potential for future crop development. Most of the species covered are native, but a few are introduced species that have since naturalized. A thorough understanding of the species that occupy North America, including their distributions, potential value to agriculture, and conservation statuses and needs, will give agricultural and conservation communities the basic knowledge they need to take steps to conserve our natural heritage of wild plants important to food and agriculture. The overarching goal of this book is to help ensure that these valuable but overlooked species continue to persist, both in their natural habitats and in gene banks, where they can be made available as resources to address compounding agricultural challenges. This book is authored by a broad range of experts, working diligently to protect crop genetic resources. Regardless of their backgrounds, they have come together to compile the latest information on the most important North American wild plant genetic resources. Although North America formally includes other countries, this book focuses on Canada, the United States and Mexico; three countries whose combined area covers most of the continent.

The chapters within Volume 2 focus on groups of important wild genetic resources in North America and are organized using the standardized categories of economic plants found in *World Economic Plants: A Standard Reference* (Wiersema and León 2013). Readers interested in specific species can use the indices of scientific names and common names to quickly find the relevant information. Most of the chapters focus on food crops: three chapters cover cereals, including maize (*Zea* L.), minor cereals (*Amaranthus* L., *Avena* L., *Chenopodium* L., *Echinochloa* P. Beauv., *Fagopyrum* Mill., *Hordeum* L., *Panicum* L., and *Setaria* P. Beauv.), and wildrice (*Zizania* L.). A single chapter covers beans (*Phaseolus L.*), whose areas of domestication include Mexico and for which there are significant wild genetic resources in the region. Four chapters cover vegetables, including lettuce (*Lactuca L.*), pumpkins and squash (*Cucurbita* L.), peppers (*Capsicum L.*), and the following root crops: carrot (*Daucus* L.), sweetpotato (*Ipomoea* L.), potato (*Solanum* L.), Jerusalem artichoke (*Helianthus* L.), jicama (*Pachyrhizus* Rich. ex DC.), cocoyam (*Xanthosoma* Schott.), cassava (*Manihot* Mill.), and beet (*Beta L.*). Fruits are covered by four chapters, focusing on temperate small fruits such as strawberry (*Fragaria* L.), currants and gooseberries (*Ribes* L.), blackberries and raspberries (*Rubus* L.), and blueberries and cranberry (*Vaccinium* L.); a separate chapter on grapes (*Vitis* L.); temperate fruit trees such as apple (*Malus* Mill.), stone fruits (*Prunus* L.), persimmon (*Diospyros* L.), and pawpaw (*Asimina* Adans.); and, finally, tropical fruit trees such as avocado (*Persea* Mill.), mamey sapote (*Pouteria* Aubl.), and cherimoya (*Annona* L.). A chapter on wild genetic resources of temperate nut crops [chestnut (*Castanea* Mill.), hazelnut (*Corylus* L.), pecan (*Carya* Nutt.), pistachio (*Pistacia* L.), and walnut (*Juglans* L.)] is also included. Industrial crops are represented by three chapters, one on sunflower (*Helianthus* L.), a second on rubber and minor oil seed crops [meadowfoam (*Limnanthes* R. Br.), lesquerella (*Physaria* (Nutt. ex Torr. & A. Gray) A. Gray), and guayule (*Parthenium L.*)], and a third on fiber crops, including cotton (*Gossypium* L.) and hesperaloe (*Hesperaloe* Engelm.). Another chapter covers forage and turf grasses (native warm season forage and turf and cool season forage species). Finally there are chapters on wild species used as ornamentals, including those in the genera *Coreopsis* L., *Rudbeckia* L., and *Phlox* L. A final chapter in this section covers species used medicinally or for social purposes, highlighting black cohosh (*Actaea* L.), cacao (*Theobroma* L.), tobacco (*Nicotiana* L.), and hops (*Humulus* L.).

All of the crop chapters follow a general outline. Authors briefly discuss the origin and use of each domesticated crop and review challenges to its cultivation. The main part of the chapter then focuses on the crop wild relative species that occur in North America, including their geographic distributions and historical, as well as potential, utilization in breeding. Taxa that have been utilized directly from the wild for food, medicine, or other purposes by Indigenous and other people are also covered. In addition, the authors discuss cultivated plants that have been semidomesticated or are essentially wild, such as many types of forage, ornamental, and medicinal taxa. All chapters within Volume 2 include maps of the geographic distributions of the taxa of interest, modeled from the most comprehensive and up-to-date occurrence records available. These should be a valuable reference for conservation planning.

There are over 20,000 wild plant species in North America, and all deserve a chance to thrive. However, a small fraction of these are distinguished by their potential to support food and agricultural production, either because they are resources that can be used to breed more productive crops or because they have commercial or cultural value when used directly. Many of these species are common, even weedy, and are easily overshadowed by rare or endangered plants. Nevertheless, because of their real or potential importance to our food and agriculture, they deserve to be recognized, celebrated, conserved, and made available to support food and agricultural security.

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Abbreviations

AAFC	Department of Agriculture and Agri-Food Canada
AFLP	Amplified fragment length polymorphism
AHLV	American hop latent virus
AHPA	American Herbal Products Association
ANSM	Universidad Autónoma Agraria Antonio Narro
AOSCA	Association of Official Seed Certifying Agencies
ApMV	Apple mosaic virus
ARS	Agricultural Research Service
ASU	Arizona State University
AZ	Arizona
BCMV	Bean common mosaic virus
BGCI	Botanic Gardens Conservation International
BLM	Bureau of Land Management
BP	Before present
Bt	Bacillus thuringiensis
BTA	Boyce Thompson Arboretum
CA	California
CAM	Crassulacean acid metabolism
CAPS	Cleaved amplified polymorphic sequences
CBD	Convention on Biological Diversity
CDFW	California Department of Fish and Wildlife
CIAT	International Center for Tropical Agriculture
CIMMYT	International Maize and Wheat Improvement Center
CLCuD	Cotton leaf curl disease
CMS	Cytoplasmic male sterility
CMV	Cucumber mosaic virus
CNHP	Colorado Natural Heritage Program
CNRG	National Genetic Resources Center
Co	County
CONABIO	National Commission for the Knowledge and Use of Biodiversity
CS	College Station Texas

CSIRO	Commonwealth Scientific and Industrial Research Organization
CSN	Counter Season Nursery
CWR	Crop wild relative (s)
DNA	Deoxyribonucleic acid
DNR	Department of Natural Resources
EC	Electrical conductivity
ECOS	Environmental Conservation Online System
ELISA	Enzyme-linked immunosorbent assay
FAO	Food and Agriculture Organization of the United Nations
FGP	Frost grape polysaccharide
FRRL	Forage and Range Research Laboratory
GBS	Genotyping by sequencing
GG	Germplasm Resource Information Network-Global database
GH	Greenhouse
GLIFWC	Great Lakes Indian Fish and Wildlife Commission
GLS	Gray leaf spot
GMP	Good Manufacturing Practice
GP	Genepool
GPS	Global Positioning System
GRIN	Germplasm Resource Information Network database
GS	Genome selection
GWAS	Genome-wide association study
HPLC	High-performance liquid chromatography
HpLV	Hop latent virus
HpMV	Hop mosaic virus
HPTLC	High-performance thin-layer chromatography
HRT	Hormone replacement therapy
ICAR	Indian Council on Agricultural Research
ICRISAT	International Crop Research Institute for the Semi-Arid Tropics
INDR	Indiana Department of Natural Resources
INIFAP	National Institute of Forestry, Agriculture and Livestock Research
INRA	French National Institute for Agricultural Research
INTA	Instituto Nacional de Tecnología Agropecuaria
IPK	Leibniz-Institut für Pflanzengenetik und Kulturpflanzenforschung
ISSR	Inter-simple sequence repeat
ITIS	Integrated Taxonomic Information System
ITPGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
LGCS	USDA Lactuca Germplasm Collection in Salinas
LGRCD	Lactuca Genetic Resources Collection at the University of California in Davis
MCMV	Maize chlorotic mosaic virus
Mha	Million hectares
MLN	Maize lethal necrosis

MLS	Multilateral system
MS	Flow injection mass spectrometry
MT	Metric tons
MTA	Material Transfer Agreement
n/d	Not determined
NA	North America
NALPGRU	National Arid Land Plant Genetic Resources Unit
NARO	National Agriculture and Food Research Organization
NASS	National Agricultural Statistics Service
Nc	Census population size
NCGC	National Cotton Germplasm Collection
NCGR	National Clonal Germplasm Repository
NCGR-Davis	National Clonal Germplasm Repository in Davis, California
NCRPIS	North Central Regional Plant Introduction Station
NILs	Near isogenic lines
NLGRP	National Laboratory for Genetic Resources Preservation
NLR	Nucleotide binding-leucine rich repeat receptor
NM	New Mexico
NMFS	National Marine Fisheries Service
NMR	Nuclear magnetic resonance
NOM-059	NOM-059-SEMARNAT-2010-Mexican standard that lists all threatened native wild species
NORGEN	North American Regional Network for Agricultural Research-Genetic Resources Task Force
NPGS	USDA, ARS National Plant Germplasm System
NPS	National Park Service
NRCS	USDA, Natural Resources Conservation Service
NS SEME	Novi Sad Institute of Field and Vegetable Crops
OPGC	Ornamental Plant Germplasm Center
OR	Oregon
OSU	Ohio State University
PacBio	Pacific Biosystems
PCR	Polymerase chain reaction
PEO	USDA, ARS Plant Exchange Office
PGRC	Plant Gene Resources of Canada
PGRFA	Plant Genetic Resources for Food and Agriculture
PMC	USDA, Natural Resources Conservation Service Plant Material Center
PRV	Papaya ringspot virus
PVG	Pre-variety germplasm
QTL	Quantitative trait loci
RAPD	Random amplified polymorphic DNA
SBBG	Santa Barbara Botanic Garden
SCMV	Sugarcane Mosaic Virus

SDBG	San Diego Botanic Garden
SEINet	Southwestern Environmental Information Network
SINAREFI	National Program of Plant Genetic Resources for Food and Agriculture
SNP	Single nucleotide polymorphisms
SNWA	Southern Nevada Water Authority
SS	Sequence-tagged site
SSR	Simple sequence repeat
SWD	Spotted wing drosophila
TEX	University of Texas
TNPD	Texas Native Plants Database
TX	Texas
UC Davis V&E	The University of California, Davis Viticulture and Enology Department
UCBG	University of California Botanical Garden
UMA	Wildlife Conservation Management Units
UNAM	National Autonomous University of Mexico
UNESCO	United Nations Educational, Scientific and Cultural Organization
UNFAO	United Nations Food and Agriculture Organization
UPOV	International Union for the Protection of New Varieties of Plants
URL	Uniform Resource Locator
USA	United States of America
USD	United States Dollars
USDA	United States Department of Agriculture
USDA-ARS	United States Department of Agriculture – Agricultural Research Service
USFS	United States Forest Service
USFWS	US Fish and Wildlife Service
UT	Utah
VASCAN	Database of Vascular Plants of Canada
VIR	Vavilov All-Russian Research Institute of Plant Industry
VNIIMK	All Russian Research Institute of Oil Crops
WGD	Whole genome duplication
WMV	Watermelon mosaic virus
WRPIS	USDA, ARS Western Regional Plant Introduction Station
WUS	Wild utilized species
WY	Wyoming
ZWMV	Zucchini yellow mosaic virus

Part I
Cereals and Legumes

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

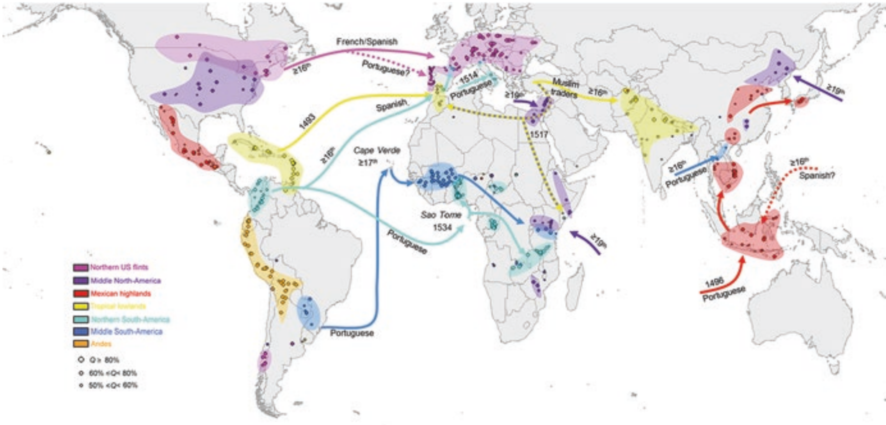

Fig. 1.1 Map of hypothetical major routes of global maize diffusion out of the Americas (Mir et al. 2013)

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